Contributions in Biology and Geology

Number 17 May 6, 1978

ON THE SEASONAL INCIDENCE OF TROPICAL SNAKES

Robert W. Henderson
Milwaukee Public Museum

James R. Dixon
Texas A&M University

Pekka Soini
Iquitos, Peru

MILWAUKEE PUBLIC MUSEUM

Milwaukee Public Museum Press
Published by the Order of the Board of Trustees
Milwaukee Public Museum
Accepted for publication March 9, 1978

REVIEW COMMITTEE FOR THIS CONTRIBUTION:
William S. Brown, Skidmore College
Henry S. Fitch, University of Kansas
Harry W. Greene, University of Pennsylvania
C. J. McCoy, Carnegie Museum of Natural History
Max A. Nickerson, Milwaukee Public Museum

ON THE SEASONAL INCIDENCE OF TROPICAL SNAKES

Robert W. Henderson
Vertebrate Division
Milwaukee Public Museum
Milwaukee, Wisconsin 53233

James R. Dixon
Dept. of Wildlife and Fisheries Science
Texas A&M University
College Station, Texas 77843

Pekka Soini
P.O. Box 621
Iquitos, Peru

Abstract: The seasonal incidence of snakes from several Old and New World tropical localities (with emphasis on the Iquitos, Peru region) is discussed. Variation in rainfall probably causes differences in the monthly incidence of snakes. Incidences of snakes that are arboreal and snakes that prey on anurans are most often positively correlated with rainfall. Peaks of snake activity in times of depressed rainfall but high incidence of prey species may be due to an endogenous circannual rhythm of activity.

* * *

Snakes, although famous denizens of the tropics, have for many years remained mysterious and elusive. Most aspects of their ecology are virtually unknown with the exception of macrohabitat and fortuitous observations on food habits and reproduction. At most localities in the lowland tropics snakes may be among the least conspicuous vertebrates, but they are probably important secondary and tertiary consumers.

Apparent low population densities of most tropical snake species (there are exceptions; see Greene, 1975, and papers cited therein, and Myers, 1974: 221) have made it difficult to study specific aspects of their ecology, although some attempts have been made (Henderson, 1974; Nickerson et al., in press; Oliver, 1947; Scott, 1969; and others). Therefore, when a large collection of snakes from a single locality or from several localities in relative proximity is accumulated it presents an opportunity to examine broader patterns of snake ecology.

Here we will analyze and discuss the seasonal incidence of snakes from the Iquitos region of Peru. This subject has been discussed previously by Duellman (1958) and Oliver (1947) but only for single species. Some comparisons are made with another neotropical site at a higher latitude and also with several Old World tropical sites.

MATERIALS AND METHODS

Between 1965 and 1973 Soini made semi-monthly trips to various localities in the region of Iquitos, Depto. Loreto, Peru, in the Upper Amazon Basin. At each of the localities local hunters made collections for Soini which he gathered on his regular excursions. Dixon made several visits to collaborate with Soini, and Henderson spent 6 weeks in the region visiting major collecting sites. Details of collecting sites, habitat, vegetation and a map of the region were set forth by Dixon and Soini (1975, 1977). A total of 900 snakes was accumulated. The month of capture was known for all, and the exact date of capture was available for most. Each specimen was examined for the presence of prey items in the stomach. Rainfall data for the Iquitos region for the years 1970-1972 were available from the Estacion Meteoroligica de Zungarococha. We have examined seasonal incidence in the entire sample of snakes, and also in subsamples based on habitat (primary forest, edge, etc.), adaptive zone (terrestrial, arboreal, etc.), food class (frog predator, mammal predator, etc.) and on selected taxa.

Seasonal incidence of snakes at a site in northern Belize has been discussed in detail elsewhere (Henderson and Hoevers, 1977), but field data from that study are re-examined here for comparison with the Iquitos data. Meteorological data for the Orange Walk area, Orange Walk District, Belize were provided by the National Meteorological Service of Belize for the years 1967-1975 (see Henderson and Hoevers, 1977, for details). In addition, the seasonal incidence of snakes at Iquitos is also compared with that for localities in Ghana (Leston and Hughes, 1968), and Java (de Haas, 1941).

For convenience, we have analyzed seasonal incidence in terms of amount of rainfall per month. Thus, all data are grouped in 12 monthly categories. The Iquitos data were analyzed only in terms of rainfall since temperature was relatively constant, but mean monthly minimum and maximum temperatures are also used in the Belize analysis. Since there is no time of the year in the Iquitos area when rainfall ceases, we will refer to periods of reduced rainfall as "drier" seasons. At Orange Walk in Belize, there is a pronounced dry season of little precipitation; it will be referred to as the "dry" season.

Spearman's rank correlation procedure, a nonparametric test, was used throughout to detect correlations between seasonal differences in environmental variables and abundance of snakes. To protect against the inflated error rates of multiple comparisons, we have set conservative α values for our tests. Error rates for a given family of comparisons are held at .05. We have assumed that collecting effort was uniform throughout the year.

