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**GEOGRAPHIC VARIATION IN SIZE AND SHAPE OF  
NEOTROPICAL FROGS:  
A PRECIPITATION GRADIENT ANALYSIS**

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**ABSTRACT** Anuran species richness in the Yucatán Peninsula diminishes dramatically from south to north and, especially, to the northwest. Species richness covaries positively with mean annual precipitation and negatively with seasonality of precipitation; together these two abiotic variables statistically explain 71% of interlocality variation in anuran species richness at 27 sites in the Yucatán Peninsula. Those few species that occur in the arid northwest portion of the peninsula are a nonrandom subset of the anuran fauna with respect to body size and reproductive mode. As a group, pan-peninsular species tend to be large species, and there is a highly significant rank correlation between body size and the extent to which species penetrate the most arid portion of the peninsula. In terms of reproductive mode, none of the seven species that deposit eggs out of water penetrates the driest areas of the Yucatán Peninsula. The hypothesis that large size and small appendages convey an advantage in a desiccating environment due to favorable surface-volume relationships is tested for a pan-peninsular species, *Smilisca baudinii*. This species exhibits highly significant interlocality variation in size, but a multivariate morphometric analysis reveals that this variation is not organized in a manner consistent with expectation. Thus, with respect to body size, the interspecific pattern is not recapitulated by an intraspecific one. However, independent of overall size, frogs from drier, more seasonal areas have smaller appendages, as predicted by a surface-volume desiccation argument.

**Key words:** Anura, Size, Geographic variation, Yucatán.

**RESUMEN** La abundancia de las especies de ranas en la península de Yucatán disminuye notablemente de sur a norte y, en particular, de sur al noroeste. La



abundancia de las especies retrocede positivamente en el promedio de la precipitación anual y negativamente en la medida de la periodicidad estacional de precipitación; estas dos variables abióticas explican la existencia de la variación estadística interlocal de 71% en las especies de ranas. Las pocas especies que existen en la zona árida del noroeste de la península no son una variedad fortuita: como grupo estas ranas tienden a ser grandes y hay una correlación sumamente importante entre el tamaño y el grado de penetración de la zona noroeste. En terminos del modo de reproducción, ninguna de las especies que depositan los huevos en situaciones terrestres o en hojas ocurre en la árida zona noroeste de la península. La hipótesis de que un tamaño grande confiere una ventaja debido a una relación favorable de superficie-volumen en un ambiente deshidratador, está probada explícitamente por la especie pan peninsular, *Smilisca baudini*. Esta especie presenta una variación interlocal muy significativa en tamaño y forma características, pero el análisis de correlación revela que la variación no está organizada de una forma consistente con la hipótesis. Por eso, el modelo interespecífico no está recapitulado por uno intraespecífico. No obstante, independientemente del tamaño del cuerpo, ranas de las zonas áridas tienen apéndices más pequeños, como se predijo en la hipótesis de superficie-volumen.

*Palabras claves:* Anura, Tamaño, Variación geográfica, Yucatán.

Biogeographic work in the Yucatán Peninsula of southeastern México and northern Central America has documented a steep gradient in frog species richness (Lee, 1980). From south to north-northwest, over a distance of about 600 km, the number of frog species diminishes from about 22 at the base, to 10 at the northwest corner of the peninsula. Frog species richness varies directly with amount of precipitation and inversely with seasonality of precipitation, based upon data from seven sites (Lee, 1980).

That fewer species of frogs should exist where precipitation is scanty and highly seasonal is by no means counterintuitive, given the necessity of aquatic or moist situations for reproduction and the fact that water evaporates from the typical amphibian integument at a rate comparable to that of evaporation from a free water surface (Jorgensen, 1950). However, it not clear how or to what extent aridity serves to set distribution limits for amphibians in the Yucatán Peninsula.

Amphibian adaptations to xeric environments can take many behavioral and physiological forms (Bentley, 1966; Shoemaker and Nagy, 1977; Pough et al., 1983). An additional evolutionary adjustment to xeric conditions to which authors sometimes allude, but of which there exists no rigorous examination, concerns modification of size and shape. Because rates of evaporative water loss are in part a function of surface-to-volume ratios (Thorson and Svihla, 1943), larger individuals are expected to lose water at slower mass-specific rates than are smaller individuals. This expectation has been documented experimentally (Farrell and MacMahon, 1969; Ralin and Rogers, 1972). Among amphibians of the same size, differences in

rates of water loss have been attributed to differences in shape (Cohen, 1952; Schmid, 1965; Spight, 1968; Thorson, 1955).

Thus, for amphibians, adaptive modifications of morphology represent one of several possible evolutionary adjustments to a xeric environment. Such modifications have been advanced, *post hoc*, to explain observed patterns of geographic variation in size and shape of frogs (e.g., McDiarmid, 1968; Nevo, 1973), but there exists no detailed and comprehensive morphometric analysis evaluating this idea.

The intent of this study is to (1) explore further the relationship between climate and frog species richness, bringing greater quantification to bear on that issue; (2) ascertain whether those species that penetrate the xeric northwest corner of the Yucatán Peninsula are a nonrandom subset of the Yucatecan frog fauna; and (3) evaluate the proposition that a drying environment favors large body size and small appendages. Examination of this latter idea involves the test of two specific predictions. First, variation in body size within species should exhibit interlocality variation and be organized such that larger individuals occur in xeric areas and smaller individuals in mesic areas. Second, variation in appendage size should exhibit interlocality variation that is organized such that individuals with relatively small appendages occupy xeric situations and those with relatively longer appendages occupy more mesic areas.

