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A GEOGRAPHIC VARIATION GRADIENT  
IN FROGS

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CURATOR OF AMPHIBIANS AND REPTILES

Variation gradients in body size and relative length of appendages, correlated with geographic distribution, have been studied in birds and mammals for nearly a hundred years. Bergmann, in Europe (1847), and J. A. Allen, in this country (1876, 1905), were pioneer investigators of this subject. The generalizations known as the Bergmann and Allen Rules state respectively that animals of the same species tend to be larger in a cooler climate and to have relatively shorter appendages. While there are numerous exceptions and anomalies, these rules have received renewed and critical attention in recent years. The corollary of the Bergmann Rule, that cold-blooded animals may be expected to be larger in warmer regions, requires much further study. In general, poikilothermous animals increase in size with approach to their optimum climatic conditions. Rensch (1933, pp. 37-43) summarizes and gives references to some of the recent literature for both the Bergmann and the Allen Rules.

In the course of taxonomic studies of both amphibians and reptiles, measurements are frequently taken of large series of individuals, and from certain studies of my own I wish to describe what appears to be a geographic variation gradient in the leg-length of frogs. One of the characters most frequently employed in the discrimination of the species of frogs and toads is the relative length of the hind legs, expressed either in measurements or by the point reached by the heel or toes when the leg is laid forward alongside the body. It is well known that shortness of the legs is correlated with burrowing, and great elongation of the limbs with more active habits. The fact that there is a varying amount of sex dimorphism in leg-length in frogs has not had as much attention

as it deserves. My friend C. C. Liu has recently canvassed this matter in the Saliencia for the Chinese fauna (Liu, 1936).

My attention was first drawn to what I believe to be a quite different general trend of variation in the leg-length character by two male wood-frogs from Labrador, collected by Dr. William Duncan Strong in the course of the Rawson-MacMillan Subarctic Expedition of Field Museum. At first sight these frogs seemed to represent a distinct undescribed form. Their stocky bodies, short limbs, and extreme fullness of web give them an appearance quite different from that of the familiar wood-frogs of Wisconsin. On further investigation, the Labrador wood-frogs proved to be referable to *Rana sylvatica latiremis* Cope, in spite of the fact that the type locality of *latiremis* is Lake Aleknagik, Alaska, at the opposite side of the continent. Indeed, the fact that these frogs range along the border of the arctic tundra means that a continuous uniform habitat is available to them, extending from the Pacific coast of Alaska to the Atlantic Labrador coast. This supports the probability that there is only a single form of wood-frog at the north in North America. The wide east-west range of *Rana temporaria temporaria* in Eurasia parallels that of *R. sylvatica latiremis*.

The wood-frog of the middle west, *Rana sylvatica cantabrigensis*, with short limbs, is usually distinguished from the eastern, longer legged *R. sylvatica sylvatica*. In connection with studies on the amphibians and reptiles of Wisconsin in which my brother, the late F. J. W. Schmidt, was associated with me, we found that the relative leg-length of the wood-frog of our region, in Clark County, was intermediate between that of the wood-frogs of Manitoba and that of eastern specimens of *sylvatica*. Furthermore, it was evident from published data that the Manitoba wood-frog, in turn, was intermediate in this character between *latiremis* and our Wisconsin wood-frogs, supposedly *cantabrigensis*. It had caught our attention also that a similar variation in leg-length with latitude could be discerned in *Pseudacris triseriatus*, and in the doubtfully distinct short-limbed *P. septentrionalis*.

It was my brother's plan to collect extensively both in Wisconsin and in boreal America, and we laid aside our notes for the accumulation of further material. As there is now no expectation of adding to our northern collections, and as Dr. E. B. S. Logier, of the Royal Ontario Museum, is engaged in a study of the wood-frog problem, it is unlikely that I shall have occasion to study this subject at greater length. My supposition of the identity of the Labrador



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form with the Alaskan *latiremis* was mentioned in identifying wood-frogs of the Chicago region as *Rana cantabrigensis cantabrigensis* (Schmidt and Necker, 1935, p. 66).

Turning from the taxonomic questions involved to the problem in ecological zoogeography presented by the correlation between the leg-length character and latitude, I find definite clues in our notes to such a relation, corresponding in a minor way with the Bergmann and the Allen Rules. My attention has been especially drawn to such relations by my share in the publication of *Ecological Animal Geography* (Hesse, Allee, and Schmidt, 1936).