RESULTS

Seasonal Incidence of Iquitos Region Snakes

Total snakes. — Eighty-six species of snakes were collected from one to 88 times for a total of 900 specimens. Detailed accounts of the species, habitat, reproductive data and stomach contents appear in Dixon and Soini (1977). A graph showing mean monthly rainfall for 1970-1972 appears in Dixon and Soini (1975: Fig. 2). Figure 1 of this paper shows the relationships between rainfall and incidence of snakes. There is no

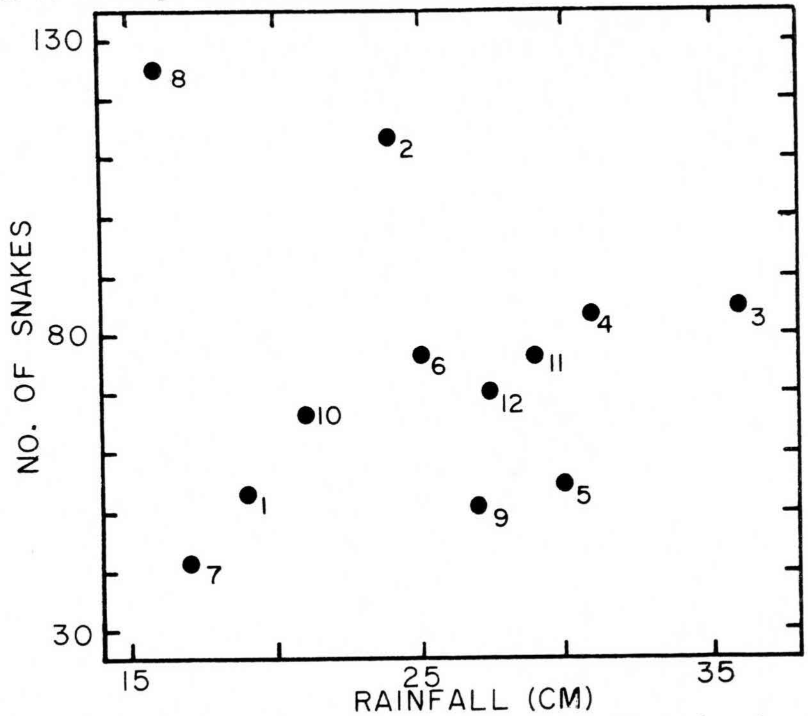

Figure 1. Relationship between rainfall and the incidence of the total number of snakes from the Iquitos region. Numbers beside the points refer to the months of the year.

significant correlation ($P > .05$). There are two peaks of snake activity which, when combined, account for over 25% of the total number of snakes taken. One peak occurs in February at the beginning of the rainy season and the other occurs in August, the drier time of the year. Excluding those two extreme months of activity, the data show a significant positive correlation between rainfall and monthly snake incidence ($P < .025$).

Adaptive Zones. — Our four zones of adaptation are all considered "equal" (i.e., the arboreal zone, for example, is not considered a subzone of the terrestrial zone in the sense of Wake, 1966). Four zones of adaptation were chosen within the horizontal or vertical dimensions of a given habitat.

Thus, snakes were classified as arboreal, terrestrial, subterrestrial or aquatic except for some species or genera, such as *Chironius* and *Pseustes*, which were found about as often on the ground as in an arboreal situation; these were classified as both arboreal and terrestrial. For the twelve-month samples there were no significant correlations between rainfall and incidence of snakes in any of the four adaptive zones, but arboreal snakes had by far the highest correlation coefficient of the four zones. With February and August eliminated, both arboreal (Fig. 2) and terrestrial (Fig. 3) snakes show a significant positive correlation ($P<.0005$ for arboreal and $P<.025$ for terrestrial; .025 set as the critical level for each of

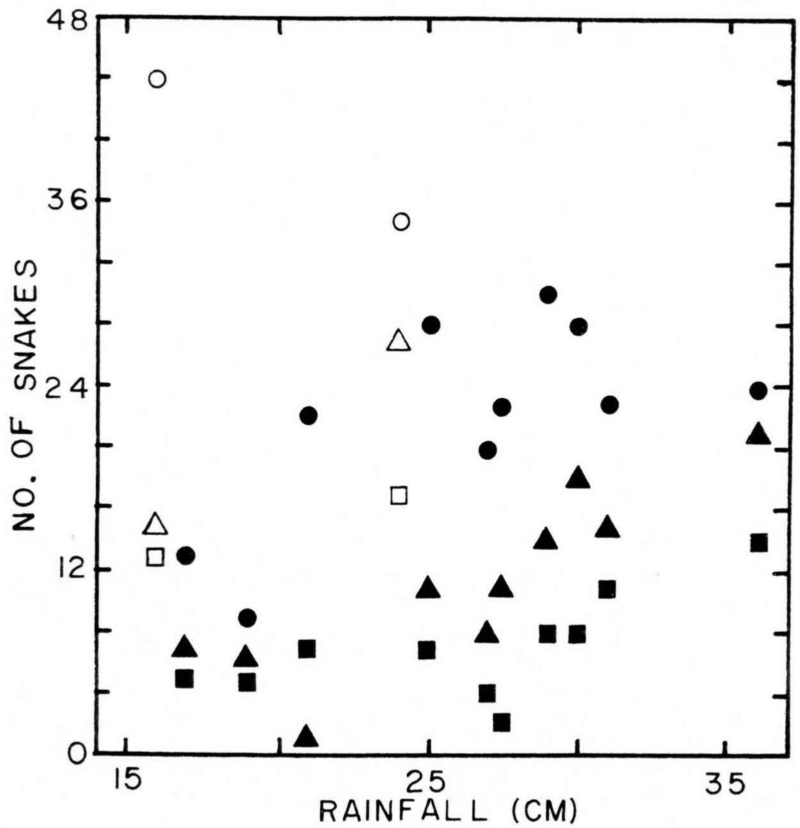

Figure 2. Relationship between rainfall and the incidence of arboreal snakes from three habitats in the Iquitos region of Peru. Dots = primary forest; squares = edge; and triangles = open. Open points = February and August incidence in each of the habitat types.

the two tests, for a combined α of .05). Similar ten-month correlations were not attempted for subterrestrial and aquatic snakes because of small sample sizes.

