A COMPARATIVE STUDY OF MONTANE AND LOWLAND LARVAL POPULATIONS OF LEPTODACTYLUS ALBILABRIS IN PUERTO RICO

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ABSTRACT

A COMPARATIVE STUDY OF MONTANE AND LOWLAND LARVAL POPULATIONS OF *Leptodactylus albilabris* IN PUERTO RICO

by William R. Bhajan

Significant morphological differences were determined between tadpole samples of *Leptodactylus allbilabris* found at El Yunque, a highland region of Puerto Rico, and comparable samples obtained at Rio Piedras, a lowland area in the same island.

These differences might be explained in that the montane population made climatic adjustments with such success that morphological differences resulted.

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By

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INTRODUCTION

A comprehensive study of the taxonomy and ecology of *Leptodactylus albilabris* in Puerto Rico was undertaken in 1963 by Dr. Harold Heatwole, then a staff member at the University of Puerto Rico. The project, reported herein, was undertaken at the suggestion of Dr. Heatwole as a contribution to his research on this species of frog.

The field and laboratory research was conducted from January, 1964 to December, 1964, in Puerto Rico under the direction of Dr. Heatwole. In October, 1964, I was admitted to the Graduate School at Michigan State University where the research program was concluded.

Leptodactylus albilabris, a relatively small frog with an average snout-vent measurement approximately 100 mm. exhibits a great variability in coloration and pattern but shows relative uniformity in structural characters throughout its range. Stejneger (1902) described the living adult as having "general color above olive, the dusky marking dark grayish brown, nearly blackish brown below the dorso-lateral fold and on femur; the dorso-lateral fold and narrow edges around the dark markings pale olive gray; the transocular band and cutting edge of lip dark grayish brown; the supra-labial light band pale straw yellow; underside whitish; throat finely sprinkled with dark chocolate brown; iris olive silvery, overlaid with blackish."

Morphologically, the species is described as having the vomerine teeth in two curved series behind the choanae; tongue large, slightly indented behind; nostrils nearer the tip of snout than eye; tympanum circular about two-thirds the diameter of the eye; interorbital space equals width of upper eye-lid; first finger much longer than second, which equals fourth; toes slightly webbed at base; third much longer than fifth; subarticular tubercles well developed and numerous smaller tubercles in series on the sole; two metatarsal tubercles, the inner connected with a slight tarsal fold; heels overlapping when hindlimbs are folded at right angle to axis of body; tarso-metatarsal joint reaching tympanum when hind limbs are carried forward along the body; skin smooth above and below; numerous small, pointed tubercles on the outer surface of the tibia; a narrow dorsolateral glandular fold and another similar one, though less prnounced, on sides from shoulder to groin; a strong glandular fold from posterior angle of eye over tympanum to shoulder; ventral disk plainly marked by two transverse dermal folds, one between the forelimbs, the other across the belly, these joined by a longitudinal dermal fold on each side.

Leptodactylus albilabris is found on the Caribbean islands of Puerto Rico, Vieques, Culebra, St. Thomas, Tortola, Jost Van Dyke, Anegador, and St. Croix. In the Antilles, it is restricted to the Virgin Islands, St. Croix, Vieques and Puerto Rico.

In Puerto Rico (Figure 1) the species occurs where suitable moisture conditions exist from sea level to an altitude of about 2000 feet. In the Northern Coastal Plain, Leptodactylus albilabris is abundant at the lower altitudes and populations extend into the highlands behind. The animals are especially abundant in moist meadows and irrigated fields of sugar cane. Stomachs examined contained land snails, spiders, and a variety of insects including beetles, ants, flies, catepillar and cockroaches.

The breeding season of this frog seems to be early in the year. Eggs were found in January and March at El Yunque and Rio Piedras respectively. Full grown tadpoles were observed in the Catalina planatation on March 1, and on April 7, eggs and all stages of tadpoles were observed in a little stream begind the town of Utuado (Figure 1).

The tadpole of Leptodactylus albilabris is distinctive and readily identified by "length of body about one and one-third its width and slightly less than one-half the length of the tail; nostrils nearer the eyes than the end of the snout' distance between eyes one-fifth more than distance between the nostrils and considerably less than width of

