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*The American Naturalist*, Vol. 106, No. 948 (Mar. - Apr., 1972), 220-236.

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*The American Naturalist* is currently published by The University of Chicago Press.

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## SPECIES DENSITIES OF PREDATORS AND THEIR PREY

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Varied explanations have been offered for the fact that numbers of coexisting animal species differ from place to place and, in particular, that species density tends to increase toward the equator. Factors related to species density or other indices of species diversity include means and variability of climatic variables (Pianka 1967), plant species diversity (MacArthur and MacArthur 1961), and structural characteristics of vegetation (MacArthur and MacArthur 1961; MacArthur, MacArthur, and Preer 1962; MacArthur 1964; MacArthur, Recher, and Cody 1966; Pianka 1967; Recher 1969). Many of these studies dealt with predators. The above factors probably influence the number of sympatric predator species through effects upon predator-prey relations and competition. If so, one of the most proximate factors influencing the number of sympatric predator species might be prey species density. According to this hypothesis, predator species density should increase with the number of available sympatric species of prey.

Snakes are particularly well suited for testing this hypothesis. Since many snakes feed upon vertebrates whose geographic distributions are well known, the number of *potential* prey species at specific localities can be accurately estimated. Many snakes eat a restricted class of prey (e.g., small rodents, or lizards, or anurans and fish). One can determine the number of sympatric prey species at many localities, the number of sympatric snake species likely to prey upon them, and the number of sympatric snake species unlikely to prey upon a given class of prey. A test for strong positive relationships between predators and their prey is thus possible; moreover, there should be no relationship between prey species density and the number of species of predators which do not eat those prey.

## PREDATOR-PREY RELATIONSHIPS AMONG SYMPATRIC SNAKE SPECIES

If predators are competing for food, spatial or temporal differences in habitats of sympatric predators will most effectively reduce competition when these differences coincide with spatial or temporal habitat differences of prey species. In general, natural selection should favor differences in

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habitat and in various aspects of foraging behavior which minimize overlap among predators in prey species eaten.

Snake species are *not* usually restricted to a single, or even to a very few, prey *species* at specific localities or throughout their geographic range. Instead, most snakes eat a wide variety of prey, belonging to one or a few prey types (e.g., small mammals, lizards, anurans, or fish) (Fitch 1963*a*, 1963*b*, 1965); Klimstra 1959).

Sympatric snake species tend to eat different species of prey. Stomach contents based upon large local samples of sympatric snakes often show pronounced differences in prey taken by different snake species (Fitch 1949, 1960, 1963*a*, 1963*b*, 1965; Uhler, Cottam, and Clarke 1939; Hamilton and Pollack 1956). In those few cases where extensive stomach content data are available for sympatric snake species *which eat the same basic prey type*, different snake species tend to concentrate on different prey species (Carpenter 1952; Fitch 1949, 1960, 1963*a*).

Some mechanisms causing sympatric snake species to eat different prey species might be: (1) habitat differences which coincide with habitat differences of prey species, (2) temporal differences in foraging activity which coincide with temporal differences in activity or availability of prey species, (3) differences in prey sizes eaten which coincide with different-sized prey species, and (4) innate differences in the tendency to strike different prey species.

In any group of sympatric species, it is difficult to separate the relative contributions of each of these mechanisms to observed differences in prey species eaten. At any given locality all of these mechanisms probably play some role.

For example, Carpenter (1952) studied the ecologies of three sympatric species of garter snakes, *Thamnophis sauritus*, *Thamnophis sirtalis*, and *Thamnophis butleri*. The two most terrestrial species, *T. sirtalis* and *T. butleri*, fed mainly upon earthworms, while the more arboreal, bush-dwelling species, *T. sauritus*, ate principally anurans. Carpenter found that within populations of both *T. sauritus* and *T. sirtalis* larger specimens switched to larger individuals and species of prey. There is some evidence, too, that larger individuals of *T. sirtalis* ate larger species of anurans more often than did *T. sauritus*.

Fox (1951) found that, in the field, aquatic *Thamnophis* ate aquatic prey (e.g., anurans, fish), while more terrestrial *Thamnophis* ate terrestrial prey (e.g., rodents, plethodontid salamanders, slugs). These differences persisted in captivity even when alternative prey were offered. Prey odor seemed to play a major role in eliciting feeding (Fox 1952).

Some snake species enter the world with predisposed feeding preferences. Burghardt (1967, 1968, 1969) found that naïve newborn or newly hatched specimens of three species of *Natrix*, five species of *Thamnophis*, *Storeria dekayi* and *Ophiodryx vernalis* all showed species differences in the number of tongue flicks and attacks given to chemical extracts of different potential prey studies. Species differences in chemoreceptive and attack response of

these naïve young snakes remarkably parallel published accounts of species differences in prey type.