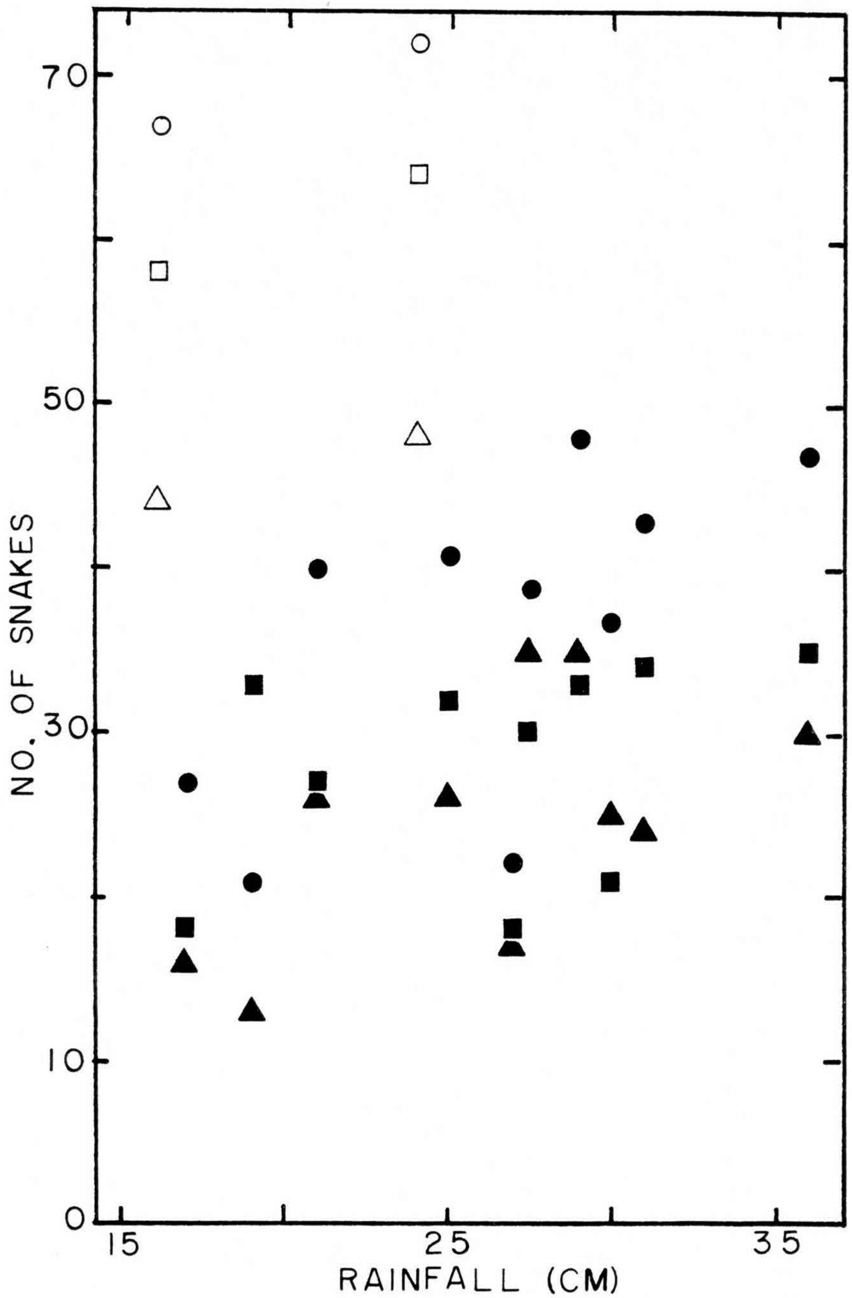

Figure 3. Relationship between rainfall and the incidence of terrestrial snakes from three habitats in the Iquitos region of Peru. Symbols as for Fig. 2.

Habitats. — Snakes of the Iquitos region were found in a variety of habitats, but for convenience we looked for correlations in three major habitat types: primary rainforest, forest edge, and open; "ubiquitous" species, found in all or many habitats, constituted a fourth category. For each habitat we further divided the snakes into their respective adaptive zones in order to determine if certain zones in a given habitat were more sensitive to seasonal conditions than others. There were no significant correlations in any adaptive zones in any habitat (including for ubiquitous species) during the twelve-month span. Arboreal snakes show the highest correlation coefficients in two out of the three habitat types and those arboreal snakes that are ubiquitous had a higher correlation coefficient than either terrestrial or aquatic ubiquitous species. Arboreal and terrestrial species were tested with the February and August samples excluded (critical value = .008 for each of the 6 tests). Arboreal snakes showed significant correlations in edge habitat ($P<.0005$). The other probability values which showed a trend toward significance were as follows: arboreal species in primary forest and open, both $P<.025$, and terrestrial snakes in primary forest and open habitats (both $P<.05$).