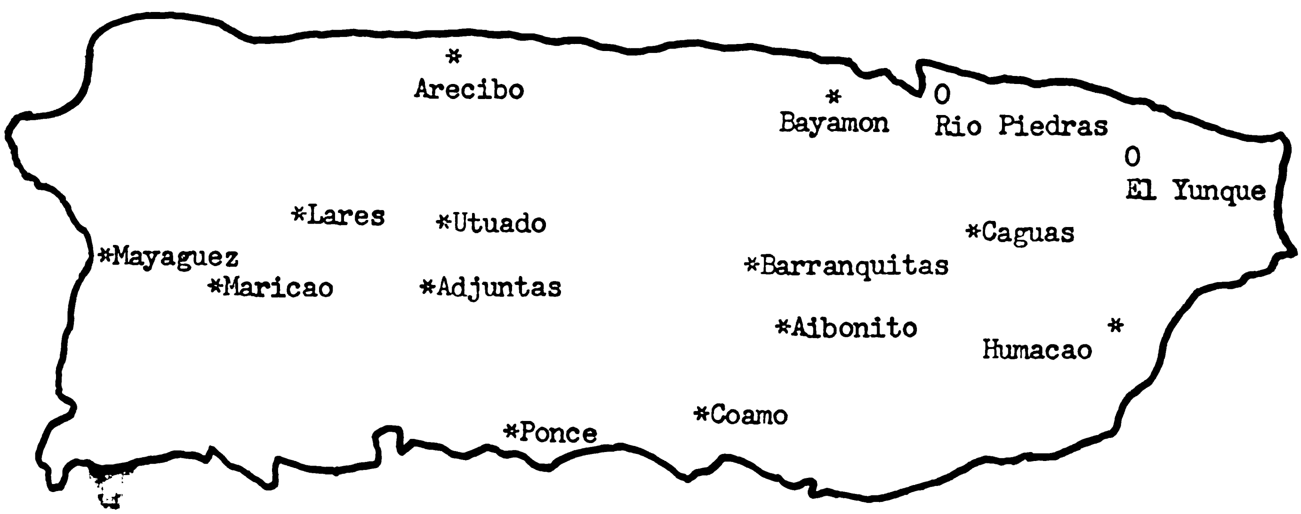


Figure 1. Localities known for Leptodactylus albilabris in Puerto Rico. The circles (0) indicate the locations of the study areas.

mouth; distance between nostrils equals their distance from eyes, as well as the diameter of the eyes; spiraculum on left side, directed backward and upward, situated above a line drawn between the base of the muscular part of the tail and the mouth and nearer to the posterior extremity of the body, being about halfway between anterior border of eye and insertion of hind legs; anus a long tube, median and larger than the spiraculum, tail about four times as long as deep, ending in an obtuse point; both upper and lower crests confined to the tail and nearly equal in depth, their edges being nearly parallel until the terminal third; the depth of the muscular part of the tail at its base about two-thirds the greatest total depth" (Stejneger, 1902).

Objectives of the Study

The tadpoles of *Leptodactylus albilabris* in Puerto Rico differ morphologically in accordance with habitat. In the lowlands, at a temperature of approximately 30° C. the tadpoles are smaller in body than the montane population. The montane population also exhibits longer appendages. The question therefore, arises as to whether the two populations represented distinct subspecies of *Leptodactylus albilabris*, or merely express clinal responses to their habitats. The findings of the data are examined in the light of Allen's and Bergmann's Rules.

I will present a morphological comparison of the larvae from highland and lowland populations to further delineate the problem. Next, experimental rearing of larvae under controlled conditions was conducted. The objective was to ascertain if morphological and/or behavior responses of the two populations that would develop. A montane population group was cultured in montane conditions and another in lowland conditions. Securing these conditions in the laboratory was effected through temperature control. The same procedure was followed for a lowland population sample.

Furthermore, the possibility that acclimatization might be responsible for morphological differences between populations was of interest.

Acclimatization is a process in which organisms adjust to new climatic conditions and embraces the whole complex of adaptation to the varying factors in the new environment.

Adaptation to environmental temperatures is important for the survival of a species. Animals must be able to function under available temperatures and these temperature relations are of paramount importance to the complete ecological understanding of any animal species.

The nature of these adjustments is of great interest. Oxygen consumption in cold adapted fishes is several times as great as in the warm adapted fish (Wells, 1935; Peiss and Field, 1950; Scholander, et al., 1953). Stuart (1951) found that only an increase in haemoglobin could balance the oxygen carrying capacity of the blood in cold adapted fish. Fishes acclimated to cold water are less tolerant to higher temperatures than those acclimated to warm water (Hathway, 1927; Brett, 1944; Fry, 1947). That such phenomena are characteristic of most aquatic poikilotherms is well established (Prosser, et al., 1950).

Considerable literature involving temperature acclimatization is avialable for adult amphibians. Among the more notable are those Bullock (1955), Ruibal (1955), Prosser (1955) and Highton (1962). These authors have shown that the compensatory metabolic rates exhibited by northern or cold adapted anurans are in keeping with the general concept that activity rates are greater at a given temperature in cold blooded animals from northern latitudes when compared with the same or closely related forms from southern latitudes.

