

RELATIVE ABUNDANCE OF SOME PANAMANIAN SNAKES ^{c. 1}

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This paper is primarily a consideration of the relative abundance and distribution of the 69 snake species known to inhabit the Panama Canal Zone and the adjacent Pacific side lowlands of the Panamanian provinces of Herrera, Coelé, Panama, and Darien. It is the result of the examination and identification of 11,763 individuals, and the basic facts concerning these specimens are set down in table VII. In this table the material from the region is divided into four main groups: "Coelé-Herrera" combines the material from these two provinces; material from the Province of Panama and the Pacific side of the Canal Zone is called "Sabanas" for brevity, and that from the Atlantic side of the Canal Zone and part of the Province of Colon is called "Chagres" for the same reason; the fourth group is the material from Darien.

The bulk of the material was sent to me for identification and report, during the years 1933 to 1945 inclusive, by Dr. H. C. Clark, Director of the Gorgas Memorial Laboratory in Panama City. The primary aim of this census was to ascertain the relative abundance of dangerously venomous snake species, and it was made as much at random as was humanly possible. The Clark collection accounts for 10,690 of the specimens. It contains 63 species; nine not previously known from the region, three of them new to science. I am greatly indebted to Dr. Clark for the privilege of examining his extraordinary collection, which included some 1,500 specimens from other regions of the Republic.

The remainder of the material consists of museum collections of snakes from the region. I have examined nearly all such material in this country, and, as a holder of a John Simon Guggenheim Fellowship in 1929, in England and in Europe. I have not seen the 28 specimens in the

Turin Museum, but the list of these published by Peracca in 1896 indicates nothing additional to the specimens I have seen. The museum material amounts to 1,073 specimens and contains 60 species, six of which are additional to the 63 in the Clark collection.

In faunistic and distributional discussions I have utilized all the material; for statistical comparisons of relative abundance I have used only the Clark collection, as the museum material has been subjected to an unknown amount of selection. Prior to 1933 Dr. Clark sent in between 1,100 and 1,200 snakes from the region. The majority of these were discarded, but 138 of them were selected for incorporation in museum material and are so recorded in this paper. Among them are two species, *Dryadophis plœci* from the Chagres and *Bothrops nasuta* from the Sabanas, which have not since appeared in Clark material from those areas.

It may be appropriate to mention that I here include only specimens seen prior to June 1946, when I began the calculations of percentages. A few specimens seen since that date have not been added.

The specimens of the Clark collection were collected by a very considerable number of people, i.e., by everybody in a village, or in a working gang, who could be induced by a small reward to bring in a killed snake or the head of one. The specimens were delivered to some one person in the vicinity, who preserved them in formol, kept a sort of score, received the money from Dr. Clark and passed it out to the actual collectors. When the container was full it was shipped to the Laboratory. Occasionally men came into the Gorgas Laboratory with snakes from the Sabanas area, and Dr. Clark regularly visited the Chagres villages and Agua Clara.

The fee was 25 cents for vipers and coral snakes, 10 cents for others. At first Dr. Clark paid a flat rate of 10 cents a head, but sometime prior to 1933, suspecting the sum was not sufficient to induce collectors to tackle the larger vipers, he established the differential rate. In neither case was any attention paid to the size or condition of the specimen. Theoretically this differential rate might affect the value of the figures for relative abundance, but actually I do not think it does. In the first place, the average campesino thinks a great many more species poisonous than are so in actual fact, and is thus debarred from making too discriminatory a catch. Second, because of the very large number of harmless snakes turned in. Third, because the discrimination of the paying bureau was not always infallible when it came to coral snakes and their mimics. Fourth, because of a certain scepticism on my part as to the extent to which the differential rate was passed on to the actual collectors by the middleman, and whether, in some cases at least, the flat rate of ten cents a head for any and all snakes was not all that the collectors really got.

A well known herpetologist once expressed considerable scorn for, and lack of interest in, any collection of snakes made by such untrained and ignorant fellows. The facts as listed speak for themselves. They got as many secretive and burrowing species as the herpetologists have collected (they got Caccilians and Amphishaenids too, thinking in their ignorance that they were snakes, or hoping in their guile that they would pass as such); they had better success than herpetologists with nocturnal, arboreal snakes (*Dipsas nicholsi*, *Rhinobathrum*); they even got some of the nocturnal, thoroughly aquatic snakes of the genus *Tretanorhinus*. After repeated attempts, the failure of the late Dr. Ditmars to get a bushmaster in the Canal Zone region was the subject of a joke in the "New Yorker," and may be contrasted with the 62 specimens taken for Dr. Clark.

It must not be forgotten that many of the small secretive snakes in Museum collections were taken by the fine toothed comb of the entomologists, and that most of the specimens of *Liotyphlops*, *Trimetopon*, *Enulius*, and *Tantilla*, small and secretive, and of *Tretanorhinus*, in the Museum columns for the Chagres and the Sabanas were taken by gangs of workmen engaged in ditching and draining and otherwise sanitating the cleared and inhabited parts of the Canal Zone. An account of 1,564 such specimens, 182 of which were kept in a museum, is given by Bates ('28).

The Clark collection is manifestly not perfect, but I maintain that it gives a better picture of the number of species and relative number of individuals in the region than the only other source of information—the museum material.

I am responsible for the identification of all the specimens. I hope that no errors have been made, but think it my duty to point out the spots where they are most likely to have occurred. There are certain pairs of species that can be distinguished from each other without error or difficulty if one has entire specimens, but in the Clark collection, except for small individuals, the specimens are heads with a varying amount of neck attached, and in cases where the head is cut off at the nape proper identification may be quite difficult. In such cases I have preferred to make the possible error in the more plausible direction. Thus some of the *Thalerothis occidentalis* individuals in the Clark figures may have been the much rarer *T. riveti*, especially in the Chagres area where *T. riveti* is known to occur. So also some *Chironius carinatus* may have been wrongly identified *C. fuscus*; some *Dryadophis boddaertii* may have been *D. pleci*; and some *Leptodeira rhombifera* may have been *L. annulata*. On the other hand, in the case of the almost equally abundant *Imantodes cenchoa* and *I. gemmistratus* I am just as likely to have misidentified one as the

other, and the possible errors may well cancel out.

CLIMATE

The lowlands of Panamá, cut by the parallel of latitude nine north, are, of course, tropical, and have almost no change of temperature from month to month throughout the year. The areas on the Pacific side with which we are concerned receive an annual rainfall of from 65 to 73 inches; highest in Coclé, lowest in Darién. There is a "low sun" (winter) dry season composed of two to four months, each with less than two inches of rain. The dry season is longest in Coclé (January to April inclusive), shortest in Darién (February and March). This climate does not support forest except where the water table comes near the surface, and is "tropical savanna with galeria forest" (Awí of the Köppen classification).

The Atlantic slope of the Canal Zone has from 100 to 129 inches of rain a year, but has a dry season very similar to that of the Pacific side. This climate supports a general forest cover, and is

"tropical deciduous forest," "monsoon forest" (Amwi of the Köppen classification). There are numerous references in literature to "tropical rain forest" in this area, but none exists. Gatun, now deforested, has the least severe dry season in the area, but it is too severe for the climate to be called Af, "tropical evergreen forest." The rainfall for February is 2.02 inches, and that for March 1.71; both well below the minimum requirement, which is 2.40 for the driest month.

DISTRIBUTION

Twenty species are known from lowland Coclé; none are peculiar to it. Of these twenty, 19 occur in the Sabanas, 18 in Herrera, 17 in the Chagres area, and 15 in Darién (see fig. 1).

Twenty-nine species are known from lowland Herrera; one is peculiar to it. Twenty-seven of them occur in the Sabanas, and the same 27 are in the Chagres area, but only 23 of them occur in Darién.

