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Resource Partitioning in Amazonian Snake Communities

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Abstract: Resource partitioning among snakes at three localities in the Peruvian Amazon near Iquitos is qualitatively analyzed and discussed. Con- and heterogenerics occurring in primary rainforest which are active at the same time (i.e., diurnal or nocturnal) can usually be segregated on the basis of size, adaptive zone or food preference. Snakes tend to be highly stenophagous and species that feed on potentially high-density prey groups (anurans, lizards) are more abundant than those that feed on low-density prey groups (mammals). Numerous cases of complementarity are evident. Among congenics, when four or more species occur together, none are very common or one or two species predominate in abundance.

* * *

The study of neotropical rainforest snake ecology is in its infancy and most likely it will never reach maturity. Although more and more herpetologists are working in the tropics, rainforest snakes tend to be found at lower densities than temperate species, rainforests are rapidly being destroyed, and large collections of snakes from one locality that can be utilized to gather natural history data are rare. For these reasons, a brief analysis of resource partitioning in Amazonian snake communities is not premature. The collections made by Soini between 1965 and 1973 total 900 specimens. It is one of the largest collections to come from the area.

Resource partitioning among snakes that are not congeneric has received little attention for temperate species (Fitch, 1949; Henderson, 1974; Shine, 1977; and, most notably, Brown and Parker, *in press*), and even less for tropical snakes (but see Duellman, 1963, 1978; Leston and Hughes, 1968; Henderson and Hoivers, 1977).

The purpose of this paper is to examine the species composition of three

snake faunas, all in proximity to one another, and to discuss briefly resource partitioning among syntopic con- and heterogenerics in a diverse snake fauna. Our treatment is largely qualitative.

Methods

Our analysis of resource partitioning is based on collections from the Iquitos region, Loreto, Peru. Collecting methods, a complete list of species and localities, the geographical relationship of the study areas, photographs, climatic and physiographic data, and discussion of ecology and faunal similarities appear elsewhere (Dixon and Soini 1975, 1977; Henderson *et al.*, 1978).

Snakes were classified by habitat type, prey preference, size (length-over-all [LOA]), usual time of activity, and adaptive zone (see Henderson *et al.*, 1978, for definition). If a particular species was found in more than one kind of habitat or in more than one adaptive zone, it was scored equally for each habitat and/or zone in which it occurred. Our analysis concentrates on three localities in the Iquitos area. They are Centro Union, Mishana and Moropon.

Unless otherwise stated, whenever we discuss the relative abundance or density of a snake species or group of species, we are doing so only in terms of our sample. It is possible that our samples are biased in favor of bolder (i.e., less likely to retreat at the approach of humans), and more conspicuous species (such as *Bothrops atrox*), while canopy and subterrestrial species may be under-represented.

Results and Discussion

Only species collected five or more times at a site are considered in analysis of resource partitioning. Table 1 summarizes resource partitioning at each of the three localities. The Moropon site is represented by more species (21) and specimens (217) than the other two, and we have therefore singled it out for more extensive discussion. The Moropon site is the most diverse in microhabitat and elevation/slope differences. The ridges and hills between stream courses are higher, steeper, and have less leaf litter in some microhabitats due to the steepness of slope and physiognomy of tree growth associated with slope and soil type. Soil moisture, and the depth, width and flow of streams at the Moropon site are all affected by slope. All of these factors may influence the composition and abundance of prey items during all or some parts of the year. Our per-species sample sizes prohibit quantification of niche breadth and overlap, but it is one of the most diverse snake communities ever studied.

Seventeen of the 21 (81.0%) species occur in primary forest at least occasionally. Only one species (5.9%) appears to be restricted to it, and eight species (47.1%) are restricted to primary and secondary forest. Of those species occurring in primary forest, nine (52.9%) are arboreal about 50% of the time. About 60% of the arboreal snakes are diurnal and 40% are nocturnal. All diurnal species feed on frogs, lizards, or birds, but primarily frogs. The nocturnal species feed on mollusks, frogs, lizards, or small mammals.