Food — Only about 6% of the 900 snakes had identifiable food items in their digestive tracts. There is no correlation between rainfall and the seasonal incidence of stomachs with food, but among specific prey groups, the reptiles (primarily lizards) and amphibians (almost exclusively anurans) show different trends. The seasonal incidence of reptiles in stomachs is approximately parallel to that for all prey groups combined, but there is a positive correlation between rainfall and the number of stomachs containing anurans ($P<.025$).

Selected genera and species. — The following genera and species were examined in terms of seasonal incidence: *Atractus*, *Chironius*, *C. fuscus*, *Helicops*, *Imantodes*, *Leimadophis reginae*, *Leptodeira annulata*, *Leptophis ahaetulla*, *Xenodon*, *Micrurus* and *Bothrops atrox*. Since the critical level with eleven groups is so small (.0045), no species achieved a significant correlation. However, it is worth reporting those tests with low probabilities in that they may be suggestive of trends which are obscured by small sample size and the number of comparisons. *L. reginae* showed a positive correlation ($P<.025$) with rainfall over a 12-month period and the *B. atrox* showed a negative correlation ($P<.05$) with rainfall over a 12-month period. Other genera or species showed no such correlations, but for the 10-month period (excluding February and August), *Chironius*, *Leptodeira annulata* and *Leptophis ahaetulla* all showed positive correlations (at $P<.025$, $P<.05$ and $P<.05$, respectively). *Bothrops atrox* did not show a similar level of correlation for the 10-month span. No other genera or species showed strong trends toward correlation although *Helicops* showed some trend toward negative significance for 12 months (it was not tested for 10 months).

Previously published data. — Duellman (1958), Fitch (1970) and

Oliver (1947) all used specimens in the American Museum of Natural History's Bassler Iquitos snake collection to discuss reproductive cycles and/or seasonal abundance. Oliver (1947) presented rainfall data from two sources for the Iquitos area. One set of data was collected by Bassler during 1927-1929 and the other set came from Knoch (1930). In a footnote, Oliver (1947:2) wrote that "Bassler made careful rain gauge observations for an extended period. He informs me (in litt.) that the rainfall data of Knoch are not typical for the locality." Except for a sharp decline in rainfall in April, the Knoch rainfall data agree more closely with our rainfall data from 1970-1972 than do Bassler's data, and Oliver found that the relationship between rainfall and number of snakes collected/month was less apparent from Bassler's data than from Knoch's. Oliver (1947) and Duellman (1958) examined seasonal incidence in *Leptophis ahaetulla* (Oliver's *Thalerophis richardi)* and *Leptodeira annulata*, respectively. Neither noted any direct correlation between snake activity and rainfall, and, examining it on a 12-month basis, neither could we. However, after exclusion of their two months of peak snake activity (again, one in the wet season [March] and one in the "drier" season [August]) obvious trends appear. The Knoch rainfall data show weak positive correlations at $P<.10$. Fitch (1970) provided data on the seasonal incidence of *Bothrops atrox* (N= 191) in the Iquitos area. He divided his sample into four age/size classes. On a twelve-month basis, neither the total snakes nor any of the age/size classes showed any trends toward correlation with rainfall (Bassler data), but the subadult class showed a trend toward positive correlation ($P<.05$) using the Knoch rainfall data. However, after excluding March and August the remaining snakes of all age/size classes combined show an obvious (but not significant) trend and his subadult (600-999 mm) size class (which was the largest size/age class sample [N = 34 for 10 months]) showed a positive, although not significant correlation ($P<.05$) (Knoch data).

Seasonal Incidence of Snakes at Sites in Belize, Ghana and Java

Belize. — In the area of Orange Walk Town, Orange Walk District in northern Belize, Central America, there was, from 1967 through 1974, a mean annual rainfall of 1270 mm. There is no correlation between rainfall and the incidence of total species of snakes. If, however, the aquatic colubrid *Tretanorhinus nigroluteus* is eliminated, a highly significant positive correlation ($P<.01$) between snake incidence and rainfall occurs (see Fig. 1 in Henderson and Hoevers, 1977).

In different adaptive zones, the following significant correlations were found with rainfall: arboreal species, positive correlation ($P<.05$); terrestrial species, positive correlation ($P<.025$); acquatic species, negative correlation ($P<.025$). A $P<.0125$ would have been required for significance, but the trends are as expected. Subterrestrial and leaf litter species showed no significant correlations.

The following frog predators showed trends toward positive correlations of incidence with rainfall: *Leptodeira frenata* and *L. septentrionalis* combined (P<.025); and *Leptophis mexicanus* (P<.05). There was no correlation between rainfall and incidence of *Drymobius margaritiferus*. Total frog predators combined showed a significant positive correlation (P<.005). There was no correlation between rainfall and occurence of mammal predators.

No significant correlations resulted from comparisons of the seasonal incidence of total snakes, total snakes less the aquatic *Tretanorhinus nigroluteus*, or any adaptive zone, with monthly mean minimum and maximum temperatures for 1967-1974.