Thirty-one species are known from the combined Coclé-Herrera area, two being confined to it. There are 29 in common

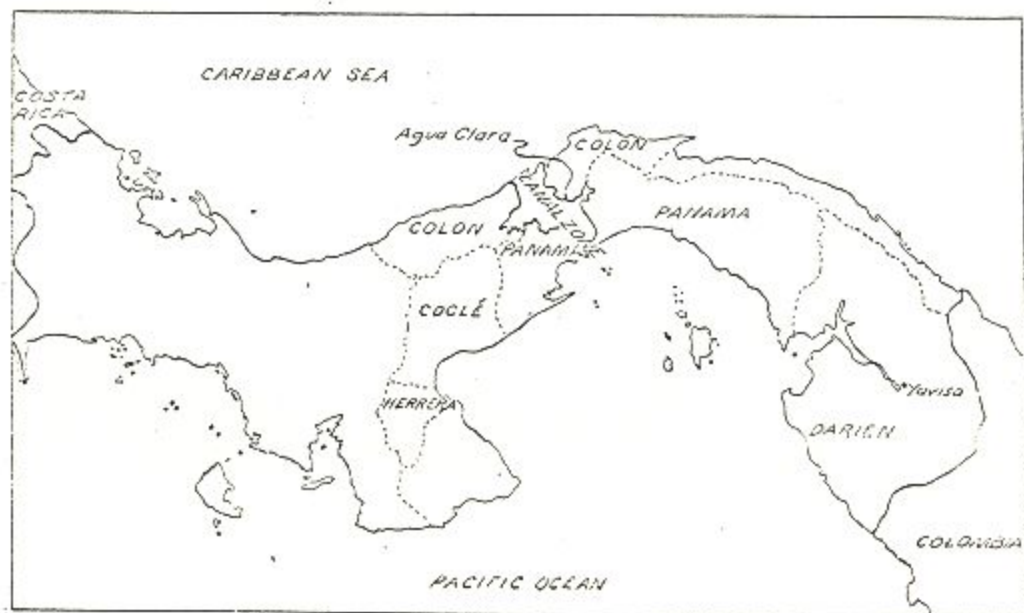


FIG. 1. Outline map of the Republic of Panamá, showing the Canal Zone, the Provinces of Herrera, Coclé, Colon, Panamá, and Darién, and the localities Agua Clara and Yavisa.

with the Sabanas, 27 with the Chagres, and 23 with Darien.

Forty-four species are known from Darien: none are peculiar to it. Forty-two of them are found in the Sabanas and 42 in the Chagres area, the fauna being either an impoverished Chagres fauna with two Sabanas species or an impoverished Sabanas fauna with two Chagres species.

The Sabanas fauna of 58 species shares 51 of them with the Chagres fauna. The seven others are: Sabanas only, three; Sabanas-Coelé, one; Sabanas-Coelé-Herrera, one; Sabanas-Darien, two.

The Chagres fauna of 60 species shares 51 of them with the Sabanas fauna. The nine others are: Chagres only, seven; Chagres-Darien, two.

Faunistically, any two of the contiguous areas do not differ remarkably, in spite of the fact that the Chagres area is climatically different from the other three.

G. G. Simpson ('47) advises the use of a figure derived from the formula $100 C/N_1$, as the best simple measure of the degree of taxonomic resemblance between two faunas, C being the number of species in common, and N_1 being the number of species in the smaller fauna. I have expressed the numerical data above, and the indices derived from Simpson's formula follow.

Coelé-Sabanas	95
Darien-Sabanas	95
Darien-Chagres	95
Coelé-Herrera-Sabanas	94
Herrera-Sabanas	93
Herrera-Chagres	93
Coelé-Herrera	90
Sabanas-Chagres	88
Coelé-Herrera-Chagres	87
Coelé-Chagres	85
Herrera-Darien	79
Coelé-Darien	75
Coelé-Herrera-Darien	74

DOMINANCE AND RARITY

The opinion of most naturalists, including myself before I studied the snakes of the Clark collection, was fairly well stated by Hesse, Allee and Schmidt ('31). Speaking generally, they say (p. 30),

"In the tropics the favorable conditions (combined with the intensity of the competitive struggle) permit almost unlimited speciation, but the individuals of each species are for the most part not abundant," and, speaking of snakes (p. 40+), "the small number of individuals which characterize most of these species is in direct contrast to the great number of species by which the tropical fauna is characterized. . . . A collector of snakes in Cameroon took 50 species, and of only two of these did he obtain as many as four individuals."

The "collector of snakes in Cameroon" was Sjöstedt. On reading his paper I find that far from taking 50 species he took only 14. Of these, two were represented by four specimens apiece, one by two specimens, and eleven by a single specimen each; a total of 21 specimens. The collection made by Sjöstedt shows less dominance and less rarity than any Panamanian one, but is fairly similar to the Agua Clara catch of 1943. The figure of "50 species" was taken from a snake list compiled by Sjöstedt for the whole of the Cameroon country.

The Clark material indicates that many of the species are indeed rare. Five are represented by only a single specimen apiece, and six species known from the region do not appear at all in a collection of 10,690 specimens. However, the extreme relative rarity of many species expresses only half the truth, as, in the same collection of 10,690, one species was represented by 1,440 specimens, a second by 1,019, and a third by 895. This is equally extreme relative abundance.

It would be awkward and futile to try to give ordinary graphic expression to a curve of this hyperbolic nature, in which the ordinate (number of species represented by a given number of individuals) would require five lines, and the abscissa (number of individuals in a species) 1,440! Seeking for a fairly vivid but non-graphic mode of expression, I decided to cut both the ordinate and the abscissa and contrast the two ends of the

curve thus cut from the central portion.

One end of the curve contains 1/2 the individuals in the collection and a certain relatively small percentage of the species. The other end of the curve contains 1/2 the species in the collection and a certain relatively small percentage of the individuals. These two percentages may now be contrasted. If both are low there is great discrepancy in relative abundance; if both are high there is little. Half the collection, 5,345 individuals, accounts for those of the six most abundant species plus 6% of those representing the seventh, i.e., 6.06 species. This number of species is 9.6% of the 63 in the collection. Thus a little less than 1/10 of the species make up half the catch. The rare 31.5 species account for 398.5 individuals, which is 3.7% of the collection. Thus 1/2 the collection makes up 9.6% of the species, and 1/2 the species make up 3.7% of the collection. Figures for the four areas and for the localities Agua Clara in the Chagres area and Yavisa in Darien are given below.

	1/2 the collection	1/2 the species
Coclé-Herrera	9.8% of the species	4.6% of the collection
Sabanas	7.2% of the species	2.9% of the collection
Chagres	12.8% of the species	5.8% of the collection
Agua Clara	12.6% of the species	6.8% of the collection
Darien	8.0% of the species	5.4% of the collection
Yavisa	9.3% of the species	7.3% of the collection

These figures do not express specific variety, but the dominance and rarity of species in a fauna. In these two respects tropical snake populations will be found to differ little from temperate snake populations, as I have obtained quite similar percentages from a collection, made in the United States, which contained only 17 species.

The dominance of the commonest species is slightly less marked in the Amw deciduous forest climate of the Chagres area than it is in the Aw savanna climate of the other three. But it would not be too far wrong to say that 1/10 of the species make up half a collection, and that half the species make up less than 1/10 of a collection. From three

(Coclé-Herrera) to seven (Chagres) species are so abundant that they make up over half of the collection from any one area, but in order to show the seven dominants of each area it is necessary to list 15 species.

In other words, the dominance shifts from one set of species to another as one goes from one area to another. I noticed this phenomenon very early in the work. I had not received many shipments before I found that I could correctly predict the locality whence they came by merely glancing at the mass of specimens jumbled on the table. A lot largely composed of *Bothrops atrox* and *Boa constrictor* meant Darien; a high number of *Xenodon* meant Chagres; etc. This remarkable shift in relative abundance of dominant species from one contiguous area to another is even more novel and noteworthy than the fact of dominance itself.

To show these shifts I have prepared a table (table I) giving the relative abundance of 15 species in each area, expressed in terms of percentage of the

catch for the area. For each species I have added the number in the total catch and the percentage of the total catch that it makes. The list includes every species that makes up as much as 5% of any areal catch, as well as the seven species which make up as much as 1% of each areal catch. The symbol "+" indicates presence in the area, but less than 1% of the areal catch. The symbol "-" indicates absence from the area.