## MATERIALS AND METHODS

Distributional data for frogs are from updated versions of the spot maps of Lee (1980), from which distributional limits for each species were inferred. As in the earlier study, species richness was estimated for each of 144 grid squares, each representing  $50 \times 50$  km, and superimposed on a map of the Yucatán Peninsula. Data on mean annual precipitation (ANRN) are available for 31 localities and the percent of annual precipitation (PCTRN) falling from May through October (a measure of seasonality of precipitation) are available for 27 localities in the peninsula. These are from published (Page, 1933, 1938; Lundell, 1937; Arias, 1959; Vivó Escoto, 1964; García, 1965) and unpublished (R. Waide, pers. comm.) sources.

To characterize size for each species, snout-vent lengths (recorded to the nearest mm with a plastic ruler) were measured for samples of preserved specimens in the University of Miami Reference Collections (UMRC) and the private collection of Jay M. Savage (the Costa Rica Expeditions Collection [CRE]). Some species were excluded from the analysis owing to their restricted habitat requirements. *Rana juliani* and *Agalychnis moreletii* are restricted to montane situations; their absence from the peninsular lowlands likely involves the lack of habitat of suitable elevation. *Hyalinobatrachium fleischmanni* was excluded because it deposits its eggs

on vegetation overhanging streams, which are absent in the northern third of the Yucatán Peninsula. *Eleutherodactylus alfredi* was excluded because there are so few locality records for the peninsula that its distribution cannot be inferred with any confidence. Finally, *Eleutherodactylus yucatanicus* was excluded because of its extreme habitat specificity—it is apparently an inhabitant of mesic situations associated with caves and cenotes at the northern end of the peninsula.

The analysis of interspecific size was restricted to adult males, as those are generally better represented in collections than are females. Samples were usually those drawn from the Yucatán Peninsula, although occasionally, when peninsular samples were unavailable, measurements are for specimens collected elsewhere and, occasionally, measurements were taken from published sources. Here the emphasis was on interspecific size differences: at this phase of the analysis, intraspecific geographic variation was ignored.

Intraspecific variation in size and shape was analyzed for male *Smilisca baudinii*, a pan-peninsular species, in order to test the prediction that a xeric environment results in the evolution of large body size and reduced appendage size. Specimens used were those in the collections of the Museum of Natural History, The University of Kansas, and the University of Miami. Specimens had been in preservative for various lengths of time, but never less than 2 yr. Thus, preservation-induced distortion is assumed to have been stabilized and to be comparable for all samples (Lee, 1982). Museum numbers of the specimens examined are given in the Appendix. Sample sizes and localities from which samples were drawn are given in Table 1. Each specimen was scored for the 18 morphometric characters defined elsewhere (Lee and Crump, 1981). The characters are: snout-vent length (SVL), femur length (FL), tibia length (TL), foot length (FTL), metatarsal length (ML), diameter of the disk of Digit IV of foot (DD), head length (HL), head width (HW), eye diameter (ED), tympanum diameter (TD), interorbital distance (IOD), internarial distance (IND), snout length (SL), diameter of disk on Digit IV of hand (HDD), radioulna length (RUL), hand length (HDL), axilla-groin length (AGL), and snout depth (SD). Two technicians scored the specimens, and inter-observer variation might contribute to the variability in the morphometric data (Lee, 1990). However, covariation between measurements made on the same specimens by the two technicians is extremely high ( $r = 0.999$ ;  $df = 34$ ), indicating that interobserver variation is tolerably slight.

To explore character covariation and to obtain a multivariate index of overall size, principal components of variation were extracted from a matrix of product-moment correlation coefficients between the 18 morphometric characters. Interlocality variation in mean PC scores for the samples was analyzed by analysis of variance (ANOVA). To provide an explicit test



Table 1. Localities and sizes of samples of *Smilisca baudinii*. Sample numbers correspond to those in Figure 4.

Locality	Sample Number	Sample size
Yucatán: Mérida	1	4
Yucatán: Tecóh, 1.7 km S	2	9
Yucatán: Dzitás	3	14
Yucatán: Río Lagartos: 24.2 km S	4	6
Quintana Roo: Cobá	5	7
Campeche: between Dzibalchén and Becanchén	6	14
Campeche: Dzibalchén	7	17
Campeche: Chekubúl, 7.4 km S	8	19
Campeche: Escárcega	9	19
El Petén: Tikal-Uaxactún	10	15
El Petén: Chinajá, 20 km NNW	11	42
TOTAL		166

of the prediction concerning appendage size, the various measurements of fore- and hindlimb segments were regressed on SVL and their adjusted sample means analyzed by analyses of covariance (ANCOVA) and by a principal components analysis.

## RESULTS

### INTERSPECIFIC PATTERNS

**Geographic variation in anuran species richness and its environmental correlates.**—The geographic pattern of anuran species richness in the Yucatán Peninsula is displayed in Figure 1. From south to northwest, the number of species of anurans diminishes dramatically from about 22 at the base, to 10 at the northwest corner, a 55% reduction in species richness over a distance of about 600 km.

Covariation between frog species richness and annual precipitation and seasonality of precipitation is highly significant ( $P < 0.01$  for both); species richness varies directly with the amount, and inversely with the seasonality, of precipitation (Fig. 2). In a multiple regression analysis, these two variables statistically explain 71% of interlocality variation in frog species richness at 27 localities ( $Y = 6.00 + 6.17 \text{ ARN} - 0.27 \text{ PCTRN}$ ;  $R^2 = 0.71$ ). Clearly, frog species richness is greatest where annual precipitation is high and more evenly distributed among months, a finding that confirms and extends the conclusions of an earlier study (Lee, 1980), based on seven localities.