In summary, available information on snake species and their prey defies any simple notion of resource partitioning by habitat segregation in time or space. It is clear, however, that sympatric snake species tend to eat different species of prey, and that this is accomplished by a variety of complex mechanisms.

#### METHODS

Forty-five mainland localities were chosen where good estimates could be made of the numbers of sympatric lizards, anurans, and snakes, and where snake species occurred whose feeding habits were well documented.

Some of the many pitfalls in determining the number of sympatric species in an area can be avoided, but others cannot. Simpson (1964) discussed difficulties in determining the number of species which occur in quadrants 150 miles on a side. It is still more difficult to estimate the number of sympatric species at specific localities.

Fortunately, distributions of lizards, snakes, and anurans are quite well known in many geographic areas. Even so, distributions of most species in these taxa are discontinuous within recorded ranges. In some areas, point localities were available, which often show major discontinuities in distribution. Where only "solid" range maps were available, however, discontinuity of distribution undoubtedly led to some error in estimating species densities. Localities at junctions of major biotic provinces, life zones, or plant community types were avoided, since at such places species densities are overestimated. Similarly, localities in areas of high local topographic relief were avoided to eliminate pooling species which replace each other altitudinally.

Estimates assembled for each locality represent the number of sympatric species (species densities) in a quadrant of a few square miles (Appendix).

Of the 45 sample localities, 28 are in the United States, six in Mexico, four in Rumania, four in Sweden, two in England, and one in West Pakistan (data on distributions were taken from Conant 1958; Duellman 1965; Fuhn 1960; Fuhn and Vancea 1961; Gislén and Kauri 1959; Klauber 1956; Leviton and Banta 1964; Minton 1966; Savage 1960; Stebbins 1954, 1966; Taylor 1963; Wright and Wright 1957).

Several authors have classified snakes into major feeding types based on the prey they consume (Ditmars 1912; Mell 1929; Pope 1935). The classificatory scheme I devised is surprisingly similar to Mell's scheme for Chinese snakes.

A total of 187 species of snakes occurred at the 45 sample localities. Each species was assigned to one of the following feeding types or guilds (Root 1967):

1. *Lizard-eating snakes*.—Species feeding upon lizards *but not* anurans (e.g. *Salva-*

*dora hexalepis*, *Phyllorhynchus decurtatus*, *Lampropeltis getulus*). Some also eat small mammals or invertebrates.

2. *Anuran and lizard eating snakes*.—Species feeding upon lizards as well as anurans (e.g. *Heterodon nasicus*, *Coluber constrictor*, *Drymobius margaritiferus*). A few also eat mammals.

3. *Anuran-eating snakes*.—Species feeding upon anurans but not lizards (e.g. *Thamnophis sauritus*, *Natrix sipedon*, *Heterodon platyrhinos*). Many species also eat fish, some eat invertebrates, and a very few eat mammals.

4. *Mammal-eating snakes*.—Species feeding exclusively or predominately upon mammals but not anurans (e.g. *Lichanura trivirgata*, *Elaphe obsoleta*, *Crotalus viridis*). Juveniles of some species feed upon lizards.

5. *Invertebrate-eating snakes*.—Species feeding exclusively upon invertebrates (e.g. *Ophedrys vernalis*, *Carphophis amoneus*, *Natrix septemvittata*).

The vast majority of snake species fall unambiguously into one of these feeding guilds. Each species was assigned to a feeding guild on the basis of published analyses of stomach content or feeding data pooled from many localities. In a few species without published information on feeding habits, museum specimens were X-rayed for stomach contents. In the absence of other information, data on feeding habits of captive specimens were used. In a few cases (e.g., *Coluber constrictor*), species with geographic or seasonal variation in feeding habits were assigned to one feeding guild on the basis of data pooled from throughout their range.

Variance in species densities increases toward the equator (fig. 1). In analyses to follow, logarithmic transformations of species densities were used *throughout* to render variance homogeneous with latitude and give unbiased estimates of correlation with latitude. One was added to all species densities before taking natural logarithms because at some localities there were no species in some predator and prey categories.

Product moment correlation coefficients and partial correlation coefficients with latitude held constant were calculated for all pairs of variables (table 1).