Ghana. — Leston and Hughes (1968) examined size, composition, origin and natural history of the snake fauna at Tafo, a forest cocoa-farm locality in Ghana, West Africa, where mean annual rainfall is 1651 mm falling on 129 days.

There is no correlation between the total number of snakes and rainfall. There are, however, trends toward positive correlations (.017 required for significance) between rainfall and incidence of arboreal snakes (P<.05) and of terrestrial snakes occurring in "shaded" habitat (P<.05), but not for terrestrial snakes in open, "unshaded" habitat. Those snakes that include amphibians in their diet showed no correlation, nor did those that feed exclusively on amphibians, nor those that are reptile predators. However, those that are mammal predators showed a trend toward positive correlation (P<.025; .0125 required for significance), but of the 42 individuals of 7 species that are mammal-eaters, 40.4% were either *Boiga pulverulenta* or *Dendroaspis viridis*, both of which are arboreal.

Java. — De Haas (1941) reported on a large collection of snakes from two districts of West Java. The mean annual rainfall for Nandjoeng Djaja over a 23-yr period was 3434 mm in 156 days of rain. During the years (1932 and 1933) that De Haas collected the snakes, rainfall was 3242 mm and 3080 mm, respectively, and this is one of the driest localities of West Java. The other site, Bandjarwangi, is one of the wettest areas of West Java with a 26-yr average of 4866 mm of rain. During 1938, when the collection analyzed here was made, rainfall was 4143 mm. At Nandjoeng Djaja, where collections of 111 and 250 snakes were collected in 1932 and 1933 respectively, there was no correlation with rainfall. At Bandjarwangi, there was a significant negative correlation (P<.05) between rainfall and the 2444 snakes collected. This may suggest that, in terms of rainfall, "the more the better" is not necessarily true. No attempt was made to find correlations in different adaptive zones, with different prey groups, etc., or to eliminate months of minimum and maximum activity as we did for the Iquitos analysis.

Kopstein (1938), in an analysis of a large collection of snakes from Central Java, found that the appearance of hatchling snakes occurs in the rainy season, coinciding with the time of year when anuran prey is most abundant. Henderson and Hoevers (1977) suggested the same possibility for the Orange Walk area of Belize.

DISCUSSION

Three factors are involved in the changing seasonal incidence of tropical snakes: 1) Seasonal change in the activity of the humans who are doing the sampling; 2) Seasonal change in the actual number of snakes; and 3) Seasonal change in the activity of the snakes.

Factor 1 can be readily dismissed. Although native farmers are usually more active in their fields during periods of low rainfall (January, July, August), proportionately higher numbers of snakes were not collected during all three months. August shows the highest peak of snake incidence, but July has the lowest incidence and January also has one of the lowest monthly totals.

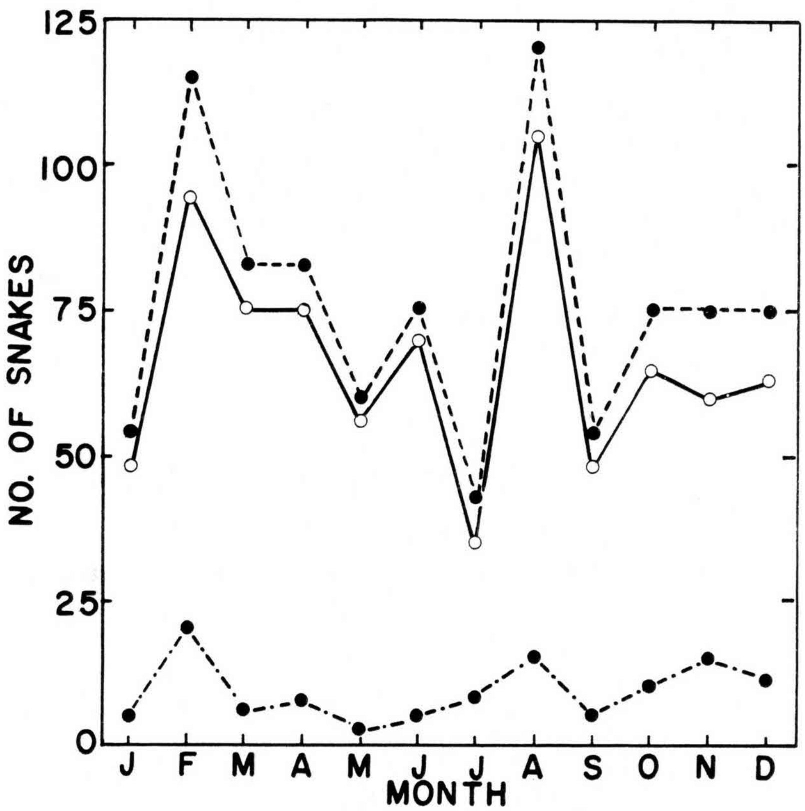

Figure 4. The monthly incidence of all snakes (solid circles, dashed line), of newborn snakes (solid circles, dash-dot line), and of all snakes less newborn snakes (open circles, solid line) from the Iquitos region, Peru.