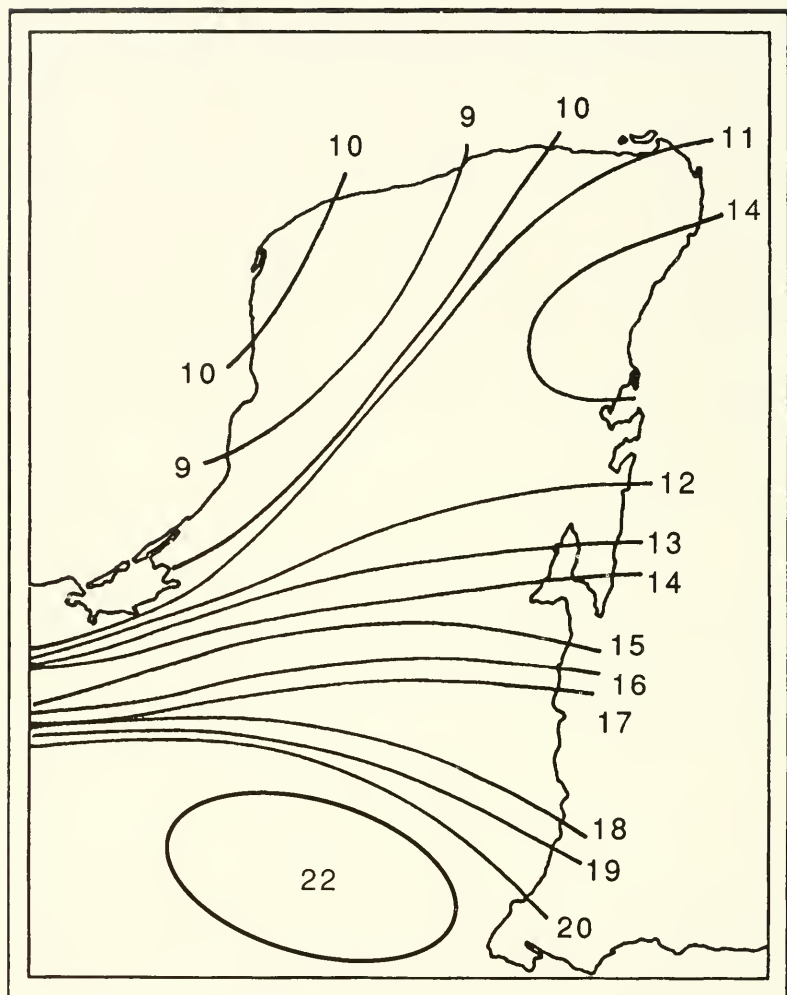


Fig. 1. The pattern of anuran species richness in the Yucatán Peninsula. Lines represent isopleths of equal numbers of species, with an interval of one species. Note the conspicuous reduction in the number of species from south to north north-west.

**Species richness and body size.**—Mean body size of males and its rank order for each of the 25 species is displayed in Table 2, together with the rank order of the extent to which each species penetrates the xeric north-west corner of the peninsula. Enormous interspecific variation in size exists between the largest (*Bufo marinus* = 110.6 mm SVL) and the smallest (*Hyla picta* = 17.5 mm SVL) species. Moreover, seven of the 10 largest

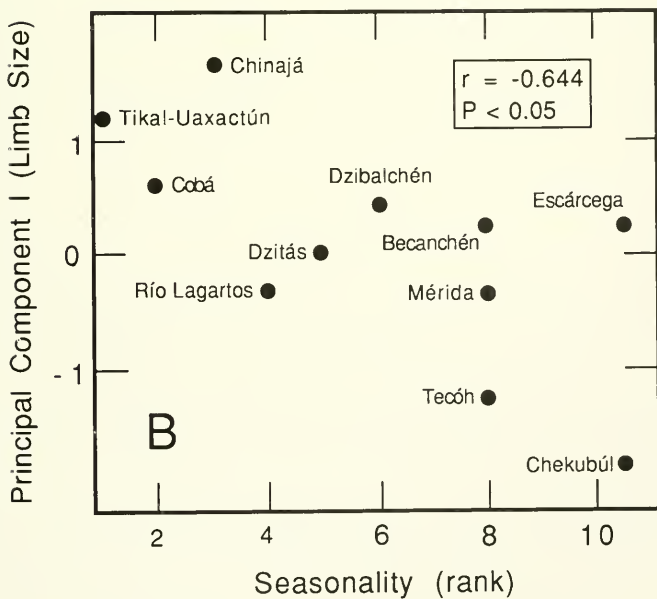
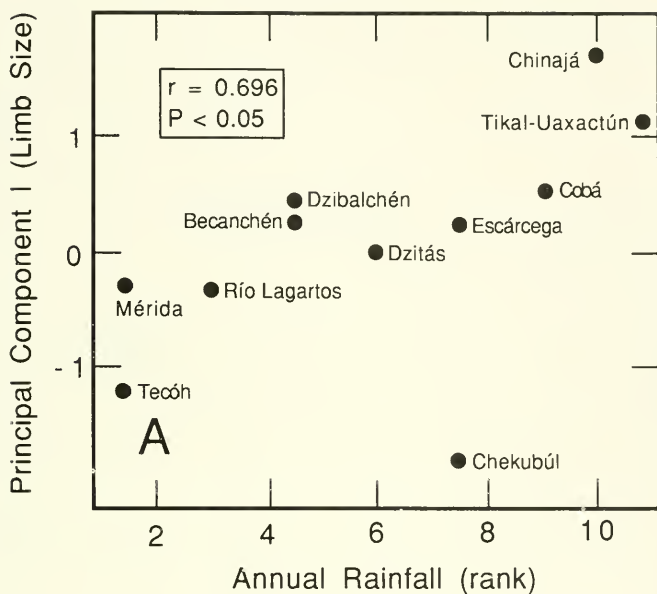


Fig. 2. Covariation of anuran species richness with seasonality of precipitation, expressed as the percent of annual precipitation falling May–October (A) and with mean annual precipitation (B). Some data points are superimposed.