In the column giving the total catch figures the first 14 species are also the first 14 in actual abundance, and all those which make up as much as 2% of the catch. But the fifteenth species, *Lygophis*, would be twenty-second from the top were this a complete list of species

TABLE I

	Coeló-Herrera	Sabanas	Chagres	Darién	Total catch	
					No.	%
<i>O. aeneus</i>	19.4	22.2	10.9	1.9	1440	13.5
<i>L. rhombifera</i>	20.5	6.1	3.8	14.2	1019	9.5
<i>B. lansbergi</i>	10.6	16.7	2.9	1.3	895	8.4
<i>B. atrox</i>	+	3.1	5.6	18.3	824	7.7
<i>D. boddaertii</i>	2.8	4.9	8.0	6.3	618	5.8
<i>C. carinatus</i>	+	2.4	3.6	11.1	522	4.9
<i>Xenodon</i>	1.1	4.9	9.8	+	478	4.5
<i>M. nigrocinctus</i>	1.5	6.5	6.9	+	460	4.2
<i>T. occidentalis</i>	5.9	4.2	4.9	2.1	422	3.9
<i>Constrictor</i>	3.9	4.7	4.2	1.7	388	3.6
<i>Epicrates</i>	3.1	3.8	3.2	3.9	385	3.6
<i>Boa conkii</i>	+	+	+	11.3	372	3.5
<i>Leimadophis</i>	—	+	7.6	3.4	314	2.9
<i>D. margaritifera</i>	7.5	4.6	+	—	284	2.7
<i>Lygophis</i>	9.2	—	—	—	113	1.1

arranged in order of abundance in the total catch.

The great changes from area to area in the relative abundance of most of these species are obvious. Attention is called to the almost constant relative abundance of *Epicrates* and, to a lesser degree, of *T. occidentalis*, *Constrictor*, and *D. boddaertii*.

The generic name alone is used unless more than one species of the genus is mentioned in the paper. For the full name and systematic position see table VII.

ABUNDANCE AND RANGE

In order to see if any relationship exists between relative abundance and range, I have divided the species into four groups.

(1) Nine species seem to be endemic, or practically so, in the region. None of them form as much as 1% of any population.

- Anomalepis mexicanus*
- Scaphiodontophis zeteki*
- Tretanorhinus moquardi*
- Hydromorphus clarki*
- Dipsas viguieri* (also known from upland Darién)
- Dipsas nicholsi*
- Trimetopon barbouri*

Tantilla albiceps
Micrurus dunni

(2) Six species seem to have their southern limit in the region, none of them entering South America. I give, in general terms, the northernmost country inhabited.

- Tretanorhinus nigroluteus*: Mexico.
- Ninia maculata* (also upland Darién): Nicaragua.
- Amastidium veliferum*: Nicaragua.
- Rhadinaca decorata* (also upland Darién): Mexico.
- Imantodes gemmistratus*: Mexico.
- Micrurus clarki* (also upland Darién): Costa Rica.

The *Imantodes* makes up 2.5% of both the Coeló-Herrera and the Sabanas collections. None of the rest make up as much as 1% of any population. The *Tretanorhinus* is unknown between the Canal Zone and Nicaragua.

(3) Seven species seem to have their northern limit in the region, none of them entering North America farther than Herrera Province. I give the southernmost country inhabited.

- Leptotyphlops gondotii*: Colombia.
- Leptotyphlops macrolepis*: Brazil.
- Lygophis lineatus*: Argentina.
- Siphlophis cervinus*: Brazil.

Phimophis guianensis: Argentina.

Dryadophis pleei: Venezuela.

Thalerophis riveti: Peru.

The *Lygophis* makes up 9.2% of the Coeló-Herrera collection. The *Dryadophis* makes up 2.5% of the same collection. None of the rest make up as much as 1% of any collection. All these species show marked discontinuities in their known ranges, and the *Siphophis* is the only one of them known to occur in Darien.

(4) The remaining 47 species have ranges which extend from South America to western Panama at least, and in some cases to the United States. In this group are to be found the 18 species most abundant in the total catch, the six species which attain to more than 10% in any of the areal catches, and 12 of the 13 species which reach over 5% in any of the areal catches. Twenty-eight species make up more than 1% of the catch in at least one area. Eight species of this group have not yet been taken in Darien, and there are a number of striking discontinuities in the known ranges of many of them.

Another method of investigating the relationship between range and abundance is to divide the species into four groups on the basis of distribution within the region.

(1) Twelve species occur in only one of the four areas. Of these only one amounts to more than 1% of the collection in which it is found.

(2) Thirteen species have been taken in two of the areas. Only one amounts to as much as 1%, and that in one area only.

(3) Twenty-one species have been taken in three areas. Nine make up from 1% to 7.6% of one or two of the populations.

(4) Twenty-three species occur in all four areas. Twenty of these form from 1% to 22.2% of one or more of the populations. Seven are more than 1% and two are more than 3% of all four

areas. This group contains the three most abundant snakes of each area, and all six species that make up more than 10% of any area.

Both of these methods indicate some degree of positive correlation between wide range and relative abundance. It is surprising that the endemics should be so rare, as they are in the center of their known range. It is not surprising that the forms which reach their range limit in the region should be relative rarities, and the abundance of *Lygophis* in Coeló-Herrera is very extraordinary. Nor is it surprising that forms which range beyond the limits of the region, and widely within it, should, on the whole, be the more abundant species.

RELATIONSHIP BETWEEN ABUNDANCE AND SIZE OF SYSTEMATIC GROUP

It has frequently been suggested that the number of named forms in a systematic group has a positive correlation with the number of individuals in a state of nature. To examine the Clark material on this basis I have tabulated the five best represented groups. The three families Boidae, Elapidae, and Viperidae are each represented in the collections by approximately the same number of species. The Colubrid subfamily Xenodontinae is represented by approximately the

TABLE II. Representation by species

	Boidae	Elapidae	Viperidae	Xenodontinae	Colubrinae
Coeló-Herrera	9.7	6.5	6.5	29.0	48.0
Sabanas	6.9	6.9	8.6	34.5	36.2
Chagres	6.7	5.0	8.3	38.3	36.7
Darien	9.1	6.8	9.1	36.4	38.6

Representation by individuals

	Boidae	Elapidae	Viperidae	Xenodontinae	Colubrinae
Coeló-Herrera	7.5	1.6	10.9	16.6	63.5
Sabanas	8.9	6.9	20.0	12.3	51.8
Chagres	7.6	7.9	12.3	23.8	48.3
Darien	17.1	1.5	20.4	10.9	50.1

same number of species as is the subfamily Colubrinae.

The table makes it fairly obvious that equal representation by species is very far from equal representation by individuals. The Viperids and Colubrinae are more numerous as individuals, and the Xenodontines less so, than their relative numbers of species would suggest.

In table II the figures for representation by species are percentages of the total number of species in each area. The figures for representation by individuals are percentages of the total areal catches.

THE COCLÉ-HERRERA COLLECTION

This collection consists of 1,232 specimens representing 30 species. The Coclé material comes from:

Río Grande and Río Coclé (1933)	68 specimens
Río Grande (1940)	183 specimens
Río Hato (1940)	3 specimens

The Herrera material comes from:

Río Santa María near Portuga (1933)	42 specimens
Parita to Río Santa María (1939)	936 specimens

The collections from Herrera and Coclé have 18 species in common. The following 11 species from Herrera do not occur in the catch from Coclé:

- Boa hortulana cookii*
- Dipsas nebulatus*
- Enalius flavitorques*
- Coluber mentovarius subocularis*
- Oxybelis fulgidus*
- Imantodes gemmistratus*
- Chironius carinatus*
- Lampropeltis triangulum micropholis*
- Tantilla ruficeps*
- Stenorhina d. degenhardtii*
- Bothrops atrox*

With the exception of the *Coluber* these have all been taken in the Province of Panama and are to be expected in intervening Coclé.

The following two species do not occur in the catch from Herrera and there is

no evidence as yet that they range west of Coclé:

- Phimophis guianensis*, "Coclé."
- Micrurus dunni*, Río Hato.