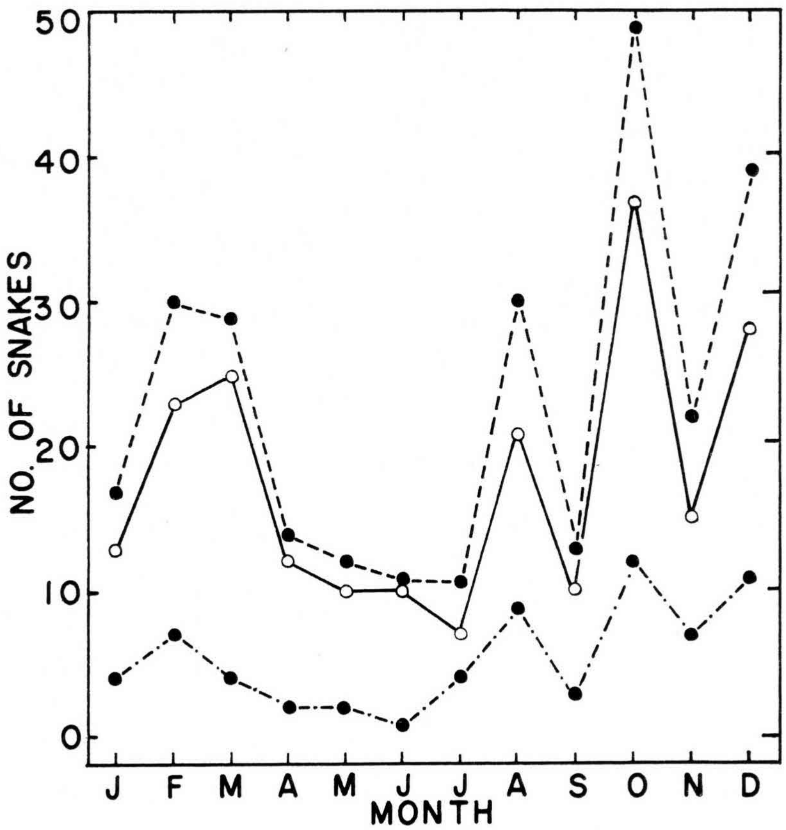

Figure 5. The monthly incidence of the total number of *Bothrops atrox* (solid circles, dashed line), newborn *Bothrops atrox* (solid circles, dash-dot line), and total number less newborn (open circles, solid line) of *Bothrops atrox* from the region of Iquitos, Peru.

Factor 2 would be accomplished by the addition of new individuals to the population from births. If times of highest seasonal incidence were correlated with births and hatchings this might explain why peaks occur when they do. Figure 4 illustrates the monthly contribution newborn snakes made to the total numbers of snakes collected each month. There appears to be no disproportionate number of births and hatchlings at a particular time of the year to account for seasonal peaks of the occurrence of snakes. Figure 5 illustrates the monthly contribution of births to the seasonal incidence of one species, *Bothrops atrox.* We have combined our data with that of Fitch (1970: Table 9) for a total of 279 specimens. As in Fig. 4, the incidence of newborn snakes closely follows the incidence of total snakes less newborn snakes and there is no disproportionate increase in any one month (except July which has a depression in overall activity). We therefore feel that unevenness in seasonal incidence is not caused by births and hatchings. There is no correlation between rainfall and seasonal incidence of hatchling snakes, all species combined. The remainder of our discussion will be addressed to Factor 3.

The temperature at Iquitos is relatively constant throughout the year and probably does not alter snake activity, and Allee (1926a) and Evans (1939) have shown that humidity shows little annual variation in the rainforest habitat. Wind can have a desiccating effect, but it too is probably of little significance in the rainforest (Richards, 1966). The most conspicuous, readily-measured variable, then, is precipitation.

The seasonal incidence of tropical snakes appears to be related to rainfall. Correlations supporting this observation were found for each of four localities we examined. However, the habitat and zone of adaptation occupied by a particular species affects the degree of importance rainfall may have. At Iquitos, Orange Walk and Tafo, arboreal snakes invariably showed significant correlations or trends toward correlation with rainfall including, at Iquitos, in three habitat types. Activity of terrestrial snakes is also correlated with rainfall at Iquitos and Orange Walk whereas aquatic, leaf litter and subterrestrial species are apparently more independent of rainfall. At Orange Walk, where there was a negative correlation between rain and incidence of aquatic snakes, this is probably just an artifact of sampling ability (Henderson and Hoevers, 1977:351).

More arboreal snakes are found in primary rainforest than in any other habitat in the Iquitos region (Dixon and Soini, 1977), and it has been demonstrated that humid forest snake species are more sensitive to dehydration than non-humid forest species (Gans et al., 1968). Furthermore, the arboreal adaptive zone is probably a less stable environment (i.e., it is subject to more measureable fluxes in environmental variables) than is the terrestrial zone (Allee, 1926a; Hardy, in press) and both are probably more unstable than aquatic and subterrestrial adaptive zones. Also, most arboreal snakes are anuran predators and anuran activity may be closely linked with rainfall. Scott (1969) found that in Middle American snake faunas, arboreal species decrease and terrestrial species increase as aridity increases and that subterrestrial species remain fairly constant (although the highest percentages of occurrence occur at the arid end of the range). In an analysis of the Costa Rican snake fauna he determined that wet forest species are most easily exterminated by man and that "many arboreal snakes, especially nocturnal forms, are not tolerant of drastic changes in the natural vegetation" and he included in this category such genera as *Corallus*, *Chironius*, *Leptophis*, *Oxybelis* and *Bothrops*.