Table 2. Rank correlation between mean SVL and km NNW for species of frogs in the Yucatán Peninsula.

Species	Mean SVL (mm)	Size rank	Km NNW rank
<i>Bufo marinus</i>	110.6	1	5.5
<i>Rana vaillanti</i>	82.7	2	18.0
<i>Rana berlandieri</i>	76.8	3	5.5
<i>Phrynobates venulosa</i>	72.9	4	5.5
<i>Bufo valliceps</i>	71.6	5	5.5
<i>Rhinophrynus dorsalis</i>	62.0	6	5.5
<i>Smilisca baudinii</i>	52.9	7	5.5
<i>Triprion petasatus</i>	49.3	8	5.5
<i>Agalychnis callidryas</i>	45.2	9	13.0
<i>Smilisca cyanosticta</i>	45.0	10	25.0
<i>Eleutherodactylus laticeps</i>	40.6	11	22.5
<i>Leptodactylus melanonotus</i>	35.8	12	5.5
<i>Eleutherodactylus rugulosus</i>	35.7	13	24.0
<i>Hyla loquax</i>	35.1	14	13.0
<i>Hypopachus variolosus</i>	34.6	15	5.5
<i>Leptodactylus labialis</i>	32.2	16	5.5
<i>Eleutherodactylus rhodopis</i>	27.0	17	20.5
<i>Hyla ebraccata</i>	25.0	18	16.0
<i>Physalaemus pustulosus</i>	24.7	19	18.0
<i>Scinax staufferi</i>	24.5	20	3.0
<i>Eleutherodactylus chac</i>	24.0	21	20.5
<i>Eleutherodactylus leprus</i>	23.5	22	22.5
<i>Gastrophryne elegans</i>	23.0	23	18.0
<i>Hyla microcephala</i>	22.4	24	13.0
<i>Hyla picta</i>	17.5	25	13.0

species are pan-peninsular, whereas only one of the 10 smallest species is pan-peninsular (Table 2). Along the precipitation gradient, anuran species tend to drop out in inverse rank order of their snout-vent length ( $r_s = 0.54$ ,  $n = 25$ ;  $P < 0.01$ ). Although they constitute a taxonomically diverse assemblage of eight genera representing six families, pan-peninsular species (i.e., those that penetrate the xeric northwest corner of the peninsula, mean rank of 5.5 in Table 2) have one trait in common—viz., they tend to be large species. This fact is represented graphically in Figure 3, which displays statistics of location and dispersion for the grand mean snout-vent lengths of pan-peninsular and mesic-restricted species; the grand means for the two groups show a highly significant heterogeneity by analysis of variance (mean = 59.9 vs. 33.6;  $df = 1, 23$ ;  $F = 11.0$ ;  $P = 0.003$ ).

**Species richness and reproductive mode.**—Four of the reproductive modes defined by Crump (1974) are represented among the anurans of the

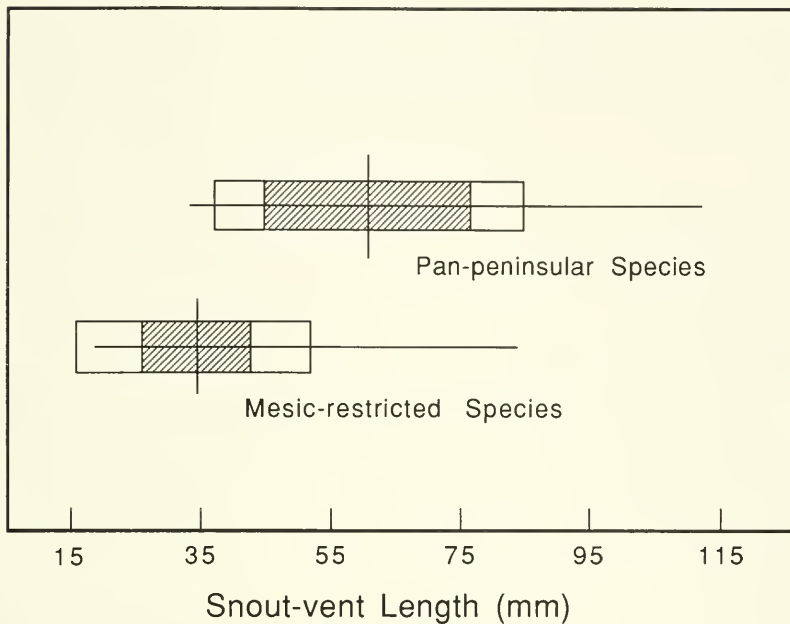


Fig. 3. Statistics of location and dispersion for mean snout-vent lengths of pan-peninsular and mesic-restricted species of anurans in the Yucatán Peninsula. Horizontal lines = range; vertical lines = grand mean; open rectangles encompass  $\pm$  one standard deviation of the grand mean; solid rectangles encompass 95% confidence limits for the grand mean.