Río Hato was a United States airfield. The 1940 Río Grande collection was made by the personnel of the University of Pennsylvania archeological dig, and probably the Río Grande-Río Coclé collection was made by the Harvard dig at the famous Sitio Conte, in the same vicinity.

Dr. Clark says of the Río Santa María area, "dry table land area near the mouth of the river." I have visited none of the localities, but I have traveled through Coclé and Herrera and on into Veragua (from Antón to Santiago and Océ) without seeing any physiographic or floristic change. The rainfall data for Penonomé in Coclé is 73 inches a year; four months (January to April) each with under two inches.

All of the localities are below 500 feet elevation.

The Clark material adds 19 species to the fauna of the area. The Museum material of 98 specimens contains a specimen of *Phimophis guianensis* from "Coclé," a species that does not occur in the Clark collection. Two species (*Lygophis lineatus* and *Coluber mentovarius*) are known from definite Panamanian localities only by means of this collection.

The families and subfamilies are represented as follows:

	No. of species	% of species	Individuals in collection	% of individuals
Boidae	3	9.7	92	7.5
Xenodontinae	9	29.0	204	16.6
Colubrinae	15	48.4	782	63.5
Elapidae	2	6.5	20	1.6
Viperidae	2	6.5	134	10.9

Species are represented by from 252 individuals (*Leptodeira rhombifera*, 20.5% of the collection) to one individual (six species).

Sixteen species are each more than 1% of the collection. These add up to 1,189 individuals or 95.5% of the collection.

Fourteen species are each less than 1% of the collection. These add up to 43 individuals or 3.5% of the collection.

The contrast between 1/2 the collection, as made up by the few dominant species, and that part of the collection made up by the rarer 1/2 of the species is:

1/2 the collection, 616 individuals (2.9 species), 9.8% of the species.

1/2 the species (15 species), 57 individuals, 4.6% of the collection.

THE SABANAS COLLECTION

This collection consists of 3,914 specimens representing 52 species. The specimens come from the Pacific side lowlands: from Capira to the west to Canita in the mid-basin of the Bayano to the east; in the Canal Zone from Miraflores, near the divide, to the Pacific ocean. The majority of the specimens come from the true "Panama sabanas" which lie between Panama City and Chepo. One lot of specimens was labeled "Miraflores to Chepo," and many others have similar but less inclusive titles. Frequent remarks such as "mostly Juan Diaz to Pacora" indicate the probable provenance of most of these, but it is not possible to give any big lot separate year by year analysis.

From west of the Zone come 730 specimens: Capira, 1; Chorrera, 29; Chorrera to Arraijan, 700. The last collection contains the only specimens of *Rhadinaea decorata* and *Tantilla ruficeps* known from the area.

From Miraflores to Chepo come 3,105 specimens. Some of the rarer forms in this lot can be localized (*Amastridium velliferum* and *Erythrolamprus m. micrurus* were allocated to Panama-Ancon-Corozal; *Micrurus clarki* to Panama City and the Canal Zone). The following forms are not known to occur farther west on the Pacific side than this Canal

Zone to Chepo area: *Boa annulata*, *Tretanorhinus moquardi*, *Siphlophis cervinus*, *Rhinobothryum bovalli*, *Amastridium velliferum*, *Erythrolamprus m. micrurus*. The last is represented much farther west by *E. m. impar*. Miraflores-Chepo forms not known from farther east are: *Tretanorhinus moquardi*, *Amastridium velliferum*, *Micrurus dunni*.

From east of Chepo come 79 specimens from Canita in the mid-basin of the Rio Bayano. This collection contains the only specimens of *Leptotyphlops macrolepis* and *Ninia atrata* known from the area.

I have traveled over this area from Old Panama in the east through to the Atlantic side of the Zone, west past Capira, and on over the wooded uplands which make a sort of barrier between this area and that of Coeló-Herrera. Dr. Clark's description is: "a dry table-land, very little above sea level, and without trees except for narrow stretches near rivers and creeks." To this I would add that there are occasional isolated "inselberge," steep-sided, and with forest on top. Of these, Ancon Hill (654 feet) is the only one likely to have furnished any snakes to this collection, or to the Museum material from the same area.

The area has a yearly rainfall of 69 inches (Balboa); three months (January to March) each have less than two inches.

The Clark collection contains 14 species additional to those in any Museum. The Museum collections of 401 specimens contain 6 species not taken by Clark's collectors in recent years. They are:

Leptotyphlops goudotii; La Joya I air-field, between Pacora and Chepo.

Scaphiodontophis seteki; Ancon.

Trimetopon barbouri; Ancon, Pedro Miguel.

Pliocercus e. dimidiatus; Pedro Miguel.

Chironius fuscus; Pintupe on the Bayano.

Bothrops nasutus; "Sabanas," Chepo.

The Sabanas area has three species not known from elsewhere in Panama or in North America.

Leptotyphlops macrolepis; Canita, otherwise known from Colombia, Venezuela, and Brazil.

Leptotyphlops goudotii; La Joya 1, known from the Magdalena valley in Colombia.

Scaphiodontophis seteki; Ancon, not known from any where else.

The families and subfamilies are represented as follows:

	No. of species	% of species	Individuals in collection	% of individuals
Leptotyphlopidae	2	3.4	1	—
Typhlopidae	1	1.7	1	—
Boiidae	4	6.9	350	8.9
Sibynophiinae	1	1.7	0	—
Xerodontinae	29	34.5	482	12.3
Colubrinae	21	36.2	2026	51.8
Elapidae	4	6.9	270	6.9
Viperidae	5	8.6	784	20.0

Species are represented by from 868 individuals (*Oxybelis aeneus*, 22.2% of the collection) to one individual (six species).

Sixteen species are each more than 1% of the collection. These add up to 3,604 individuals or 92.1% of the collection.

Thirty-six species are each less than 1% of the collection. These add up to 310 individuals or 7.9% of the collection.

The contrast between 1/2 the collection, as made up by the few dominant species, and that part of the collection made up by the rarer 1/2 of the species is:

1/2 the collection, 1,957 individuals (3.8 species), 7.2% of the species.
1/2 the species (26 species), 112 individuals, 2.9% of the collection.

THE CHAGRES COLLECTION

This collection consists of 2,500 specimens representing 53 species. It comes from the Atlantic slope of the Canal

Zone and the Chagres Valley, from France Field on the coast to the head of Madden Lake (where the Rio Peluca joins the Boquerón at an elevation of 260 feet). The majority of the specimens (2,434; 53 species) were taken in the Chagres valley between the normal Canal Zone boundary and the head of Madden Lake. Dr. Clark says: "this collection is almost entirely from the mid-basin . . . in the rocky, forested portion," and "practically all of the snakes that we caught in the Madden Lake area were collected from the 5-1/2 square miles of the bottom that they cleared of trees and bushes."

The collection may be broken up as follows:

Localities	Specimens
France Field	5
Goodyear Farm near Gatun	18
Gigante Island in Gatun Lake	42
Gamboa to Summit	1
Chagres villages between Zone border and Madden Dam	711
Agua Clara village	1103
Madden Dam road	14
Madden Lake area	606

The villages on the Chagres are all rather new, were made by clearing forest, and are due to the exodus from the Canal Zone as a result of the decision not to renew leases. Agua Clara lies about two miles from the river, just outside the Zone border, and almost directly north of Gamboa. It is not on any map. As this village has the largest number of species for any single Panamanian locality, and a collection record of nine years, I give this material a separate analysis.

I have been over most of the area, but my visits were after the flooding of Gatun Lake and of Madden Lake. My impression is that the entire area was forest in prehuman days, but that there was probably some forest clearing by Indians, and certainly a good deal of clearing from Spanish colonial times up to the present. The rainfall data are as follows:

Madden Dam, 100 inches, three months each below two inches.

Barro Colorado Island (Gatun Lake), 110 inches, three months each below two inches.

Cristobal (Atlantic coast), 129 inches, two months each below two inches.