Moore (1939, 1940, 1942, 1946, 1949), Volpe (1953) and Goin (1962) have investigated the adaptation of frog embryos to temperature. These authors demonstrated that warm adapted species have a more rapid rate of development. They also found that the time of tadpole transformation into the adult is progressively greater to the north.

Most of the above work was done in the United States and very little in the tropics. Part of the data to be presented in this paper areconcerned with the adaptation of the embryonic characters of *Leptodactylus albilabris* for the lower temperatures which occur at the montane rain forest of El Yunque, Puerto Rico.

METHODS AND MATERIALS

Description of the Sampling Areas

Schmidt (1930) provides the following pertinent and precise account:

> Puerto Rico includes a wide range of habitat conditions from the extremely wet mountain rain forest of Luquillo, where mountain palms and hardwoods are hung with lianas and draped with moss that never dries out, to the opposite extreme of aridity on the south-west corner of the island, where a cactus flora predominates.

Puerto Rico, though only 100 miles long and about 35 miles wide, is mountainous and therefore lends itself to habitats with significant temperature differences. The island is traversed by several mountain ranges with a broad northern plain. Rio Piedras is situated on this coastal plain while El Yunque is situated on the eastern end of the Luquillo mountain range. These two sites typically represent a grassland region and a tropical rain forest region and were selected as sampling areas.

Rio Piedras, at latitude 18° 25'N. and longitude 66° 04'W., has an elevation of about 75 feet above sea level. It has an annual rainfall of 77.1 inches and it is also traversed by numerous streams. The average temperature is 82°F.

El Verde, the second study area, is located 1500 feet above sea level at latitude 18° 21'N. and longitude 65° 49' on the lower montane rain forest up the side of the El Yunque mountain in the Luquillo Experimental Forest of eastern Puerto Rico. Here the average temperature is 68°F.

Laboratory Analysis of Growth and Temperature Responses

Broods of *Leptodactylus albilabris* eggs covered with foam were found near the running streams of El Yunque. Two clutches numbering about 100 eggs each, were collected on January 25, 1964, and kept in separate containers until the tadpoles emerged.

Eggs of the Rio Piedras population were found in shallow stagnant pools, under stones and near streams on March 24, 1964. Two clutches, also of approximately 100 eggs each, were obtained from this area. The lowland clutches were treated similarly as highland clutches by using separate containers.

The tadpoles of the montane populations emerged on January 26, 1964. Forty tadpoles from each clutch were measured and placed in individual open containers. These tadpoles were arranged in groups as follows:

Group 1 (a): 25 tadpoles each in its individual container were cultured at 20°C.
Group 2 (a): also 25 in number from Group (a) was cultured at 30°C.

Group 1 (b): 15 in number was cultured at 20°C.
Group 2 (b): 15 in number from group (b) was cultured at 30°C.

The purpose of the grouping was to culture the montane population in montane temperature conditions (group 1a and 1b) and also to culture montane population in lowland temperature conditions (group 2a and 2b).

The lowland population sample was similarly cultured, No feeding was necessary during the first week due to food nutrients present in the yolk sac. Tap water, aerated for at least 24 hours, was used for culturing tadpoles. The water was changed daily. The individual tadpoles were fed daily with canned spinach. During the process of metamorphosis, the water level was reduced gradually. When forelegs appeared, small pebbles were inserted in the cheese cloth covered jars. Culturing was stopped when the entire tail had been absorbed.

Since data on geographic variation is usually based upon morphological characteristics, attempts were made to obtain morphometric data.

The specimens were measured weekly and replaced in their containers. Measurements were made by removing the specimens to a petri dish which was placed over graph paper that was calibrated in millimeters. The animals were then examined through a binocular dissecting scope.

Comparative Larval Morphology of Natural Populations

Samples from the field were needed for comparison with live tadpoles being reared in the laboratory. Tadpoles were caught by a net in various pools and running streams in both sampling areas. The montane tadpoles were collected at El Yunque in July and August, 1964, and samples from the lowland Rio Piedras were collected in May and June, 1965. These samples were fixed in 10% formalin and after fixation were transferred to 70% alcohol.

Two hundred and fifty tadpoles, from a population estimated roughly at 1,000, were collected from El Yunque and 175, from a population of approximately 800, from Rio Piedras were randomly chosen and examined. The larvae were measured, tooth morphology diagrammed, and developmental stages determined, based on Gosner's (1960) simplified table for staging anuran embryos and larvae. Those tadpoles showing variations from normal tooth morphology were separated in bottles and labelled for future reference.

RESULTS

Larval Culturation

Relationship of Temperature and Developmental Rate: The rearing of larvae under controlled laboratory temperature produced the following observations:

(1) The montane population cultured at the temperature approximating its environment (20°C.) metamorphosed within 111 days whereas the lowland population cultured at the temperature approximating its environment (30°C.) metamorphosed within 25 days (Table 1).