Yucatán Peninsula. The modes, their abbreviations, and the species exhibiting them are, as follow: eggs in foam nest (FN—2 species of *Leptodactylus*, *Physalaemus pustulosus*); eggs on leaves, aquatic larvae (ELAL—*Agalychnis callidryas*, *Hyla ebraccata*); terrestrial eggs, direct development (TEDD—5 species of *Eleutherodactylus*); aquatic eggs, aquatic larvae (AEAL, the 15 remaining species). The anuran fauna was divided into two groups—those species that are pan-peninsular and those that are mesic-restricted (i.e., those species that fail to penetrate the xeric northwest corner of the peninsula). Table 3 gives the results of a  $2 \times 4$  contingency analysis testing the proposition that geographical group membership (pan-peninsular vs. mesic-restricted), is statistically dependent upon reproductive mode. Eight of the 10 species that exhibit a specialized reproductive mode (FN, ELAL, TEDD) are mesic-restricted species, yet the analysis provides no firm support for the idea that reproductive mode is a determinant of geographical group membership, for the chi-square value falls just short of achieving statistical significance ( $\chi^2 = 6.67$ ,  $df = 3$ ,  $P = 0.083$ ). If, however, those reproductive modes that involve oviposition



Table 3. Contingency analysis of reproductive mode versus distribution for frogs in the Yucatán Peninsula. FN = eggs in foam nest; ELAL = eggs on leaves, aquatic larvae; TEDD = terrestrial eggs, direct development; AEAL = aquatic eggs, aquatic larvae.

Distribution	Reproductive mode			
	FN	ELAL	TEDD	AEAL
Pan-peninsular	2	0	0	8
Mesic-restricted	1	2	5	7

$$\chi^2 = 6.67; df = 3; P = 0.083$$

sites out of the water (ELAL, TEDD) and which presumably expose eggs to the greatest risk of desiccation are contrasted with those modes in which eggs are deposited in water (FN, AEAL), a  $2 \times 2$  contingency analysis reveals that geographical group membership is significantly dependent upon reproductive mode (Yates corrected  $\chi^2 = 4.37$ ,  $df = 1$ ,  $P = 0.037$ ). Apparently, reproductive mode and particularly oviposition site, provide a partial explanation for the decline in species richness along the precipitation gradient. None of the seven species that deposit their eggs out of water has been able to penetrate or persist in the dry northwest portion of the Yucatán Peninsula. Excluding these seven species, a decline in anuran species richness along the precipitation gradient is nonetheless apparent, from 18 to 10, a 44% reduction. Moreover, the magnitude of the difference between the grand means of the snout-vent lengths of pan-peninsular and mesic-restricted species is changed little by the exclusion of those seven species, and remains significant by analysis of variance (mean = 59.9 vs. 34.4;  $df = 1, 16$ ;  $F = 5.43$ ;  $P = 0.03$ ). Something in addition to reproductive mode is responsible for the diminution in anuran species richness along the precipitation gradient in the Yucatán Peninsula.

The interspecific pattern of snout-vent lengths is consistent with the idea that large body size conveys an advantage in a desiccating environment. However, because the various pan-peninsular species represent diverse taxonomic groups, unknown historical factors confound any attempt to interpret body size patterns in light of contemporary ecological factors. To minimize the influence of historical factors, an intraspecific analysis of geographic variation in body size of a pan-peninsular species, *Smilisca baudinii*, was undertaken.

#### INTRASPECIFIC PATTERNS OF SIZE AND SHAPE

**Analysis of overall size.**—Factor loadings associated with the first three principal components of variation extracted from a matrix of product-

moment correlation coefficients, together with their percents of trace, are presented in Table 4. Principal component one (PC I), which statistically explains 72.3% of the variation in the data, is clearly a size factor upon which all variables load heavily and positively. PC I thus ordines individuals of *Smilisca baudinii* on the basis of overall size.

Samples of *Smilisca* from throughout the Yucatán Peninsula exhibit highly significant geographic variation in overall body size, as indexed by mean PC I scores (ANOVA;  $F = 41.37$ ;  $df = 10, 155$ ;  $P < 0.0001$ ). Statistics of location and dispersion for the PC I scores are displayed in Figure 4, together with a Student-Newman-Kuels (0.05 level) procedure identifying homogeneous subsets of sample means. Frogs from Chinajá, the most southern locality, are significantly larger than any of the other samples and constitute a unique subset. The Cobá, Becanchén, and Tikal-Uaxactún samples comprise a homogeneous subset of moderately large individuals. The seven remaining samples represent relatively small frogs, distributed through the northwest portion of the peninsula. Certainly the prediction that the largest individuals should occur in the northwest corner of the

Table 4. Factor loadings and percents of trace associated with principal components extracted from a matrix of product-moment correlation coefficients between 18 morphometric variables of *Smilisca baudinii*.

Variable	PC I	PC II	PC III
HL	0.955	0.033	-0.001
TL	0.951	0.219	0.042
SVL	0.950	0.041	0.125
FTL	0.936	0.194	0.111
HDL	0.925	0.120	0.064
IOD	0.911	-0.064	-0.073
HW	0.861	-0.217	-0.248
FL	0.846	0.363	-0.164
SL	0.839	-0.010	-0.133
ML	0.838	0.362	-0.057
HDD	0.827	-0.227	0.195
DD	0.822	-0.201	0.172
AGL	0.815	0.177	0.357
SD	0.792	-0.102	0.011
ED	0.787	-0.285	0.014
RUL	0.766	-0.131	-0.168
TD	0.731	-0.223	-0.466
IND	0.690	-0.509	0.165
Percent of trace:	72.3	5.3	3.5