Of those species found 15 or more times at Iquitos, 91.3% were recorded during 8 or more months. Of those found 20 or more times, 90.9% were recorded in 8 or more months, 63.6% in 9 or more months and 36.4% in 10 or more months. Thus, many species were encountered throughout most of the year, and there is no correlation between rainfall and the number of species unrecorded each month. There is a marked dry season in Belize and for the six species collected 12 or more times, there is a significant inverse correlation (P<.025) between rainfall and months in which the snakes were not collected. That is, all six species were collected each month during the wet season (July-November), but during the dry season (December-June) anywhere from one to all six species were not collected in a given month.

In the Iquitos region, anuran and saurian prey are generally active throughout the year, but seasonal fluctuations can possibly account for the activity peaks in the wet season and drier season. Although anurans are active throughout the year, their breeding activity is correlated positively with rainfall. Crump (1974) has shown that in the Upper Amazon Basin of Ecuador many frogs, especially hylids, are opportunistic breeders (i.e., they breed regularly following heavy rains) while others "breed after heavy rains, but sporadically rather than regularly." We have shown that there is a correlation between rainfall and the incidence of snakes with anurans in their stomachs. Furthermore, in those species of known prey preferences there are significant trends during February (wet season peak) and August (drier season peak). Of the 99 individuals collected in February, 40.4% were frog predators and 3.0% were lizard predators. In August, of the 98 snakes taken, 26.5% prey primarily on anurans while 14.3% feed on lizards. Of 66 frog predators collected in those two months 44.4% were from February and 28.9% in August, whereas of the 17 lizard predators 17.6% were taken in February and 82.4% in August. Also, there is a significant negative correlation (P<.05) between rainfall and appearance of hatchling lizards (all species; Dixon and Soini, 1975). There are more species of hatchling lizards available for food from June through November than from February to May. The low number of hatchling lizards corresponds to the rise of the Amazon and its tributaries and their overflowing onto the floodplain. This flooding may provide breeding sites for frog species with opportunistic and sporadic breeding strategies.

Evidently most or all snakes are active throughout the year in the Iquitos region, but rainfall influences seasonal activity either directly or indirectly. At Orange Walk there seems to be a definite hiatus in snake activity during the dry season directly or indirectly related to rainfall, or both. Anuran prey is greatly decreased at Orange Walk during the dry season (Henderson and Hoevers, 1977), perhaps having retreated to safe refuges to avoid desiccation or perhaps having been greatly reduced by predator pressure. After anuran populations decrease or disappear in the beginning of the dry season, snakes probably still forage for prey. However, continued activity under desiccating conditions would force the snakes to secrete themselves in microhabitat protected from the unfavorable environment of the dry season (Gans et al., 1968, have shown that active snakes dehydrate faster than inactive snakes). Onset of the rains brings conditions physiologically favorable for activity of both snakes and anurans. An example of such dry season inactivity is provided by records of *Imantodes*. Henderson and Nickerson (1976) have discussed their proclivity for bromeliads. Those collected from bromeliads were all taken in the dry season in every instance in which the author mentioned the time of year (Allee, 1926b; Smith 1941 and 1943). Also, Nickerson et al. (in press), using radio telemetry, have demonstrated that rainfall can affect the activity of tropical snakes. A heavy rainfall in the area of Belize City, Belize apparently caused a large *Spilotes* to descend to the ground and seek cover, and cool temperatures and almost constant rainfall seemingly caused a *Leptophis depressirostris* in Costa Rica to seek shelter. Apparently rain falling on a snake may cause it to become mobile and possibly seek shelter, but not to become inactive.

Oliver (1947) and Duellman (1958) both considered the incidence of rainfall-dependent prey (anurans) to be a possible indirect cause of the seasonal incidence of *Leptophis ahaetulla* and *Leptodeira annulata*, respectively, in the Iquitos area. The wet season maxima of snake numbers at Orange Walk and Iquitos are, probably, based upon reactions of the snakes to the immediate stimulus of rainfall. Rainfall itself may cause snakes to seek cover (Nickerson et al., in press), but activity probably resumes and peaks immediately following a rainfall. Stamps (1976) demonstrated in the field that during periods of drought, lizards *(Anolis aeneus)* that are sprinkled to provide them with abrupt artificial "rainfall" increase display frequency and aggression to non-drought levels and Smith (1941) suggested that, in parts of Mexico, dry season rains cause bromeliad-dwelling snakes to abandon their epiphytic retreats. At Iquitos during the drier season, as in the wet season, snakes are probably also cued by rainfall, but the cue comes less frequently and therefore activity is depressed.

In contrast, the drier season peak in the incidence of snakes at Iquitos (there is none at Orange Walk) may be due to an endogenous circannual rhythm of activity. Annual cycles are common among vertebrates and are ecologically beneficial in that they enable an animal to exploit abundance and avoid exposure and waste of energy in times of scarcity (Meier, 1975). A circannual rhythm would allow snakes to exploit a resource (i.e., hatchling lizards) that is not uniformly abundant throughout the year. Although field and laboratory work are necessary to determine the accuracy of this hypothesis, it is interesting to note that, over 30 years ago, Oliver (1947) suggested that "An inherent physiological cycle of activity [in *Leptophis ahaetulla* at Iquitos] conceivably might be a factor related in the seasonal incidence."