Employing what I believe to be the measurements least subject to fortuitous error in alcoholic specimens of frogs, namely, the length from snout to anus (=body length, *b*), and the calipered outside measurement of the flexed tibial joint of the leg (=tibia, *t*), the proportionate length of the tibia (*t/b*) is taken as an indicator of proportionate length of leg. Avoiding the question of the racial distinctness of the eastern *sylvatica*, and combining measurements from specimens in Field Museum with data available in Boulenger's account of the American frogs of the genus *Rana* (Boulenger, 1920, p. 457), the following table sets forth the variation gradient of *t/b* associated with latitude in the wood-frogs of the middle of the continent:

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Region	No. specimens	<i>t/b</i>		Approximate latitude
		Extremes	Average	
Great Bear Lake } Great Slave River }	4	.41-.45	.43	63°
Manitoba	4	.45-.50	.48	52°
Wisconsin	20	.50-.60	.55	45°
Northern Illinois	20	.50-.57	.54	42°
Terre Haute, Indiana	2	.57-.63	.60	39°30'
Southern Illinois	2	.60-.65	.62	38°

Field Museum is indebted to Mr. Fred Cagle of the Southern Illinois Normal College and to Mr. Clarence Shockley, of Terre Haute, Indiana, for the specimens from central Indiana and southern Illinois, which form an important addition to this tabulation. The uniformity of the populations from central Wisconsin and northern Illinois slightly interrupts the progressive increase in proportionate leg-length to the south, but this does not affect the general relation. It is by no means clear that the wood-frogs of southern Illinois are properly referable to *Rana sylvatica cantabrigensis*, but it is preferable to associate them with the western subspecies unless other characters than leg-length can be found to differentiate them.

Turning to the familiar leopard frog (*Rana pipiens* auct.), there are reasons for expecting a parallel relation. Comparison of the proportion  $t/b$  in specimens from Moose Jaw and Swift Current River, Saskatchewan, with the same proportion in my brother's specimens from Worden Township, Clark County, Wisconsin, results as follows:

Region	No. specimens	$t/b$		Approximate latitude
		Extremes	Average	
Saskatchewan.....	8	.49-.52	.52	50°
Wisconsin.....	13	.55-.64	.59	45°

It is not impossible that a difference of subspecies is involved in these two series, but the relation shown is nevertheless suggestive.

Material available is inadequate for the analysis of variation in leg-length in *Pseudacris*, in which the species *septentrionalis* was based especially on the shortness of leg in a specimen from Great Bear Lake (Boulenger, 1882, p. 335, pl. 23, fig. 1). Measurements taken from Boulenger's figure do not fit the tabulation of middle western specimens below:

Region	No. specimens	$t/b$		Approximate latitude
		Extremes	Average	
Quill Lake, Saskatchewan.....	1	....	.34	52°
Ramsey County, Minnesota....	8	.37-.41	.40	45°
Clark County, Wisconsin.....	16	.37-.43	.40	45°
Cook County, Illinois.....	20	.39-.43	.41	42°
Southern Illinois.....	9	.44-.51	.48	38°

Here the variation gradient is far from regular, but again suggests a similar change from short legs to long when populations are sampled from north to south. The discontinuity between the frogs from southern and northern Illinois suggests a taxonomic change.

In China, the common *Rana nigromaculata* (the Asiatic representative of the European *Rana esculenta*) is divided from north to south into three subspecies (Schmidt, 1927, p. 567), based on coloration, length of snout, and leg-length. In the last character they fall into a uniform gradient from north to south:

Region	No. specimens	$t/b$		Approximate latitude
		Extremes	Average	
Shansi.....	9	.43-.46	.44	42°
Shantung.....	10	.45-.51	.49	37°
Anhwei.....	10	.47-.54	.51	32°
Fukien.....	10	.48-.56	.52	27°

The various Asiatic wood-frogs, *Rana japonica*, *R. asiatica*, and their allies, will doubtless exhibit the same type of variation in the leg-length character.

Comparison of specimens of frogs in a single species from a considerable extent of vertical range should show some correlation with the gradient for latitude. I fail to find a corresponding variation in the measurements of *Hyla regilla* from California given by Storer (1925, p. 264). In *Rana boylei*, the alpine subspecies in the Sierra Nevada, *R. b. sierrae*, from above 10,000 feet in the Yosemite, has the *t/b* average 0.47, while in specimens of *R. b. boylei* from near sea level in Marin County, California, the average is 0.56 (Storer, 1925, pp. 248, 264).

*Hyla versicolor*, which has a wide north-south range, was chosen to test these results for a species of very different habits:

Region	No. specimens	<i>t/b</i>		Approximate latitude
		Extremes	Average	
Clark County, Wisconsin.....	10	.46-.50	.48	45°
Southern Louisiana.....	10	.49-.52	.50	30°

Here the difference is certainly slight, for it is necessary to take specimens separated by 15° of latitude to obtain even the small difference in leg-length shown above. It is evident, however, that there will be numerous exceptions to the leg-length rule for frogs, since this character may be influenced by other factors of environment or habits.

Subspecies have frequently been established primarily or in part on differences of this kind. It seems to the writer that unless supported by other characters, a variation gradient should not lead to the distinction of named races, since there might as well be ten as two; and if only the extremes are named, the major population is intermediate.

The north-south variation gradient in question cannot well be a corollary of the Allen Rule for the appendages of warm-blooded animals. The only suggestion I can make as to its meaning is that leg-length in frogs may be associated with the total activity of the animal; this is decreased to the north by both shorter season and lower temperature.

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