Table 1. — Utilization of time and resources by 31 species of snakes from the Iquitos, Peru region. Under "N," the first figure refers to the number of specimens taken at Centro Union, the second at Mishana and the third at Moropon; an X signifies that fewer than five specimens, or none at all, of that species were taken at that locality. Under "Habitat," C = cultivated, E = edge, F = fruit grove or orchard, O = open, P = primary rain forest, S = secondary rain forest, Sg = second growth, and U = ubiquitous. Under "Adaptive Zone," A = arboreal, Aq = aquatic, T = terrestrial, and St = subterrestrial. Under "Prey," B = birds, Fi = fish, F = frogs, I = invertebrates, L = lizards, M = mammals, Mo = mollusks, S = snakes, and Sa = salamanders. Under "When Active," D = diurnal and N = nocturnal. Under "LOA" (= Length Over All), the maximum known length of the species from the Iquitos region is listed in mm, regardless of sex.

Species	N	Habitat	Adaptive Zone	Prey	When Active	LOA
<i>Corallus enydris</i>	6,X,6	PS	A	BM	N	1700
<i>Atractus badius</i>	X,14,X	O	T	I?	D	413
<i>A. elaps</i>	X,X,7	OPS	T	I?	D	588
<i>A. latifrons</i>	X,10,X	O	T	I?	D	586
<i>A. species A</i>	X,14,X	OS	T	I?	D	425
<i>Chironius eroletus</i>	5,5,9	U	AT	FSaL	D	1360
<i>C. fuscus</i>	7,21,15	U	AT	FSaL	D	1385
<i>C. multiventris</i>	X,X,5	PS	AT	F	D	2270
<i>Dipsas catesbyi</i>	X,X,12	PS	A	Mo	N	693
<i>Drymoluber dichrous</i>	X,X,15	PS	T	FL	D	1300
<i>Helicops angulatus</i>	6,X,5	U	Aq	FiFL	N	731
<i>Imantodes cenchoa</i>	X,X,13	FPS	A	FL	N	1138
<i>I. lentiferus</i>	X,X,5	P	A	FL	N	1044
<i>Leimadophis reginae</i>	17,X,11	O	T	FiF	D	603
<i>Leptodeira annulata</i>	17,X,X	U	AT	F	N	780
<i>Leptophis ahaetulla</i>	X,7,10	U-P	A	F	D	1215
<i>Oxybelis argenteus</i>	X,X,16	PS	A	L	D	1213
<i>O. fulgidus</i>	X,5,X	E	A	BL	D	1620
<i>Oxyrhopus petola</i>	X,X,6	PS	T	L	N	991
<i>O. trigeminus</i>	X,5,6	ESg	T	M	N	1112
<i>Pseustes poecilonotus</i>	X,6,9	EP	AT	BM	D	1632
<i>Rhadinaea brevirostris</i>	5,X,11	U	T	L	D	370
<i>R. occipitalis</i>	6,X,X	PS	T	?	D	532
<i>Tantilla melanocephala</i>	7,X,X	CS	StT	?	?	345
<i>Xenodon rabdocephalus</i>	7,12,8	PS	T	F	N	875
<i>X. severus</i>	X,X,8	OS	T	F	N	995
<i>Micrurus langsdorffi</i>	X,9,9	U	StT	S	DN	761
<i>M. putumayensis</i>	8,X,X	PS	StT	S	DN	805
<i>M. spiri</i>	8,10,X	P	StT	LS	DN	1315
<i>Bothrops atrox</i>	18,25,31	U	T	FILM	N	1388
<i>B. bilineatus</i>	6,5,X	PS	A	BFM	N	737

All species of *Atractus* (Moropon, 7 species; Centro Union, 4 species), are relatively uncommon, but at Mishana, three of five species are fairly common (10 or more individuals/species). Nothing is known of food habits in *Atractus* at Iquitos, but Duellman (1978) found that *Atractus* at an Amazonian Ecuador locality fed on earthworms. We get the impression that when syntopic species are not segregated by habitat, they are segregated by size. When species of similar size are found in the same habitat (e.g., *A. elaps* and *A. latifrons* at Moropon) one is always more abundant than the other. At Mishana, where three species are common, *badius* (max. LOA = 413 mm) and *latifrons* (max. LOA = 586 mm) are found in open habitat, but *latifrons* is considerably larger. *Atractus* sp. A is about midway between the sizes of the other two and is found in different habitat.