ACKNOWLEDGMENTS

Henderson thanks Mr. James H. Kuehn and Friends of the Museum (MPM) for sponsoring the Milwaukee Public Museum's expedition to Peru, and Max A. Nickerson for a number of favors. Dixon and Soini are grateful to Srs. Francisco Pizarro, Waldemar Vargas, and Heraclito Flores, who not only helped them obtain specimens but also allowed them to stay in their homes during trips to their respective villages.

Diane E. Stevenson provided statistical consultation. W.S. Brown, H.W. Greene, H.S. Fitch, C.J. McCoy and M.A. Nickerson criticized an earlier draft of this work and offered many helpful suggestions; they do not necessarily agree with our ideas, however.

Ann S. McKinstry of Belize's National Meterological Service provided rainfall and temperature data from the Orange Walk Town area.

LITERATURE CITED

Allee, W.C. 1926a. Measurement of environmental factors in the tropical rain-forest of Panama. Ecology 7:273-302.

Allee, W.C. 1926b. Distribution of animals in a tropical rain-forest with relation to environmental factors. Ecology 7:445-468.

Crump, M.L. 1974. Reproductive strategies in a tropical anuran community. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 61:1-68.

deHaas, C.P.J. 1941. Some notes on the biology of snakes and their distribution in two districts of West Java. Treubia 18:327-375.

Dixon, J.R. and P. Soini. 1975. The reptiles of the Upper Amazon Basin, Iquitos Region, Peru I. Lizards and Amphisbaenians. Milwaukee Public Mus. Contr. Biol. Geol. 4:1-58.

Dixon, J.R. and P. Soini. 1977. The reptiles of the Upper Amazon Basin, Iquitos Region, Peru II. Crocodilians, turtles and snakes. Milwaukee Public Mus. Contr. Biol. and Geol. 12:1-91.

Duellman, W.E. 1958. A monographic study of the colubrid snake genus *Leptodeira*. Bull. Amer. Mus. Nat. Hist. 114:1-152.

Evans, G.E. 1939. Ecological studies on the rain forest of southern Nigeria. II. The atmospheric environmental conditions. J. Ecol. 27:436-482.

Fitch, H.S. 1970. Reproductive cycles in lizards and snakes. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 52:1-247.

Gans, C., T. Krakauer and C.V. Paganelli. 1968. Water loss in snakes: interspecific and intraspecific variability. Comp. Biochem. Physiol. 27:747-761.

Greene, H.W. 1975. Ecological observations on the red coffee snake, *Ninia sebae*, in southern Veracruz, Mexico. American Midl. Natur. 93(2):478-484.

Hardy, L.M. Environmental factors and microhabitats in rain forest of Tabasco, Mexico. Southwest. Natur. *In press.*

Henderson, R.W. 1974. Aspects of the ecology of the neotropical vine snake, *Oxybelis aeneus* (Wagler). Herpetologica 30:19-24.

Henderson, R.W. and L.G. Hoevers. 1977. The seasonal incidence of snakes at a locality in northern Belize. Copeia 1977:349-355.

Henderson, R.W. and M.A. Nickerson. 1976. Observations on the behavioral ecology of three species of *Imantodes* (Serpentes: Colubridae). J. Herpetol. 10:205-210.

Knoch, K. 1930. Klimakunde von Sudamerika. *In* Koppen, W. and R. Geiger, Handbuch der Klimatologie. Vol. 2. Berlin.

Kopstein, F. 1938. Beitrag zur Eierkunde und zur Fortpflanzung der Malaiischen Reptilien. Bull. Raffles Mus. No. 14:81-167.

Leston, D. and B. Hughes. 1968. The snakes of Tafo, a forest cocoa-farm locality in Ghana. Bull. de l'I.F.A.N. ser. A, 30:737-770.

Meier, A.H. 1975. Chrondoendocrinology of vertebrates. Pp. 469-549 *in* B.E. Eleftheriou and R.L. Sprott, eds. Hormonal correlates of behavior. Vol. 2, An organismic view. Plenum Press, New York.

Myers, C.W. 1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. Bull. Amer. Mus. Nat. Hist. 153(1):1-262.

Nickerson, M.A., R.A. Sajdak, R.W. Henderson and S. Ketcham. Notes on the movements of some neotropical snakes. J. Herpetol., *in press.*

Oliver, J.A. 1947. The seasonal incidence of snakes. Amer. Mus. Novitates (1363): 1-14.

Richards, P.W. 1966. The tropical rain forest. Cambridge Univ. Press.

Scott, N.J. 1969. A zoogeographic analysis of the snakes of Costa Rica. Ph.D. dissertation, Univ. So. California.

Smith, H.M. 1941. Snakes, frogs and bromelias. Chicago Natur. 4:35-43.

Smith, H.M. 1943. Summary of the collections of snakes and crocodilians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. Proc. U.S. Natl. Mus. 93:393-504.

Stamps, J.A. 1976. Rainfall, activity and social behavior in the lizards, *Anolis aeneus.* Anim. Behav. 24:603-608.

Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Mem. So. California Acad. Sci. 4:1-111.