The Clark collection contains 8 species additional to those in any museum. Museum material of 510 specimens contains 7 species not taken by Clark's collectors in recent years. They are:

Anomalepis mexicanus: Barro Colorado Island; Frijoles.

Liotyphlops albirostris: Summit; "Chagres river."

Tretanorhinus n. nigroluteus: Eight localities. One, Juan Mina, is very close to the Chagres villages; the others are mostly coastal.

Tretanorhinus moquardi: Fort Sherman.

Dryadophis pleei: "Chagres R."

Thalerophis riveti: Between the Chagres and Agua Clara.

Tantilla albiceps: Barro Colorado Island.

This area has seven species not present in the other three. Four are not known from elsewhere:

Anomalepis mexicanus: Barro Colorado Island; Frijoles.

Hydromorphus clarki: Agua Clara.

Dipsas nicholsi: Madden Lake area; Chagres villages; Agua Clara.

Tantilla albiceps: Barro Colorado Island.

One is not otherwise known from Panama, but is present in Atlantic side Nicaragua and occurs north into Mexico:

Tretanorhinus n. nigroluteus.

Two are known from other Panamanian localities:

Scaphiodontophis venustissimus: Puerto Armuelles in Chiriqui. Also: Atlantic side Costa Rica and Nicaragua; Muzo, central Colombia.

Thalerophis riveti: Cerro Campana, 3,000 feet. Also: west coast of Colombia, Ecuador, Peru, Trinidad.

The following table shows the representation of families and subfamilies for the whole Chagres area, including Agua Clara.

	No. of species	% of species	Individuals in collection	% of individuals
Typhiopidae	2	3.3	—	—
Boidae	4	6.7	191	7.6
Sibynophiliinae	1	1.7	1	—
Xenodontinae	23	38.3	596	23.8
Colubrinae	22	36.7	1208	48.3
Elapidae	3	5.0	197	7.9
Viperidae	5	8.3	307	12.3

Species are represented by from 274 individuals (*Oxybelis aeneus*, 10.9% of the collection) to one individual (three species).

Nineteen species are each more than 1% of the collection. These add up to 2,223 individuals or 88.9% of the collection.

Thirty-four species are each less than 1% of the collection. These add up to 277 individuals or 11.1% of the collection.

The contrast between 1/2 of the collection, as made up by the few dominant species, and that part of the collection made up by the rarer 1/2 of the species is:

1/2 the collection, 1,250 individuals (6.8 species), 12.8% of the species.

1/2 the species (26.3 species), 146 individuals, 5.8% of the collection.

COMMENTS ON THE AGUA CLARA COLLECTION

Nine yearly collections (1937-1945) have produced a total of 1,103 specimens representing 47 species. The catch contains a specimen of *Hydromorphus clarki*, a species otherwise unknown; a specimen of *Scaphiodontophis venustissimus*, otherwise unknown from between Chiriqui and central Colombia; specimens of *Boa annulata* and of *Rhinobothryum bovallii*, otherwise unknown from the lowlands of the Chagres basin.

It lacks, of course, the seven Museum species which are not in Clark's Chagres

collections. It also lacks six species that Dr. Clark has sent in from other localities in the Madden Dam area: *Boa cookii*, *Dipsas nebulatus*, *Enallius flavitorques*, *Drymobius margaritiferus*, *Bothrops lansbergii*, and *Bothrops nasuta*.

The make-up or structure of the collection is similar to that of the Chagres as a whole. Families and subfamilies are represented as follows:

	No. of species	% of species	Individuals in collection	% of individuals
Boidae	3	6.3	75	6.8
Sibynophiinae	1	2.1	1	—
Xenodontinae	19	40.4	264	23.9
Colubrinae	18	38.2	544	49.3
Elapidae	3	6.3	89	8.1
Viperidae	3	6.3	130	11.8

Species are represented by from 125 individuals (*Oxybelis acenus*, 11.3% of the collection) to one individual (eight species).

Eighteen species are each more than 1% of the collection. These add up to 979 individuals or 88.8% of the collection.

Twenty-nine species are each less than 1% of the collection. These add up to 124 individuals or 11.2% of the collection.

The contrast between 1/2 of the collection, as made up by the few dominant species, and that part of the collection made up by the rarer 1/2 of the species is:

1/2 the collection, 551.5 individuals (5.9 species), 12.6% of the species.
1/2 the species (23.5 species), 74.5 individuals, 6.8% of the collection.

Year	Specimens	Species	Species new to locality
1937	53	24	24
1938	176	35	14
1939	270	35	3
1940	39	29	2
1941	49	26	3
1942	41	16	1
1943	25	10	—
1944	59	18	—
1945	91	29	—

The preceding table lists the number of specimens and species in the yearly catch, and gives the number of species that appeared for the first time in any given year.

A scrutiny of the collection for yearly trends or fluctuations brings out some few matters of interest.

Bothrops atrox is the only snake that makes up 4% or more of each year's catch. It is fifth in total count.

Micrurus nigrocinctus makes up 3% or more of each year's catch, but is seventh in total count.

Dryadophis boddaertii makes up 2% or more of each year's catch, but is fourth in total count.

Oxybelis acenus is below 2% in 1937, but is first in total count.

Leimadophis epinephalus is absent in 1942, but is second in total count.

Xenodon rabdocephalus is below 2% in 1937, but is third in total count.

Stenorhina degenhardtii is below 2% in 1944 and in 1945, but is sixth in total count.

Seven species appear in each of the nine years. They are never below 1% of any year, and each makes up at least 10% of some one year. They make up all but one of the eight total counts above 60.

Eight species appear in a single year only. They are represented by one specimen in each case.

In the years 1938 to 1941 there seems to have been a steady increase in the incidence of *Oxybelis acenus* (6.8 to 20.1%), and of *Dryadophis boddaertii* (5.7 to 10.1%); a decrease in that of *Stenorhina degenhardtii* (11.5 to 3.4%). There can be little connection between these phenomena, as *Oxybelis* is scansorial; *Dryadophis* terrestrial. Both are active and diurnal, whereas *Stenorhina* is secretive and probably burrowing and nocturnal.

The first of the following tables lists the Agua Clara snakes in order of abundance. The second lists the eleven most