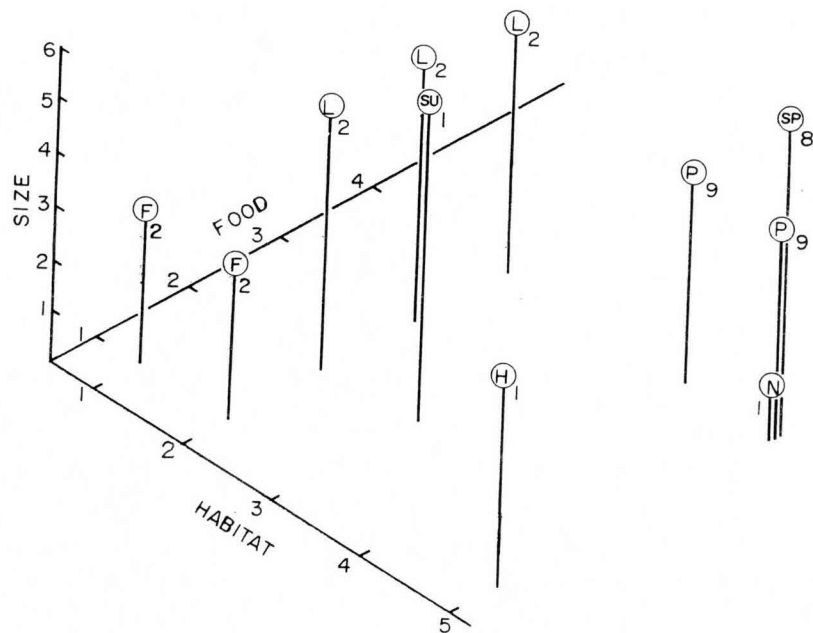


Figure 1. — Graphic representation of resource use by seven species of *Micrurus* which occur at Centro Union. The species are designated by an initial enclosed in a circle: F = *M. filiformis*, H = *M. hemprichi*, L = *M. lemniscatus*, N = *M. narducci*, P = *M. putumayensis*, SP = *M. spixi*, and SU = *M. surinamensis*. For "Habitat," 1 = edificarian, 2 = open, 3 = riparian, 4 = secondary forest, 5 = primary forest; along the "Food" axis, 1 = invertebrates, 2 = fish, 3 = amphibians, 4 = reptiles; for the vertical axis, size (LOA), 1 = < 25 cm, 2 = 25-50 cm, 3 = 50-75 cm, 4 = 75-100 cm, 5 = 100-125 cm and 6 = > 125 cm. The numbers alongside the species designations refer to total sample size/species, e.g., only two *M. lemniscatus* were taken at this site.

Chironius at Centro Union is represented by four species, none of which is very common. At Moropon, *exoletus* and *fuscus* are common, do not exhibit prey and habitat differences, and *fuscus* is more abundant than *exoletus*. At Mishana, only *fuscus* is common, represented by from 4.5 to 18 times more individuals than any other species of *Chironius*.

Micrurus is represented by seven species at Centro Union, and their ecological relationships are illustrated in Fig. 1. Where there is prey and habitat overlap, size segregates species. The same is true at Mishana and Moropon. The only two *Micrurus* species that we have nowhere found in sympatry are *M. langsdorffi* and *M. putumayensis*. They are morphologically and ecologically closer to one another than any of the other species. Both are small, unspecialized, with same shape and scale counts, and they can be differentiated only by the color patterns. They represent a case of non-compatibility of two closely related species with overlapping ecological niches, resulting in a mosaic pattern of distribution of the two species in the area.

At Centro Union there are five species of *Bothrops*, none of which are very common, including *B. atrox*. All can be segregated by prey, habitat, size or adaptive zone. At Mishana, only *B. atrox* and *B. bilineatus* occur; they are well segregated on the basis of size and adaptive zone. Three species of *Bothrops* occur at Moropon, but *B. atrox* comprises 94.1% of the number of specimens of *Bothrops* collected there.