Biological interpretation of correlation or partial correlation depends upon the particular causal scheme by which variables influence each other. The method of path coefficients (Wright 1921, 1934, 1968) provides a convenient means of determining the relative importance of various paths of influence between variables once a causal scheme has been formulated. Analysis by the method of path coefficients was used because the method demands an explicit presentation of supposed causal relationships among variables. This is of particular importance in interpreting the basis for correlation of species densities with latitude because the causal basis for such correlations could be rather complex. The causal scheme shown in figure 2 incorporates a priori knowledge that latitude might influence species densities in many ways, but species densities do not influence latitude. This very simple scheme admits many possible routes by which latitude and prey species densities might influence species densities of snake feeding guilds.

In this causal scheme, species densities of lizards and anurans are each

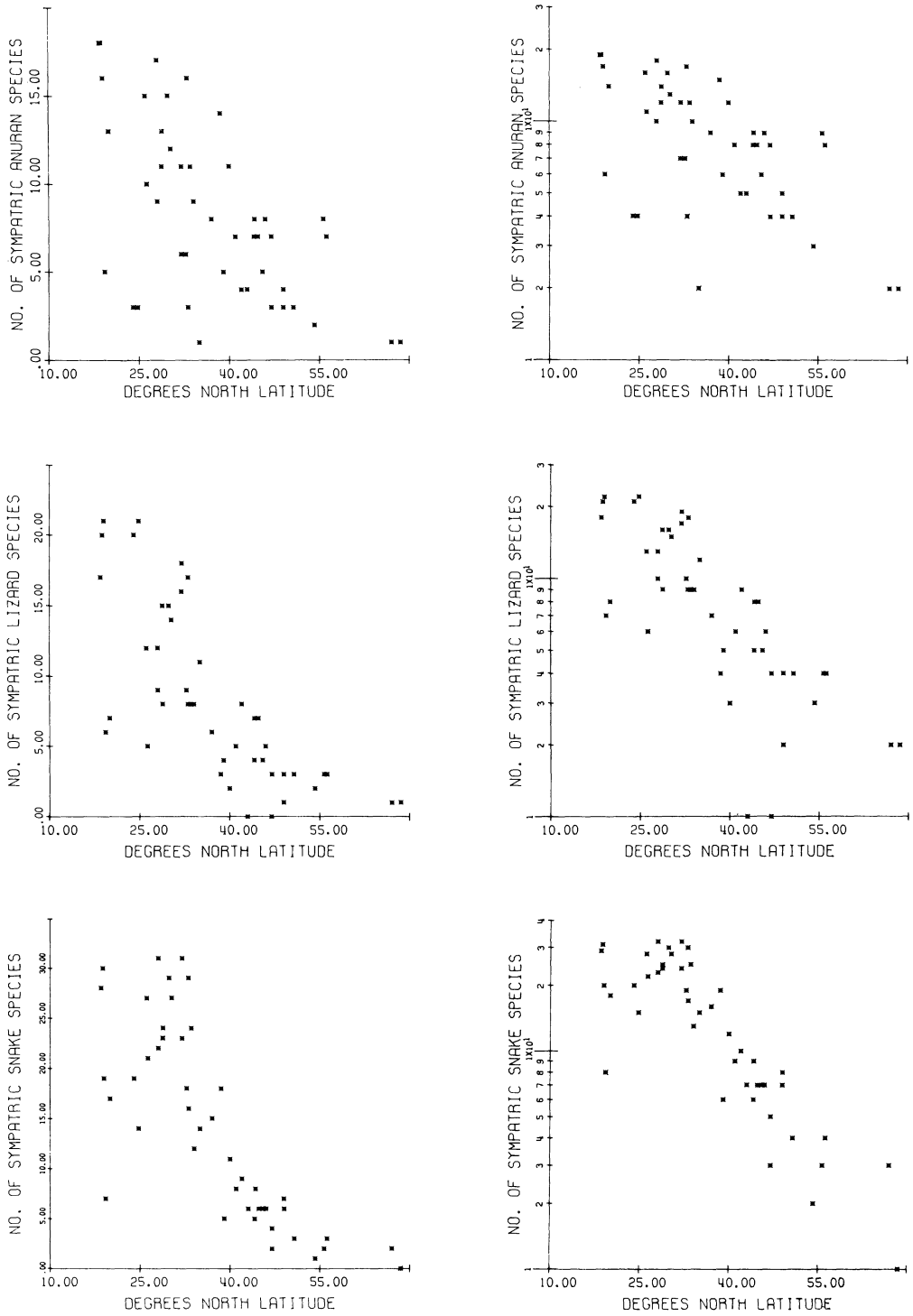


FIG. 1.—Linear and semilogarithmic plots of species densities of sympatric anurans, lizards, and snakes as a function of latitude for 45 Northern Hemisphere localities.