TABLE III. *Agua Clara, 1937-1945*

	1937	1938	1939	1940	1941	1942	1943	1944	1945	Total
<i>O. aeneus</i>	1	12	22	40	31	7	1	4	7	125
<i>Leimadophis</i>	4	7	35	26	5	—	3	12	14	106
<i>Xenodon</i>	1	10	26	10	9	5	3	9	15	88
<i>D. baldaerthii</i>	4	10	17	22	15	1	2	7	2	80
<i>B. atrox</i>	3	12	16	21	12	7	2	3	4	80
<i>Stenorkina</i>	2	20	22	22	5	1	4	1	1	78
<i>M. nigrocinclus</i>	6	9	9	16	13	3	5	8	6	75
<i>Pseustes</i>	6	10	17	9	7	3	2	1	5	60
<i>T. occidentalis</i>	1	7	19	8	5	—	2	1	3	46
<i>Lachesis</i>	—	9	8	13	5	4	—	1	1	41
<i>Epicrates</i>	6	9	8	6	6	2	—	2	1	40
<i>C. carinatus</i>	1	5	12	9	7	—	—	—	1	35
<i>Constrictor</i>	2	6	5	8	8	1	—	—	2	32
<i>L. rhombifera</i>	—	3	4	3	6	1	1	3	2	23
<i>Spilotes</i>	2	8	3	4	2	1	—	1	1	22
<i>Dendrophidion</i>	2	2	8	4	1	2	—	1	1	21
<i>L. annulata</i>	2	4	3	—	—	—	—	—	5	14
<i>I. cerrojo</i>	1	—	4	1	1	—	—	2	4	13
<i>Contiophanes</i>	—	4	4	1	1	—	—	—	1	11
<i>Phiocercus</i>	—	3	1	—	1	—	—	1	4	10
<i>B. schlegelii</i>	1	2	3	—	2	—	—	—	1	9
<i>E. bizonus</i>	—	3	2	2	—	1	—	—	—	8
<i>Drymarchon</i>	1	3	—	4	—	—	—	—	—	8
<i>T. ruficeps</i>	—	3	2	—	—	—	—	1	1	7
<i>M. mipartitus</i>	—	2	3	2	—	—	—	—	—	7
<i>M. clarki</i>	2	2	3	—	—	—	—	—	—	7
<i>N. maculata</i>	—	2	1	1	—	1	—	—	1	6
<i>Clelia</i>	—	1	3	—	1	—	—	—	1	6
<i>R. decorata</i>	1	1	1	1	—	—	—	—	1	5
<i>R. fulviceps</i>	1	1	1	—	2	—	—	—	—	5
<i>Siphlophis</i>	1	—	2	1	—	—	—	—	—	4
<i>O. fulgidus</i>	—	—	1	1	—	—	—	—	2	4
<i>Rhinobolhyrum</i>	—	—	—	1	1	—	—	—	2	4
<i>B. annulata</i>	1	—	1	—	—	—	—	—	1	3
<i>Amastridium</i>	1	1	1	—	—	—	—	—	—	3
<i>E. micrurus</i>	—	—	2	1	—	—	—	—	—	3
<i>Oxyrhopus</i>	—	1	—	1	—	—	—	—	—	2
<i>E. slateri</i>	—	1	—	—	—	—	—	1	—	2
<i>C. fuscus</i>	—	1	—	—	—	—	—	—	1	2
<i>Scaphiodontophis</i>	—	—	—	—	1	—	—	—	—	1
<i>Hydromorphus</i>	—	—	—	—	1	—	—	—	—	1
<i>D. viguieri</i>	—	—	—	—	1	—	—	—	—	1
<i>D. nicholsi</i>	—	1	—	—	—	—	—	—	—	1
<i>Trimetopon</i>	—	—	1	—	—	—	—	—	—	1
<i>Pseudoboa</i>	—	—	—	—	—	1	—	—	—	1
<i>I. gemmistratus</i>	—	1	—	—	—	—	—	—	—	1
<i>Lampropeltis</i>	—	—	—	1	—	—	—	—	—	1
Total	53	176	270	239	149	41	25	59	91	1103

abundant snakes; all that amounted to as much as 5.5% of the catch of any one year. Percentages are given for each year and for the total catch. In both tables the generic name alone is used unless more than one species of the genus is mentioned in the paper.

THE DARIEN COLLECTION

This collection consists of 3,044 specimens representing 44 species. Accord-

ing to Dr. Clark, it comes "entirely from the lowland banana and plantain farms which are in contact with . . . tidewater service." All but one of the localities are in the lowlands of the Rio Tuira basin. Material was sent in from the following localities:

Yavisa, on the Rio Chucunaque a few miles above its junction with the Tuira; tidewater; 2,321 specimens.

TABLE IV. *Agua Clara, 1937-1945*

	1937	1938	1939	1940	1941	1942	1943	1944	1945	Total
<i>O. aeneus</i>	1.9	6.8	8.1	16.7	20.1	17.1	4.0	6.8	7.7	11.3
<i>Leimadophis</i>	7.5	3.9	13.4	10.2	3.4	—	12.0	20.3	15.0	9.7
<i>Xenodon</i>	1.9	5.7	9.6	4.2	6.0	12.2	12.0	15.3	16.5	7.9
<i>D. boadartii</i>	7.5	5.7	6.3	9.2	10.1	2.0	8.0	11.9	2.2	7.2
<i>B. atrox</i>	5.7	6.8	5.9	8.9	18.1	17.1	8.0	5.1	4.4	7.2
<i>Stenorkhina</i>	3.8	11.5	8.1	9.2	3.4	2.0	16.0	1.7	1.1	7.1
<i>M. nigrocinctus</i>	11.3	5.1	3.7	6.7	8.7	7.3	20.0	13.7	6.6	6.8
<i>Pseustes</i>	11.3	5.7	6.3	3.8	4.7	7.3	8.0	1.7	5.5	5.4
<i>T. occidentalis</i>	1.9	3.9	7.0	3.3	3.4	—	8.0	1.7	3.2	4.2
<i>Lachesis</i>	—	5.1	3.4	5.5	3.4	2.7	—	1.7	1.1	3.7
<i>Epicrates</i>	11.3	5.1	3.4	2.5	4.0	4.9	—	3.6	1.1	3.6

El Real de Santa Maria, on the Tuira a few miles above its junction with the Chucunaque; tidewater; 32 specimens.

Pinogana, on the Tuira a little above Santa Maria; some eight meters above sea level; 1 specimen.

Boca de Cupe, on the Tuira above Pinogana; perhaps 60 meters above sea level; 186 specimens.

Fork of the Rio Pihuala and Rio Tucuti branch of the Tuira (the Tucuti enters the Tuira from the south below the mouth of the Chucunaque); probably below 100 meters; 359 specimens.

Rio Tucuti branch of the Tuira; 5 specimens.

Rio Sabalo headwaters and Rio Sambu (the Sabalo is a southern tributary of the Tucuti. The Sambu enters the Gulf of San Miguel but runs roughly parallel to the Tucuti. The Sabalo-Sambu divide is about 500 meters); 19 specimens of *Boc cookii*.

Punta Jaque, on the Pacific coast about halfway between Punta Escarpado (near Garachiné) and the Colombian border; 24 specimens.

"Yavisa, Boca de Cupe, and Punta Jaque"; 97 specimens.

I have not seen any of these localities. The only climatic data is for Garachiné: 65 inches of rain a year; February and March each with less than two inches.

The Clark Darien material adds 20 species to the previously known fauna of the area. No known Museum material

contains any species additional to the 44 in the Clark collection. Only 64 Museum specimens have been available. The Yavisa collection is the largest from any one Panamanian locality and will be given separate treatment.

The Darien collection contains no endemics, nor any species which does not occur in the Chagres or the Sabanas or both. The race *Pliocercus eurysonus eurysonus*, known from Darien and Colombia, is represented in the Chagres and in the Sabanas by the race *P. c. dimidiatus*.

The following table shows the representation of families and subfamilies for the whole Darien area, including Yavisa.

	No. of species	% of species	Individuals in collection	% of individuals
Boidae	4	9.1	519	17.1
Xenodontinae	16	36.4	334	10.9
Colubrinae	17	38.6	1524	50.1
Elapidae	3	6.8	45	1.5
Viperidae	4	9.1	622	20.4

Species are represented by from 556 individuals (*Bothrops atrox*, 18.3% of the collection) to one individual (five species).

Twenty species are each more than 1% of the collection. These add up to 2,823 individuals or 92.7% of the collection.

Twenty-four species are each less than 1% of the collection. These add up to 221 individuals or 7.3% of the collection.

The contrast between 1/2 of the collection, as made up by the few dominant species, and that part of the collection made up by the rarer 1/2 of the species is:

- 1/2 the collection, 1,522 individuals (3.5 species), 8.0% of the species.
1/2 the species (22 species), 163 individuals, 5.4% of the collection.

COMMENTS ON THE YAVISA COLLECTION

Five yearly collections produced a total of 2,321 individuals representing 40 species. The catch contains the only lowland Darien specimens of six species: *Boa annulata*, *Ninia maculata*, *Erythrolamprus micrurus*, *Enallius slateri*, *Tantilla ruficeps*, *Micrurus mipartitus*.

It lacks four lowland species sent in from other localities in the Darien area: *Enallius flavitorques* from Punta Jaque (reported as *Leptocalamnis torquatus* from Punta Sabana by Peracca in 1896); *Chironius fuscus*, Pihuala-Tucuti; *Imantodes gemmistratus*, Punta Jaque; *Bothrops schlegelii*, Pihuala-Tucuti.

The make-up or structure of the collection is similar to that of Darien as a whole. Families and subfamilies are represented as follows:

	No. of species	% of species	Individuals in collection	% of individuals
Bolidae	4	10.0	314	13.5
Nenocontinae	15	37.5	281	12.1
Colubrinae	15	37.5	1239	53.4
Elapidae	3	7.5	39	1.6
Viperidae	3	7.5	448	19.3

Species are represented by from 407 individuals (*Bothrops atrox*, 17.5% of the collection) to one individual (four species).