Most species of snakes are stenophagous, feeding primarily on one class of prey (e.g., fish, anurans, small mammals). Using data collected by Leston and Hughes (1968) at a forest cocoa farm locality in Ghana, West Africa, we found that of 31 species of snakes, 23 of them (74.2%) fed only on one class of prey, 7 (20.6%) fed on two classes and one species (3.2%) fed on four classes. Likewise, using data presented by Duellman (1978) for snakes from a site in the Upper Amazon Basin of Ecuador (Santa Cecilia), of 22 species represented by at least five specimens and for which there were stomach content data, 19 (86.4%) of the species fed on only one prey class. Of those species (N = 9) that had identifiable prey in three or more specimens, 66.7% had taken prey from only one class. At Moropon, of the 25 species for which food preference is known, 14 species (56%) prey on one food class, 9 species (36%) take prey from two classes, and two species (8%) prey on three classes. Nineteen of the species (76%) prey on frogs and/or lizards; 45.5% of all frog predators also take lizards and 62.5% of eight lizard predators also take frogs. Frogs and lizards are much more conspicuous than small mammals in tropical forest. Few studies are available on population densities, but Fleming (1971), in population studies of three species of rodents in the Panama Canal Zone, found maximum density for any of the species to be about 10/ha. In contrast, Sexton (1967) found the small iguanid lizard *Anolis limifrons* in the Canal Zone at a density of 1160/ha.

Figure 2 illustrates the relationship between prey group exploited and

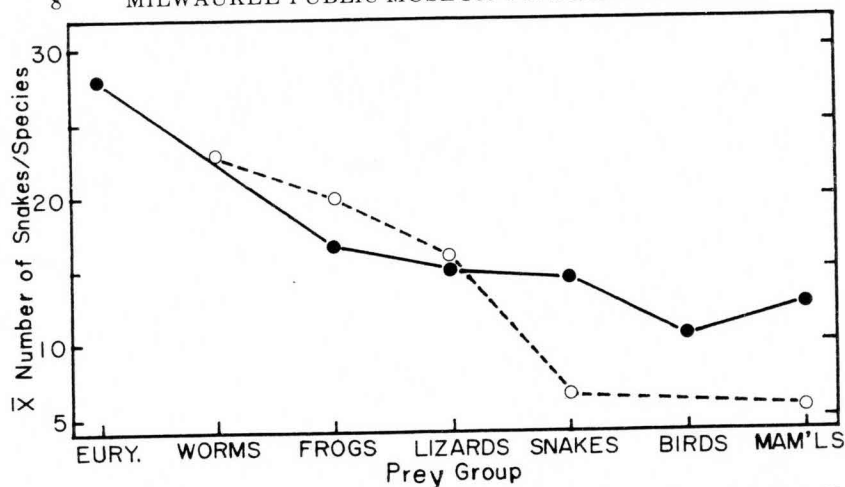


Figure 2. — Relationship between predator abundance and type of prey taken at all three Iquitos region localities combined (closed circles, solid line) and from Duellman's (1978) (open circles, dashed line) stomach content analysis of snakes from an Amazonian Ecuador site. Those species classified as euryphagous were not counted in any other predator/prey category.

relative density of the snakes that exploit that group. One of the two species classified as a euryphagic predator (i.e., exploits more than two vertebrate classes as prey items) is *Bothrops atrox* and it is the most abundant species in the collection. Otherwise, there is a general decline in numbers of individual snakes taken for phylogenetically "higher" prey groups (frog predators in higher density than lizard predators, lizard predators higher density than snake predators, etc.)