TABLE 1  
 CORRELATION COEFFICIENTS BETWEEN SPECIES DENSITIES AND LATITUDE (ABOVE MAIN DIAGONAL) AND PARTIAL CORRELATION  
 COEFFICIENTS BETWEEN SPECIES DENSITIES WITH LATITUDE HELD CONSTANT (BELOW MAIN DIAGONAL) FOR  
 45 LOCALITIES IN THE NORTHERN HEMISPHERE

	Lizards (B)	Anurans (C)	Lizard- eating Snakes (V)	Mammal- eating Snakes (W)	Inver- tebrate- eating Snakes (X)	Anuran and Lizard- eating Snakes (Y)	Anuran- eating Snakes (Z)
Latitude (A)	-.757**	-.605**	-.728**	-.628**	-.769**	-.554**	-.404**
Lizards (B)	...	.405**	.844**	.649**	.601**	.329*	.166
Anurans (C)	-.102	...	.441**	.470**	.611**	.671**	.770**
Lizard-eating snakes (V)	.654**	.001	...	.785**	.670**	.227	.330*
Mammal-eating snakes (W)	.341*	.145	.614**	...	.602**	.290	.494**
Invertebrate-eating snakes (X)	.045	.286	.251	.239	...	.482**	.481**
Anuran and lizard-eating snakes (Y)	-.166	.507**	-.309*	-.089	.105	...	.458**
Anuran-eating snakes (Z)	-.234	.722**	.057	.338*	.291	.307*	...

\* Significant at .05 level.  
 \*\* Significant at .01 level.

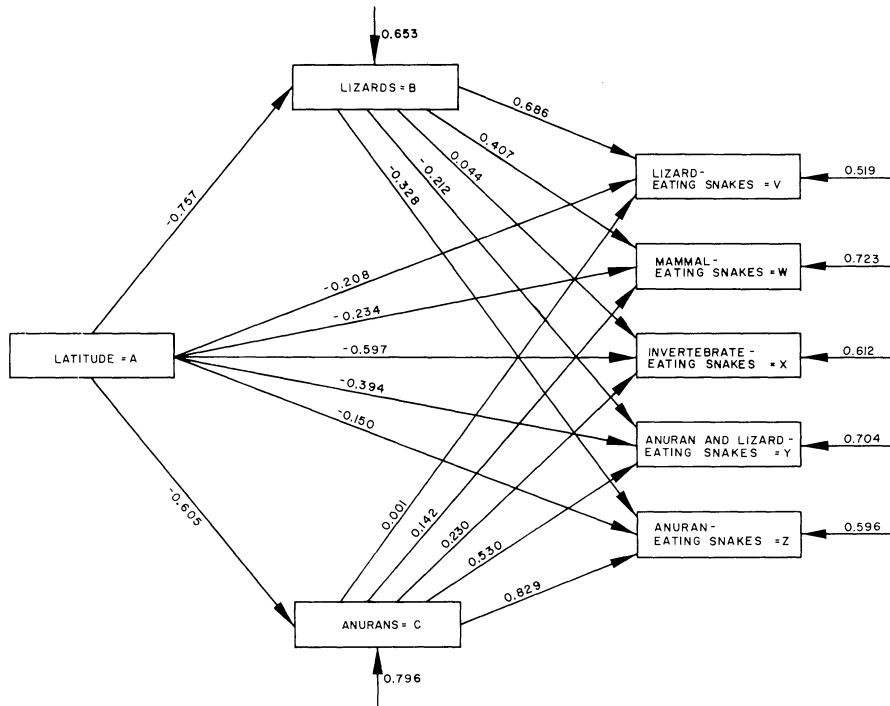


FIG. 2.—Path coefficients between variables along indicated single paths. All variables except latitude are species densities.

determined by two paths: (1) a direct path from latitude and (2) a path from an unmeasured variable (or variables). Species density of each snake feeding guild is determined by six paths: (1) a direct path from latitude, (2) a path from latitude to lizard species density to snake species density, (3) a path from latitude to anuran species density to snake species density, (4) a path from an unmeasured variable (or variables) to lizard species density to snake species density, (5) a path from an unmeasured variable (or variables) to anuran species density to snake species density, and (6) a direct path from an unmeasured variable (or variables) to snake species density.

“Direct path from latitude” to a variable is to be taken in a statistical sense. Latitude is used simply as an index of one of many variables which might be strongly correlated with latitude (e.g., climatic variables, aspects of vegetation, or unmeasured species densities or abundances of prey). A “direct path from latitude” might in reality represent many individual paths from unmeasured variables or a series of paths from variables ultimately correlated with latitude.