Nineteen species are each more than 1% of the collection. These add up to 2,120 individuals or 91.3% of the collection.

Twenty-one species are each less than 1% of the collection. These add up to 201 individuals or 8.7% of the collection.

The contrast between 1/2 of the collection, as made up by the few dominant species, and that part of the collection made up by the rarer 1/2 of the species is:

- 1/2 the collection, 1160.5 individuals (3.7 species), 9.3% of the species.
1/2 the species (20 species), 169 individuals, 7.3% of the collection.

The following table lists the number of specimens and species in the yearly catch, and gives the number of species that appeared for the first time in any given year.

Year	Specimens	Species	Species new to locality
1933	366	33	33
1934	790	35	2
1935	587	31	1
1936	310	32	0
1937	268	31	2

A scrutiny of the collection for yearly trends or fluctuations brings out a few matters of interest.

Bothrops atrox makes up more than 10% of each yearly catch. It is also first in total count.

Leptodeira rhombifera, with a minimum yearly catch of 8.2, is second in total count.

Chironius carinatus makes up 8% or more of each year's catch and is third in total count.

Boa constrictor, fourth in total count, has a minimum yearly catch of 4.4%.

Twenty-four species appear in each of the five years. They make up all but one of those whose total percentage is over 1%, and their totals run from 407 to 26. Thirteen make up at least 1% of every year. Only four fail to make up as much as 2% of some one year.

Four species occur in one year only. They are represented by a single specimen in each case.

During the five-year period there seems to have been a steady increase in the incidence of *Bothrops atrox* (14.7 to 28.7%),

and a similarly steady decrease in the incidence of *Boa constrictor* (15 to 4.4%) and of *Leptodeira rhombifera* (20.7 to 8.2%). The first is a large terrestrial snake which feeds mostly on rodents; the second is a large arboreal bird-eating form; the third is a small terrestrial form feeding largely on frogs. All three are chiefly nocturnal. Possibly the first two compete with each other, but this does not account for *Leptodeira*. The country people usually consider *Leptodeira* as a *Bothrops*, but this confusion would not cause any differential attention to them. As the decrease of the *Boa* is greater than

TABLE VI. Yavisa, 1933-1937

	1933	1934	1935	1936	1937	Total
<i>B. atrox</i>	16.7	15.0	15.3	21.2	28.7	17.5
<i>L. rhombifera</i>	20.7	19.1	12.6	10.0	8.2	15.3
<i>C. carolinatus</i>	12.0	12.7	13.1	8.0	10.4	11.8
<i>B. constrictor</i>	15.0	6.5	6.4	4.5	4.4	7.6
<i>D. bothroptilus</i>	4.6	7.3	8.6	7.0	2.9	6.9
<i>Epiplatys</i>	5.1	4.3	5.2	3.2	3.4	4.4
<i>Lalmatophis</i>	4.5	4.4	4.9	3.2	2.2	4.1
<i>L. constrictor</i>	0.8	2.2	6.4	5.2	2.7	3.5

TABLE V. Yavisa, 1933-1937

	1933	1934	1935	1936	1937	Total
<i>B. atrox</i>	54	120	90	66	77	407
<i>L. rhombifera</i>	76	151	74	31	22	354
<i>C. carolinatus</i>	44	101	77	25	23	275
<i>B. constrictor</i>	55	52	38	14	12	171
<i>D. bothroptilus</i>	17	62	51	22	3	160
<i>Epiplatys</i>	19	34	31	10	9	103
<i>Lalmatophis</i>	14	35	29	10	6	94
<i>L. constrictor</i>	3	17	38	16	7	81
<i>Dendrophiidion</i>	6	23	17	8	9	63
<i>L. annulata</i>	8	27	12	10	4	61
<i>T. occidentalis</i>	5	20	15	5	9	54
<i>Stenomochilus</i>	12	13	12	5	6	53
<i>C. arcuatus</i>	5	13	10	14	6	48
<i>M. atrata</i>	4	13	13	15	2	47
<i>Constrictor</i>	7	10	7	5	10	39
<i>Chloa</i>	6	11	5	7	6	35
<i>Pseudis</i>	2	9	12	5	6	34
<i>Caryacus</i>	2	13	7	1	3	26
<i>D. hammondi</i>	—	—	6	11	3	25
<i>D. melanostictus</i>	1	8	10	3	—	22
<i>Chilomen</i>	3	6	2	3	8	22
<i>Chamodon</i>	3	2	5	7	2	19
<i>D. rhombifera</i>	1	7	1	4	4	17
<i>Lachesis</i>	1	2	4	1	8	16
<i>M. mitchelli</i>	2	4	3	4	2	15
<i>Siphonops</i>	2	4	3	2	3	14
<i>M. clausi</i>	2	7	3	2	—	14
<i>Drymarchon</i>	—	1	4	4	1	10
<i>M. nigroocinctus</i>	3	5	1	—	1	10
<i>Pliocercus</i>	4	1	—	—	3	8
<i>E. blattus</i>	1	1	—	2	—	4
<i>E. slateri</i>	—	3	1	—	—	4
<i>Elanoides</i>	1	2	—	1	—	4
<i>T. ruficeps</i>	—	1	—	2	—	3
<i>D. aliphoi</i>	1	—	—	1	1	3
<i>R. fulvipes</i>	1	1	—	—	—	2
<i>B. annulata</i>	—	—	—	—	1	1
<i>N. maculata</i>	—	—	—	—	1	1
<i>B. micrurus</i>	—	—	1	—	—	1
<i>Pseudis</i>	1	—	—	—	—	1
Total	366	790	587	310	268	2321

the increase of *Bothrops atrox*, its place may partly be taken in the last years by the increase in the equally large *Constrictor*, *Spilotes*, and *Lachesis*.

The first of the preceding tables lists the Yavisa snakes in order of abundance. The second lists the eight most abundant snakes; all that amounted to as much as 5% of the catch of any one year. Percentages are given for each year and for the total catch. In both tables the generic name alone is used unless more than one species of the genus is mentioned in the paper.

The following table (table VII) contains all forms known from the region, listed in systematic order. The first column under each heading gives the number of museum specimens known (M); the second gives the number of specimens in the Clark collection (C). The third column (C%) expresses the figures of the second column in terms of percentage of the total catch for the area. Calculations below 1% are not given.

Thirty-three of the sixty species known from the Chagres area have been taken on Barro Colorado Island. Since many naturalists visit the Island I have indicated these species by means of an asterisk preceding the name.

SUMMARY

This paper deals with the relative abundance of the 69 snake species known to occur in the lowlands of the Panama Canal Zone and the adjacent lowlands on the Pacific slope of the Republic; in

Tropical Deciduous Forest (Anwi) climate, and in Tropical Savanna (Awi) climate. I have studied 1,073 specimens from this region in the museums of the world, specimens known to have been selected from original material of three times the number. I have also studied the 10,690 specimens of the Panama snake census collection, made, and sent to me for identification, by Dr. H. C. Clark, Director of the Gorgas Memorial

Laboratory in Panama City. This material was not subjected to any such selection, and is as near random sampling as is humanly possible.