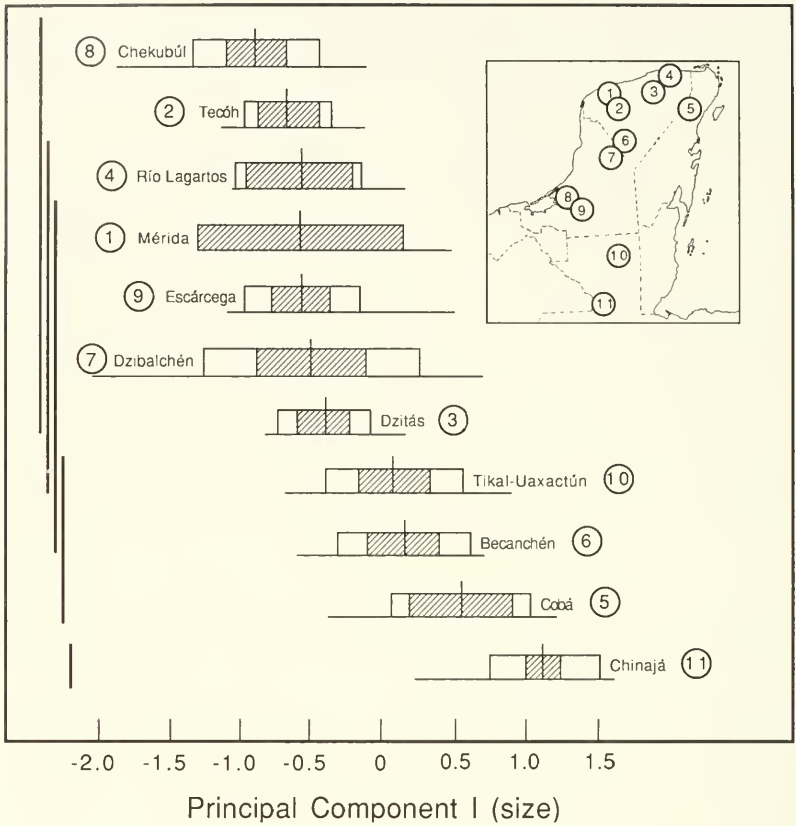


Fig. 4. Statistics of location and dispersion for principal component I scores of samples of *Smilisca baudinii* from throughout the Yucatán Peninsula. Circled numbers correspond to the sample numbers in Table 1, and the inset map gives the localities from which samples were drawn. The vertical lines at left enclose homogeneous subsets of means based on SNK tests. Symbols are as in Figure 3 except that the vertical lines within the rectangles represent means.

peninsula, reflecting a negative covariation between body size and precipitation, is not realized in this analysis. In fact, the relationship between body size, as indexed by mean PC I scores, and mean annual precipitation is, if anything, positive, for the rank correlation of 0.593 between size and precipitation is positive and just fails to achieve conventional statistical significance ( $r_{s, .05[9]} = 0.602$ ). Given the general inverse relationship between annual precipitation and seasonality of precipitation, one might expect body size in these frogs to be negatively associated with seasonality of precipitation, and this is indeed the case ( $r_s = -0.635$ ;  $P < 0.05$ ). The multivariate analyses thus provide no support for the hypothesis that a

Table 5. Spearman rank correlation coefficients between adjusted mean limb segments or mean principal component scores and mean annual precipitation (ANRN) and seasonality of precipitation (PCTRN) for 11 samples of *Smilisca baudinii*.

Variable	ANRN	PCTRN
FL	0.284	-0.497
TL	0.586	-0.566
ML	0.664*	-0.522
FTL	0.668*	-0.635*
RUL	0.046	-0.437
HDL	0.696*	-0.667*
DD	-0.041	0.133
HDD	0.220	-0.087
PC I	0.696*	-0.644*
PC II	0.023	-0.032
PC III	0.018	0.391

\* =  $P < 0.05$

xeric, desiccating environment results in evolution of large body size in *Smilisca baudinii*. Instead, and unexpectedly, the findings provide evidence, albeit weak, for the opposite relationship: body size may vary directly with annual rainfall, and inversely with seasonality of precipitation.

Principal component II explains only 5.3% and PC III 3.5% of the variation in the data. The patterns of factor loadings on the second and third components do not lend themselves to any obvious biological interpretation (Table 4); thus, PC II and III are not considered further.

**Analysis of appendage size.**—Analyses of covariance (ANCOVA) of the limb segments (FL, TL, ML, FTL, RUL, DD, and HDD), with SVL the covariate, reveal that the regression coefficients among samples are homogeneous, but the adjusted means for each of the segments are significantly heterogeneous among the 11 samples. An explicit test of the proposition that frogs from xeric environments have small appendages, independent of body size, can be had by testing for covariation between the adjusted limb segment data and the precipitation data; results of those tests are contained in Table 5. Three limb segments (ML, FTL, and HDL) show a significant positive ( $P < 0.05$ ) rank correlation with the amount of annual rainfall, and two of those (FTL, HDL) are negatively correlated with seasonality of rainfall. Thus there is some indication that when the effects of overall size are controlled, frogs from drier, more seasonal areas tend to have smaller hands and feet, a finding consistent with expectation.

However, the preceding univariate analyses ignored covariation among

the limb segments themselves; a more biologically relevant approach is to examine the limb segment data from a multivariate perspective. Results of a principal component analysis of ANCOVA-adjusted limb segment data are contained in Table 6. Five (ML, FTL, HDL, TL, FL) of the eight variables load significantly and positively on PC I, which explains 54.3% of the variation in the data. PC I thus ordines samples on the basis of limb size. PC II explains 28.8% of variation in the data, and ordines the samples primarily on the basis of toe disk diameter. Finally, PC III, which explains 12.0 of the variation in the data, is essentially a unit vector upon which RUL loads negatively.

Table 5 contains the rank correlation coefficients between the mean sample PC scores and the precipitation data. Only scores on PC I covary significantly with rainfall and seasonality. Thus, frogs having short hind limbs and hands tend to occur in areas in which rainfall is scant and seasonal; more mesic areas are inhabited by individuals with longer hind limbs and hands (Fig. 5). The multivariate analysis of the limb segments corroborates the univariate one, and together their results are consistent with the idea that a drying environment can promote the evolution of reduced appendage size.