The path coefficient for a path from variable  $a$  to another variable  $w$  is defined as the ratio of the standard deviation of  $w$  due to  $a$  to the total standard deviation of  $w$  (Wright 1921) and may be denoted  $p_{w.a}$ .

The correlation coefficient between two variables may be expressed as the



sum of products of path coefficients along each path connecting the two variables. For example, in the scheme shown in figure 2, since  $p_{b.a} = r_{ba}$  (where  $r_{ba}$  is the correlation coefficient between  $b$  and  $a$ ) and  $p_{c.a} = r_{c.a}$ ,

$$r_{wa} = p_{w.a} + r_{ba} p_{w.b} + r_{ca} p_{w.c}, \quad (1)$$

$$r_{wb} = p_{w.b} + r_{ba} p_{w.a} + r_{ca} r_{ba} p_{w.c}, \quad (2)$$

$$r_{wc} = p_{w.c} + r_{ca} p_{w.a} + r_{ca} r_{ba} p_{w.b}. \quad (3)$$

This system of three simultaneous equations was solved for unknown path coefficients  $p_{w.a}$ ,  $p_{w.b}$ ,  $p_{w.c}$ . Similarly, correlations of species densities of each snake feeding guild with latitude, with lizard species density, and with anuran species density were expressed in terms of path coefficients, and remaining unknown path coefficients were determined. Path coefficients assigned to each single path are shown in figure 2.

Squared path coefficients are called coefficients of determination and measure the proportion of variance in one variable which is determined by another variable along a particular path. Coefficients of determination along single paths are shown in table 2 and diagrammatically in figure 3, where widths of arrows are proportional to each coefficient of determination.

The theorem for complete determination of a variable states that the sum of coefficients of determination along all paths from independent variables is 1.0. This theorem was used to solve for coefficients of determination from unmeasured variables  $fb$ ,  $fc$ ,  $fv$ ,  $fw$ ,  $fx$ ,  $fy$ , and  $fz$  to species densities. These coefficients of determination represent the proportion of variance in each species density which is unexplained by the scheme of causal relationships among measured variables.

According to the scheme in figure 2, lizard species density,  $b$ , is completely determined by two independent variables, latitude and an unmeasured variable(s),  $fb$ . The coefficient of determination of lizard species density by the unmeasured variable(s)  $fb$  is  $d_{b.fb}$ . Thus  $d_{b.a} + d_{b.fb} = 1.0$ . Since  $d_{b.a} = p_{b.a}^2 = r_{ba}^2$ , then  $d_{b.fb} = 1.0 - r_{ba}^2 - p_{b.fb}^2$ . Similarly, the coefficient of determination and path coefficient (with unknown sign) were calculated for the path from the unmeasured variable(s)  $fc$  to anuran species density.

Four independent variables completely determine species density of each snake feeding guild. The expression for complete determination of species density of mammal-eating snakes,  $w$ , is, for example,

$$d_{w.a} + d_{w.fb} + d_{w.fc} + d_{w.fw} = 1.0, \quad (4)$$

where

$$d_{w.a} = (r_{ba} p_{w.b} + r_{ca} p_{w.c} + p_{w.a})^2, \quad (5)$$

$$d_{w.fb} = (p_{b.fb} p_{w.b})^2, \quad (6)$$

$$d_{w.fc} = (p_{c.fc} p_{w.c})^2. \quad (7)$$

The last three equations were substituted into equation (4) to solve for

TABLE 2  
 COEFFICIENTS OF DETERMINATION ALONG SINGLE DIRECT PATHS BETWEEN VARIABLES (SEE CAUSAL SCHEME IN FIGS. 2 AND 3)