In the material as a whole, and in all areal subdivisions of it, a few species are very abundant. These, about 1/10 of the species, make up 1/2 of the individuals in the snake populations. In contrast to this there are many less abundant species, so much less abundant that 1/2

TABLE VII

	Coclé-Herrera			Sabanas			Cintegres			Darién		
	M	C	C%	M	C	C%	M	C	C%	M	C	C%
LEPTOTYPHLOPIDAE												
<i>Leptotyphlops macrolepis</i>	—	—	—	—	1	—	—	—	—	—	—	—
<i>L. pudicill</i>	—	—	—	1	—	—	—	—	—	—	—	—
TYRANTORINAE												
<i>Anomalepis mexicanus</i>	—	—	—	—	—	—	4	—	—	—	—	—
<i>Liotyphlops albivestris</i>	—	—	—	15	1	—	3	—	—	—	—	—
BOIDAE												
<i>Constrictor constrictor imperator</i>	—	48	3.9	10	182	4.7	16	106	4.2	—	52	1.7
<i>Rhaphiodon cenchria maurus</i>	—	38	3.1	33	149	3.8	17	78	3.1	—	120	3.9
<i>Boa hartwegiana cookii</i>	—	6	—	1	16	—	—	4	—	4	302	11.3
<i>B. uncinata</i>	—	—	—	—	3	—	—	3	—	—	1	—
COLUBRIDAE SIBYRINOTINAE												
<i>Sibyrhaptophis catoki</i>	—	—	—	1	—	—	—	—	—	—	—	—
<i>S. venustissimus</i>	—	—	—	—	—	—	—	1	—	—	—	—
COLUBRIDAE XENODONTINAE												
<i>Xenodontinus n. nigrolatus</i>	—	—	—	—	—	—	15	—	—	—	—	—
<i>T. morquardii</i>	—	—	—	5	3	—	1	—	—	—	—	—
<i>Epitretomorphus clarki</i>	—	—	—	—	1	—	—	1	—	—	—	—
<i>Ninia atrata</i>	—	—	—	—	—	—	—	—	—	—	58	1.6
<i>Ninia maculata</i>	—	—	—	5	9	—	5	10	—	—	—	—
<i>Dipsas nebulatus</i>	—	1	—	7	5	—	2	10	—	2	20	—
<i>D. sigalei</i>	—	—	—	—	—	—	2	—	—	2	—	—
<i>D. nicholsi</i>	—	—	—	—	—	—	—	5	—	—	—	—
<i>A. nasiridhan voliferum</i>	—	—	—	—	1	—	2	—	—	—	—	—
<i>Rhadinaea decorata</i>	—	—	—	—	3	—	6	—	—	—	—	—
<i>R. pachyura fulviceps</i>	—	—	—	—	2	—	3	—	—	—	—	—
<i>Trinitopon barbouri</i>	—	—	—	5	—	—	1	5	—	—	—	—
<i>Phiocercus e. euryzonus</i>	—	—	—	—	—	—	—	—	—	2	9	—
<i>P. euryzonus dimidiatus</i>	—	—	—	2	—	—	3	12	—	—	—	—
<i>Contiophanes f. fissidens</i>	—	—	—	2	8	—	2	18	—	—	—	—
<i>Leimadophis e. spinophalus</i>	—	—	—	—	18	—	22	191	7.6	3	103	3.2
<i>Lygophis lineatus</i>	2	113	9.2	—	—	—	—	—	—	—	—	—
<i>Xenodon rabdocephalus</i>	1	14	1.1	30	191	4.9	44	246	9.8	1	50	—
<i>Erythrolampis bisonus</i>	1	34	2.3	10	139	3.6	5	29	1.2	—	6	—
<i>B. minus micrurus</i>	—	—	—	—	1	—	—	5	—	—	1	—
<i>Oxyrhopus petola sebae</i>	1	11	—	1	12	—	5	6	—	2	31	1.3
<i>Clelia e. clelia</i>	—	3	—	1	11	—	3	10	—	—	39	1.3
<i>Pseudoboa newwiedii</i>	2	25	2.0	8	47	1.2	7	9	—	1	2	—
<i>Siphlophis carvius geminatus</i>	—	—	—	—	5	—	4	5	—	2	15	—
<i>Phimophis guianensis</i>	1	—	—	3	10	—	—	—	—	—	—	—
<i>Enallias flavitorques</i>	—	1	—	38	17	—	8	2	—	—	2	—
<i>E. stateri</i>	—	—	—	—	—	—	3	2	—	—	4	—

TABLE VII—Continued

	Cocle-Herrera			Sabanas			Chagres			Darien		
	M	C	C%	M	C	C%	M	C	C%	M	C	C%
COLUBRIDAE COLUBRINAE												
<i>Coluber ventosarius subocularis</i>	—	1	—	—	—	—	—	—	—	—	—	—
<i>Dryadophis plecki</i>	1	31	2.5	6	32	—	1	—	—	—	—	—
* <i>D. boddaerti alternatus</i>	—	35	2.8	19	191	4.9	27	201	8.0	1	191	5.3
<i>Drymobius m. margaritifera</i>	2	93	7.5	11	179	4.6	1	12	—	—	—	—
<i>D. rhombifer</i>	—	—	—	—	7	—	—	—	—	2	19	—
* <i>Dendrophidion percarinatus</i>	—	—	—	4	16	—	13	56	2.5	1	82	2.7
* <i>Thalerophis o. occidentalis</i>	—	73	5.9	14	162	4.2	13	124	4.9	1	63	2.1
<i>T. ricotti</i>	—	—	—	—	—	—	1	—	—	—	—	—
* <i>Oxybelis aeneus</i>	1	240	19.4	3	867	22.2	26	274	10.9	—	59	1.9
<i>O. fulgidus</i>	—	2	—	7	26	—	3	13	—	—	—	—
<i>Rhinobotryum beccalli</i>	—	—	—	—	2	—	—	4	—	—	5	—
* <i>Imantodes c. conchona</i>	—	—	—	2	3	—	14	23	—	4	101	3.3
* <i>I. geministratus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Drymarchon corais melanurus</i>	4	31	2.5	17	96	2.5	5	7	—	—	1	—
<i>Pseudots. poecilomotus shropshirei</i>	—	14	1.1	3	12	—	3	15	—	—	15	—
* <i>Spilotes p. pallatus</i>	—	3	—	3	36	—	20	92	3.7	—	38	1.2
* <i>Chironius carinatus</i>	—	1	—	5	94	2.4	17	89	3.6	3	338	11.1
* <i>C. fuscus</i>	—	—	—	1	—	—	1	2	—	—	1	—
<i>Lampropeltis triangulum micropholis</i>	—	1	—	—	5	—	1	3	—	—	—	—
* <i>Leptodeira rhombifera</i>	1	252	20.5	46	240	6.1	51	96	3.8	3	431	14.2
* <i>L. a. annulata</i>	—	—	—	2	6	—	9	22	—	3	78	2.6
* <i>Tantilla ruficeps</i>	—	4	—	5	3	—	6	10	—	—	3	—
* <i>T. albiceps</i>	—	—	—	—	—	—	1	—	—	—	—	—
* <i>Stenorhina d. degenhardti</i>	—	1	—	2	9	—	8	116	4.6	—	68	2.2
ELAPIDAE												
* <i>Micurus miparitus</i>	—	—	—	3	9	—	8	15	—	—	15	—
<i>M. clarki</i>	—	—	—	—	1	—	—	8	—	—	17	—
* <i>M. n. nigrocinctus</i>	1	18	1.5	42	255	6.5	56	174	6.9	6	13	—
<i>M. dunnii</i>	—	2	—	6	5	—	—	—	—	—	—	—
VIPERIDAE												
* <i>Bothrops atrox asper</i>	—	4	—	—	123	3.1	9	141	5.6	9	556	18.3
<i>B. lansbergii</i>	80	130	10.6	5	652	16.7	1	74	2.9	3	39	1.3
<i>B. nasuta</i>	—	—	—	3	—	—	—	5	—	—	—	—
* <i>B. schlegelii</i>	—	—	—	1	6	—	—	5	—	—	—	—
<i>Lachesis muta stenophrys</i>	—	—	—	1	3	—	7	39	2.4	2	24	—

the species make up less than 1/10 of the individuals in the snake populations. These relations of dominance and of rarity are quite independent of the number of species involved.

There may be a very marked shift from place to place in the status of a species. Few maintain the same relative abundance from area to area.

There are a few fairly clear indications of steady shift of relative abundance, upwards or downwards, during the period of study (1933-1946).

A study of the material for possible relationships between relative abundance

and distribution shows that all the endemics are rare, and so are most of the forms at the periphery of their range. The species which range widely through and within the region are, on the whole, the most abundant.

A study of the material for possible relationship between relative abundance and number of species in a systematic group shows that in this region the relative abundance of individuals of Viperids would imply; that of Xenodontines much and Colubrids is much greater than their relative number of species in the fauna less.