## DISCUSSION AND CONCLUSIONS

### THE PATTERN OF ANURAN SPECIES RICHNESS

Diminution in species richness from the base to the tip of peninsulas—the so-called “peninsula effect”—has been documented for various groups of vertebrates (Simpson, 1964 for mammals; Cook, 1969, and MacArthur and Wilson, 1967 for birds; Kiester, 1971, and Means and Simberloff, 1987 for amphibians and reptiles). Lee (1980) found no evidence of a peninsula effect in the distributions of lizards or snakes in the Yucatán Peninsula, but noted that the distributions of amphibians could be interpreted as evidence of such a pattern. The generality of this phenomenon has been questioned by Busack and Hedges (1984), who found the pattern manifested by Florida lizards and snakes, but absent in the lizard and snake faunas of the Baja, Yucatán, and Iberian peninsulas. Means and Simberloff (1987) recognized three hypotheses that could be invoked, singly or in combination, to explain the peninsula effect, and these can be evaluated as they apply to the results of the present study. First, an historical interpretation posits that past environmental fluctuations eliminated species and that there has been insufficient time for an equilibrium number of species to become reestablished. As discussed by Lee (1980), an historical explanation for the gradient in anuran species richness in Yucatán is untenable because the northern end of the peninsula, although geologically only recently emergent, has



Table 6. Factor loadings and percents of trace from a principal component analysis of *Smilisca baudinii* limb segment data adjusted for covariation with snout-vent length by analysis of covariance.

Variable	PC I	PC II	PC III
ML	0.964	-0.050	-0.155
FTL	0.958	-0.019	0.080
HDL	0.953	0.122	0.222
TL	0.951	-0.062	0.279
FL	0.674	-0.635	-0.228
DD	-0.025	0.949	0.016
HDD	0.328	0.920	0.138
RUL	0.345	0.358	-0.857
Percent of trace:	54.3	28.8	12.0

nonetheless served as a notable center of vertebrate differentiation and contains many endemics (Muller, 1973; Lee, 1980).

A second hypothesis holds that the peninsula effect is a consequence of extinction-immigration dynamics played out within a peninsular geometry. This explanation, too, fails as applied to the anuran fauna of the Yucatán Peninsula, for it predicts fewest species at the point most distant from the presumed source of immigration (the base). Figure 1 clearly indicates that the reduction in species richness in Yucatán is decidedly asymmetrical, with fewest species at the northwest, rather than the more distant northeast corner.

Finally, an ecological explanation attributes the reduction in species richness to habitat deterioration along existing habitat gradients. Lee (1980) found that structural and floristic diversity of vegetation were poor predictors of amphibian species richness in the Yucatán Peninsula, and that, as confirmed for anurans by the present study, species richness covaried with the amount and seasonality of precipitation in a way suggestive of causation. The present finding that pan-peninsular species of frogs tend to be large, and that samples of *Smilisca baudinii* from dry areas have smaller appendages, supports the view that the decline in anuran species richness is a consequence of increased aridity and seasonality of precipitation.

#### THE PATTERN OF INTRASPECIFIC VARIATION IN SIZE AND SHAPE

In his review of morphological variation in the frog *Phrynohyas venulosa* throughout its extensive range in Middle America, McDiarmid (1968) noted that the largest specimens came from areas of low mean annual rainfall, characterized by distinct wet and dry seasons. He thought that large size was advantageous in dealing with problems of desiccation.

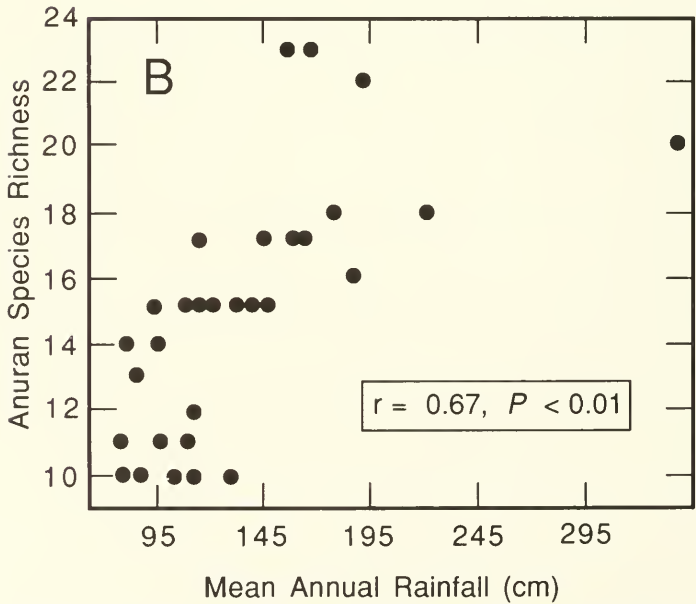
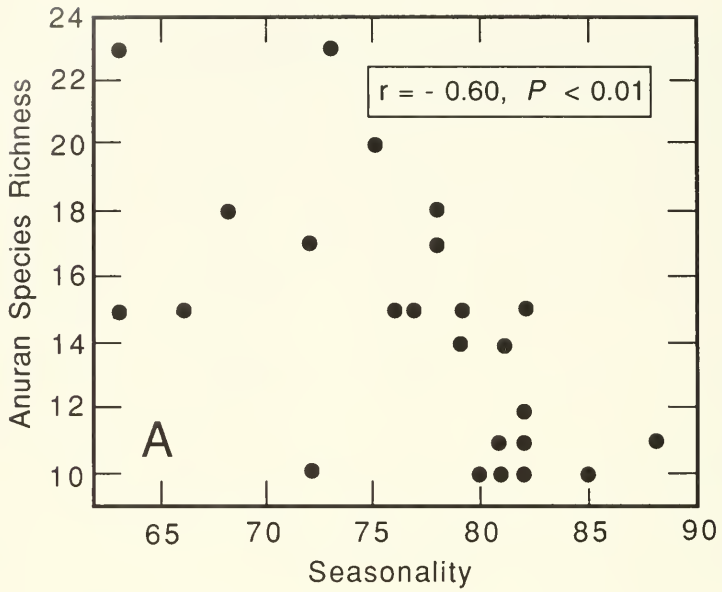


Fig. 5. Rank correlation between limb size, indexed as mean PC I scores, and annual precipitation (A) and seasonality of precipitation (B). Localities are ranked from least to greatest with respect to annual precipitation and seasonality.