	Lizards	Anurans	Latitude	Residual
Lizards ( <i>B</i> )	.....	.....	.573 = ( $d_{b,a}$ )	.426 = ( $d_{b,fb}$ )
Anurans ( <i>C</i> )	.....	.....	.366 = ( $d_{c,a}$ )	.634 = ( $d_{c,fc}$ )
Lizard-eating snakes ( <i>V</i> )	.....	.....	.043 = ( $d_{v,a}$ )	.269 = ( $d_{v,fb}$ )
Mammal-eating snakes ( <i>W</i> )	.471 = ( $d_{w,b}$ )	$1 \times 10^{-6}$ = ( $d_{w,c}$ )	.055 = ( $d_{w,a}$ )	.523 = ( $d_{w,fw}$ )
Invertebrate-eating snakes ( <i>X</i> )	.166 = ( $d_{x,b}$ )	.020 = ( $d_{x,c}$ )	.356 = ( $d_{x,a}$ )	.375 = ( $d_{x,fx}$ )
Anuran and lizard-eating snakes ( <i>Y</i> )	.002 = ( $d_{y,b}$ )	.053 = ( $d_{y,c}$ )	.155 = ( $d_{y,a}$ )	.496 = ( $d_{y,fy}$ )
Anuran-eating snakes ( <i>Z</i> )	.045 = ( $d_{z,b}$ )	.281 = ( $d_{z,c}$ )	.023 = ( $d_{z,a}$ )	.355 = ( $d_{z,fz}$ )
	.108 = ( $d_{z,b}$ )	.687 = ( $d_{z,c}$ )		

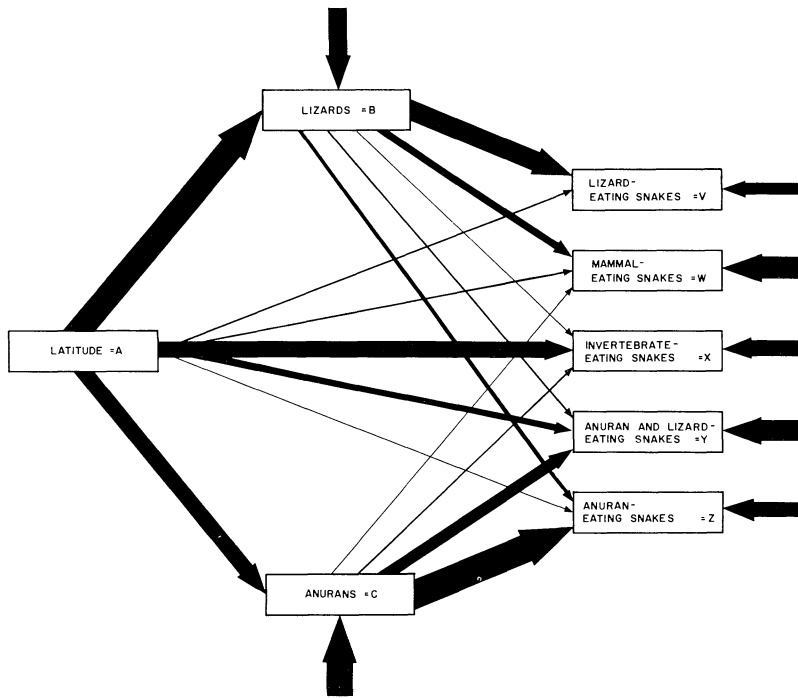


FIG. 3.—Coefficients of determination along single direct paths represented as width of arrows. All variables except latitude are species densities.

$d_{w.f.w.}$  By similar means unknown residual coefficients of determination for species densities of remaining snake feeding guilds were calculated (table 2).

#### RESULTS

Species densities of lizards, anurans, and snakes in each feeding guild are all strongly correlated with latitude (table 1). Significant correlations also exist between nearly every pair of species densities.

In light of strong correlations between all variables and latitude, many of the correlations between species densities can be attributed to common correlation with latitude. With latitude held constant (table 1, below diagonal), the only significant correlates of lizard species density are species densities of lizard-eating snakes and mammal-eating snakes. The only significant correlates with anuran species density are species densities of anuran-eating snakes and anuran and lizard-eating snakes. There are also some significant correlations between species densities of different snake feeding guilds which are not due to common correlation with latitude.

Coefficients of determination (squared path coefficients) from prey to their predators are large (fig. 3). For example, 47% of the variance in lizard-eating snakes is related to species density of lizards, and 69% of the variance in anuran-eating snakes is related to species density of anurans

(table 2). The only exception to this pattern is the rather small contribution, 4%, of lizard species density to variance in species density of anuran and lizard-eating snakes.

Coefficients of determination from prey to snake guilds which do not eat them are small. For example, only 0.0001% of the variance in lizard-eating snakes is related to species density of anurans, and only 11% of the variance in anuran-eating snakes is inversely related to species density of lizards. The only exception to this pattern is the somewhat larger contribution, 16%, of lizard species density to variance in mammal-eating snakes.