Snakes may exhibit even more refined specialization. For example, stomach contents data show that *Chironius exoletus* fed only on two genera of hylid frogs ($N = 4/4$ = four snakes had food in their stomachs, and all four had hylid frogs). (Similarly, in Amazonian Ecuador, *C. exoletus* fed only on hylids [Duellman, 1978].) *Leptodeira annulata* preyed upon frogs ($N = 6/6$) from three families and *Xenodon rabdocephalus* and *X. severus* fed only on bufonids ($N = 7/4$) and leptodactylids ($N = 7/3$). (In Amazonian Ecuador, *X. severus* fed on bufonids and leptodactylids [Duellman, 1978].) *Micrurus lemniscatus* fed on an eel ($N = 3/1$), a caecilian ($N = 3/1$) and a typhlopoid snake ($N = 3/1$). The three classes of prey, though taxonomically diverse, all are limbless with a similar body shape. In a study of stomach contents of species of *Leptophis*, Oliver (1948) found that of 106 food items, 88.7% were frogs of which 83.0% were hylids. Of 61 food items taken from *Leptophis ahaetulla*, a species known from the Iquitos region, 58 (95.1%) were hylid frogs. In a similar analysis of the stomach contents of species of *Leptodeira*, Duellman (1958) found that of 77 food items from seven species, 85.7% were frogs, and *Leptodeira annulata*, a relatively common Iquitos region species, fed exclusively on frogs. This extreme

stenophagy, which frequently reflects a predator's adaptive zone, undoubtedly alleviates competition among syntopic snake species.

Our analysis of resource partitioning is cursory at best. Although we are dealing with a large number of snakes, no one species with the possible exception of *Bothrops atrox* can be classified as abundant. Per-species sample sizes and amount of quantifiable data preclude any quantified assessment of resource segregation among the Moropon snakes (such as was undertaken by Brown and Parker, *in press*, for some Utah desert snakes). Nevertheless, our superficial examination gives some indication as to how 21 species of snakes can coexist at the same locality in the same macrohabitat.

Among those snakes collected five or more times from one site, there is always some potentially segregating factor. Among heterogenerics and congenerics there are many cases of complementarity (Schoener, 1974). A number of possible combinations of dimensions are involved in complementarity. Combinations and examples include: adaptive zone and food type—*Imantodes* and *Dipsas* are both nocturnal and arboreal, but *Imantodes* feeds on frogs and lizards whereas *Dipsas* feeds on mollusks; food type and time—*Leptophis* and *Leptodeira* are arboreal anuran predators but *Leptophis* is essentially diurnal and *Leptodeira* is nocturnal, etc.

Congenerics are most often segregated by habitat, size and food preference. Usually when there are four or more species occurring together, none is very common, or one or two species predominate in abundance. The seven species of *Micrurus* at Centro Union are apparently segregated by food, habitat and/or size. Additional data on food preference for *M. narducci*, including two specimens from Iquitos, are available in Greene (1973). Both snakes contained the tails of unidentified microteiid lizards. Beebe (1946) found lizard and snake remains in specimens of *M. hemprichi* from Kartabo, Guyana. Thus, it is possible that at Centro Union, four species of *Micrurus* share primary rainforest habitat and all are reptile predators (although *M. narducci* may feed on lizards but not snakes). If *M. hemprichi* were included in the primary forest habitat-reptile predator niche, its LOA would fall between those of *M. narducci* and *M. putumayensis*. This lends credence to Greene's (1973) suggestion that, among sympatric (or syntopic) coral snakes, "Size differences could reduce niche overlap and permit coexistence, because bigger coral snakes can eat larger prey than smaller ones."

Nevertheless, where four or more congenerics coexist, and where one or two species predominate, competitive interactions may be responsible for lower densities of the other congeners.

Conclusions

We are aware of the shortcomings of this work. Especially misleading may be the stomach content analysis since (1) only about 6% of the 900 snakes had identifiable remains in their digestive tracts; (2) there may be many cases of ontogenetic change in diet (as noted for *Bothrops atrox*), so that juveniles of large species may be competing with adults of small

species; and (3) our sample sizes preclude statistical analysis. A larger data base would possibly modify our results, but we doubt if it would contradict our interpretations.

The variables of time, habitat, adaptive zone, body size and food preference seemingly segregate species. It is likely that other, more subtle variables (e.g., soil type and moisture, vegetation structure and illumination) also play important roles in resource partitioning and further segregate potentially competitive species.

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