Similarly, Nevo (1973) found that body size in the frog *Acris crepitans* covaried negatively with annual rainfall; he interpreted large size as an adaptation to arid climates. Thus, both authors ascribed adaptive significance on the basis of a covariation between body size and climate. However, in each study, the discovery of a relationship between size and climate, and the interpretation of its biological meaning, were generated by a single data set. The conclusions of both studies, therefore, represent hypotheses to be further tested. In the immediate case of *Smilisca*, the test refutes the hypothesis: these frogs are not larger in drier areas. However, this finding is open to multiple interpretations. Individuals of *Smilisca baudinii* presumably grow indeterminately, and there is no assurance that the among-locality comparisons were based upon samples of frogs that were at equivalent points on their growth trajectories. Interlocality variation in mortality schedules could alter age structures and thus affect the size distributions of populations. Finally, in the absence of any information on heritability of adult body size in *Smilisca*, it is possible, even likely, that interlocality variation in body size is substantially affected by a variety of purely environmental effects, thereby obscuring any genotypic based pattern of covariation with climatic variables. This finding, based on a single species, does not invalidate the proposition that a desiccating environment can select for large body size, and result in its evolution, but it does impugn the generality of that hypothesis, and it underscores the difficulty inherent in interpreting patterns of interlocality variation in body size in animals that grow indeterminately.

Nevo (1973) interpreted the pattern of interlocality variation in relative foot size in *Acris gryllus* and *A. crepitans* as the result of adaptation for increased jumping efficiency, whereas Salthe and Crump (1977) tentatively invoked a thermoregulatory explanation for their finding of reduced appendage size in populations of *A. crepitans*, consistent with the ecogeographic rule of Allen that states that appendages are shorter in cold climates than in warm ones.

Owing to its tropical latitude, and the lack of major topographic relief, the thermal environment of the Yucatán Peninsula is homogeneous, and it precludes an evaluation of the idea that appendage length should vary with temperature. The data on *Smilisca* indicate, though, that significant interlocality variation in relative appendage size can be generated for reasons other than thermoregulatory ones. In particular, an osmoregulatory explanation seems warranted, for the prediction that frogs will have smaller appendages in xeric areas is sustained by the data on *Smilisca*. This supports the idea that an evolutionary adjustment in morphology has occurred in response to the rigors of a desiccating environment.

## THE PATTERN OF INTERSPECIFIC VARIATION IN SIZE

Failure to detect an inverse relationship between body size and rainfall in the intraspecific analysis does not invalidate an osmoregulatory explanation for the fact that in the Yucatán Peninsula pan-peninsular species of anurans tend to be large species, but it does encourage the search for alternative explanations amenable to further test. Because the large species that penetrate the arid portion of the Yucatán Peninsula are also large in other more mesic portions of their ranges, large body size cannot be viewed strictly as an adaptation to the aridity of Yucatán. Rather, it appears that species that are large, for whatever reason, are capable of persisting in arid portions of the Yucatán Peninsula, whereas small species cannot.

In summary, theoretical surface-volume considerations, published data on evaporative water loss in anurans, and observations on interspecific variation in size of anurans in the Yucatán Peninsula suggest that large body size confers an advantage in a drying, seasonal environment, and that such conditions can result in the evolution of reduced appendage size. Evaporative water loss and problems of water balance affecting eggs and postmetamorphic individuals are implicated as factors important in producing the steep gradient in anuran species richness in the Yucatán Peninsula. This "peninsula effect" is thus a consequence of habitat deterioration, and there is no need to invoke immigration-extinction dynamics or historical factors to explain this geographic pattern. The pattern of intraspecific variation in body size does not recapitulate the interspecific pattern and, in fact, may run counter to it. The interpretation of this finding is obscured by lack of information on heritability of asymptotic body size and on age-specific mortality in the various populations of *Smilisca baudinii*.

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## APPENDIX

Specimens of *Smilisca baudinii* examined. KU = Museum of Natural History, University of Kansas; UMRC = University of Miami Reference Collection.

GUATEMALA: *El Petén*: 20 km NNW Chinajá (KU 57199-240); 4.8 km S Tikal (KU 156952-56); 9.4 km S Tikal (KU 156948-51); Uaxactún (KU 156930-35).

MEXICO: *Campeche*: 7.4 km S Chekubúl (UMRC 84-41, 18 specimens); Dzibalchén (KU 75414-25, 75427-31); 1 km W Escárcega (KU 71391-92); 6 km W Escárcega (KU 71397-403); 7.5 km W Escárcega (KU 72377, 71380, 71382-89). *Quintana Roo*: Cobá (UMRC 84-98, 7 specimens). *Yucatán*: between Becanchén and Dzibalchén (UMRC 79-297, 14 specimens); Dzitás (UMRC 79-300, 14 specimens); Mérida (UMRC 79-302, 4 specimens); 24.2 km S Río Lagartos (UMRC 79-301, 6 specimens); 1.7 km S Tecóh (UMRC 79-299, 9 specimens).













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