Latitude influences snake species density principally by influencing prey species density. The coefficient of determination of the path from latitude to lizard-eating snakes via lizard species density is 0.27. All other effects of latitude account for only 4% of the variance in lizard-eating snakes. Similarly, the coefficient of determination for the path from latitude to anuran-eating snakes via anuran species density is 0.25, while all other effects of latitude account for only 1% of the variance in anuran-eating snakes. For anuran and lizard-eating snakes, however, latitudinal effects through prey are not larger than other latitudinal effects. The coefficient of determination for latitudinal effects via nonprey is 0.16, and for latitudinal effects via prey the coefficients of determination are 0.03 for effects via lizards and 0.10 for effects via anurans.

#### DISCUSSION

Before any explanation for tropical species diversity can be assessed, two empirical questions must be answered. (1) When specific localities are examined, does the number of sympatric species increase toward the equator? (2) When larger geographic areas are examined, are there more species with more restricted geographic ranges toward the equator? If the answer to the first question is "yes," then the explanation for tropical species diversity is to be sought in those mechanisms which permit coexistence of more species. If the answer to the second question is "yes," then the explanation must be in terms of mechanisms which enhance speciation or otherwise cause species to replace one another geographically or altitudinally. If both answers are "yes," then both sorts of mechanisms must be incorporated into the explanation.

Dobzhansky (1950) gave the numbers of snake species along transects in northern and southern (data from *Série* 1936) hemispheres, but his gradients are based upon the numbers of species in whole countries or provinces. There are more species in the tropics, but neither of the questions above can be answered unambiguously. From these gradients the explanation for tropical species diversity is unclear, even in general terms.

The numbers of sympatric species of anurans, lizards, and snakes increase toward the equator (fig. 1). Clearly, then, in these taxa part of the general phenomenon of greater species diversity in the tropics is due to factors or interactions which permit coexistence of more species toward the equator. I have no data bearing on the second question above.

Analysis by partial correlation or by path coefficients shows strong relationships between species densities of predators and their prey which are not due to common correlation with latitude, but weak or no relationships between predators and their nonprey. This strongly suggests that correlations between species densities of predators and their prey are due to prey-predator relationships and competition and are not due to common correlation with some unknown variable. Apparently snake species in a given feeding guild have competed for food and, as a result of natural selection, have evolved mechanisms which cause them to eat different prey species. Where more prey species are present, there are simply more ways to avoid prey of other predators, and more species of snakes coexist in a particular feeding guild.

Latitudinal gradients in species density of some snake feeding guilds are largely due to latitudinal gradients in species density of their prey. What factors influence the number of sympatric species of prey (e.g., lizards or anurans)? Pianka (1967) found that mean temperature during July, length of the growing season, and "plant volume diversity" were all significantly correlated with the number of sympatric species of flatland desert lizards in the southwestern United States. Pianka suggests that climatic variables influence vegetation which in turn influences the number of sympatric lizard species. Since nearly all of the lizard species that Pianka studied are carnivorous, and most are not arboreal, it seems doubtful that vegetation is the most proximate variable influencing the number of sympatric lizard species. Whether the number of potential prey species is a more proximate influence remains to be tested.

Paine (1966) argues that predators may reduce the intensity of competition between prey species by keeping their populations low, thus permitting coexistence of more prey species. This argument suggests a different causal scheme connecting variables in figure 2. Latitude might affect lizard species density directly and at the same time indirectly by affecting species density of lizard predators. In a similar fashion, latitude might affect anuran species density directly as well as indirectly through their snake predators. Such a causal scheme was constructed by reversing the direction of all arrows which connect anuran or lizard species densities directly with snake species densities in figure 2. Calculation of path coefficients for this new causal scheme leads to an impossible result. The coefficient of determination from latitude directly to anuran species density is greater than 1.0. Since there could be many reasons for this mathematical anomaly, it does not disprove Paine's hypothesis. Nevertheless, the causal scheme suggested by Paine's hypothesis is incompatible with observed correlations between variables.

#### SUMMARY

Any given species of snake tends to eat one or a very few basic prey types, and sympatric snake species tend to concentrate on different prey species. When correlations between numbers of sympatric prey species

APPENDIX  
 TABLE A1  
 NUMBER OF SPECIES OF ANURANS, LIZARDS, AND SNAKES AND NUMBER OF SPECIES OF SNAKES IN EACH OF FIVE FEEDING GUILDS AT  
 45 SAMPLE LOCALITIES

LATITUDE*	LONGITUDE*	COUNTRY	ANURANS	LIZARDS	SNAKES	FEEDING GUILDS				
						V	W	X	Y	Z
68.50	18.00	Sweden	1	1	0	0	0	0	0	0
67.00	20.00	Sweden	1	1	2	0	0	0	1	1
56.20	14.50	Sweden	7	3	3	1	0	0	1	1
55.70	13.00	Sweden	8	3	2	0	0	0	1	1
54.20	00.20	England	2	2	1	0	0	0	1	0
50.70	01.70	England	3	3	3	1	0	0	1	1
47.00	22.40	Rumania	3	3	2	1	0	0	1	0
46.00	24.00	Rumania	8	5	6	2	1	0	1	2
44.80	22.50	Rumania	7	7	6	2	1	0	1	2
44.10	27.60	Rumania	7	4	5	3	0	0	0	2
49.00	108.00	U.S.A.	4	1	7	0	2	0	2	3
49.00	118.50	U.S.A.	3	3	6	1	2	0	1	2
47.00	69.00	U.S.A.	7	0	4	0	0	2	1	1
45.50	123.60	U.S.A.	5	4	6	1	2	1	1	1
44.20	117.00	U.S.A.	8	7	8	3	2	0	1	2
43.00	96.50	U.S.A.	4	0	6	1	1	1	1	2
42.00	114.00	U.S.A.	4	8	9	4	2	0	2	1
41.00	102.00	U.S.A.	7	5	8	2	2	0	1	3
40.00	85.00	U.S.A.	11	2	11	1	1	2	2	5
39.00	103.50	U.S.A.	5	4	5	1	2	0	1	1
38.50	75.50	U.S.A.	14	3	18	3	3	5	2	5
37.00	102.00	U.S.A.	8	6	15	3	3	1	2	6

LATITUDE*	LONGITUDE*	COUNTRY	FEEDING GUILDS							Z
			ANURANS	LIZARDS	SNAKES	V	W	X	Y	
35.00	116.50	U.S.A.	1	11	14	9	3	2	0	0
34.00	103.00	U.S.A.	9	8	12	3	4	1	1	3
33.50	84.00	U.S.A.	11	8	24	5	5	8	2	4
33.10	177.70	U.S.A.	3	17	16	10	3	3	0	0
33.00	91.20	U.S.A.	16	8	29	7	3	6	2	11
32.75	117.25	U.S.A.	6	9	18	8	4	2	3	1
32.00	107.50	U.S.A.	11	18	31	13	6	6	2	4
31.95	112.80	U.S.A.	6	16	23	12	5	5	0	1
30.25	99.60	U.S.A.	12	14	27	10	6	4	2	5
29.80	101.40	U.S.A.	15	15	29	9	8	4	2	6
28.80	96.00	U.S.A.	13	8	24	6	4	3	3	8
28.75	100.60	U.S.A.	11	15	23	9	3	5	2	4
28.00	82.50	U.S.A.	17	9	31	6	4	6	3	12
28.00	98.80	U.S.A.	9	12	22	9	1	5	2	5
26.30	80.80	U.S.A.	10	5	21	6	3	3	2	7
26.10	98.00	U.S.A.	15	12	27	9	3	6	6	3
24.00	110.10	Mexico	3	20	19	10	4	4	0	1
18.75	101.00	Mexico	18	20	30	5	5	7	10	3
20.00	102.00	Mexico	13	7	17	7	3	1	3	3
19.30	101.50	Mexico	5	6	7	0	0	3	2	2
18.50	102.00	Mexico	18	17	28	6	2	11	6	3
19.00	103.00	Mexico	16	21	19	4	1	6	7	1
24.80	67.50	W. Pakistan	3	21	14	8	2	1	3	0

\* In decimal fractions of degrees.

and snake species densities in various feeding guilds are examined by the method of path coefficients, distinct patterns emerge. Much of the variance in numbers of sympatric snake species is related to prey species densities. This effect is not due to common correlation with latitude. Correlations between the number of sympatric snake species in particular feeding guilds and the number of sympatric species of nonprey are, in nearly all cases, due to common correlation with latitude. These observations support the view that where there are more species of prey, more species of predators can coexist because there are more ways to avoid competition for food. This relationship is very nearly all that is required to explain observed latitudinal gradients in number of sympatric species of snakes in some feeding guilds.

## ACKNOWLEDGMENTS

I thank Rob Colwell, James Farris, and Douglas Futuyma for many valuable discussions. Rudi Arnold, Nelson Hairston, Stephen Hubbell, Arnold Kluge, and Donald Tinkle made very useful comments on the manuscript. This work was supported by a grant from the National Science Foundation, GB-6230, to N. G. Hairston, University of Michigan, for research in systematic and evolutionary biology; by N. I. H. Graduate Training Grant 5 TO1 GM00989; and by a National Science Foundation Graduate Fellowship. Computer time was paid for by the Department of Zoology and the Museum of Zoology, University of Michigan.

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