(2) The montane population at 30°C. takes 30.5 days to transform from the tadpole stage whereas the lowland population at 20°C. required 252 days for this process (Table 1).

The results of this phase of the study indicate that a differential response to temperature was expressed as follows:

(1) The larval period of the montane population at its environmental temperature (20°C.) is 4.4 times longer than the lowland population in the latters environmental temperature (30°C.).

(2) The metamorphosis rate of samples from the montane population is increased when reared at the lowland temperature (30°C.) by 3.64 times its normal larval period.

TABLE 1.--Leptodactylus albilabris tadpole culture comparison of lowland Rio Piedras and montane El Yunque in relature to temperature.

Experimental number	Larval number	Period of larval development		Rio Piedras Length of larval stage (days)		El Yunque Length of larval stage (days)	
		Hatching	Metamorphosis	20°C.	30°C.	20°C.	30°C.
1 (a)	25	March 28	December 2	252			
(b)	15	March 28	December 2	252			
2 (a)	25	March 28	April 20		25		
(b)	15	March 28	April 20		25		
1 (a)	25	January 26	May 25			114	
(b)	15	January 26	May 18			108	
2 (a)	25	January 26	February 24				31
(b)	15	February 2	March 1				30
Average length of larval period				252	25	111	30.5

(3) The rate of metamorphosis of samples from the lowland population is 10 times slower when cultured at montane temperatures.

The results of the experiment would seem to indicate that a rise in temperature is followed by hastened metamorphosis whereas a decrease in temperature has a retarding effect on metamorphosis. The montane population at 30°C. does not duplicate the larval time span of the lowland population but takes 1.2 times longer. Similarly the lowland population at 20°C. takes 2.3 times longer than the montane population at 20°C.

The montane population appears to be more adaptable to temperature change than does the lowland population.

<u>Relationship of Temperature and Size</u>.--The growth rates of the montane and lowland tadpoles were observed by comparing the maximum weekly mean lengths, utilizing the formula:

$$\% \text{ increase/decrease} = \frac{\text{size at low temp.} - \text{size at high temp.} \times 100}{\text{size at high temp.}}$$

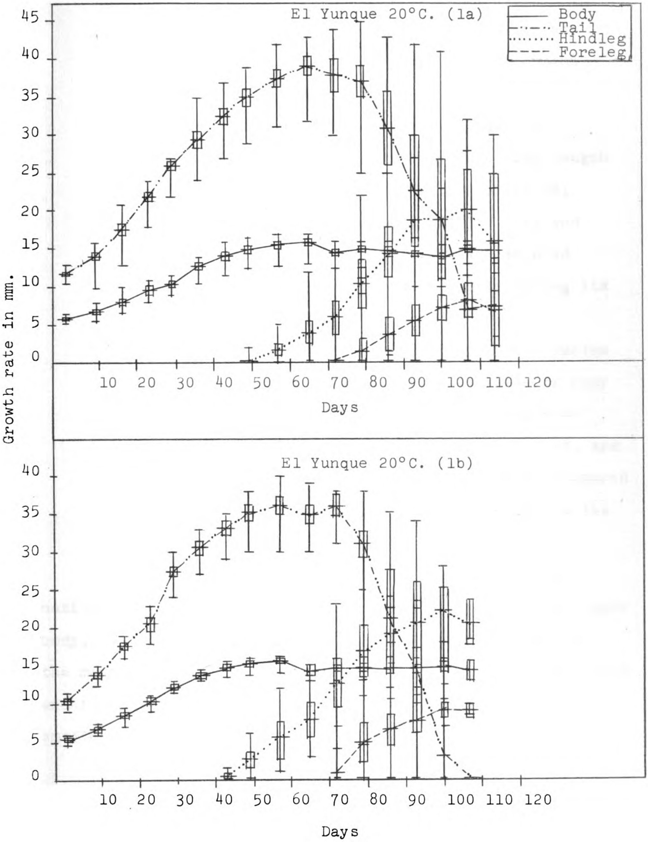
The following conclusions were made as a result of such analysis:

(1) The montane population (Table 2, Figure 2) when cultured at the temperature approximating its environment (20°C.) has an increase in body length of 8.86%; an increase in tail length of 25.12%; an increase in hind leg length of 7.74%; and an

TABLE 2.--Measurements of two groups (1a and 1b) of montane El Yunque tadpoles cultured at 20°C. $\bar{x}$ refers to the mean length and $2S\bar{x}$ denotes plus and minus twice the standard error of the mean.

Date		$\bar{x}$	$2S\bar{x}$	Range	No.	$\bar{x}$	$2S\bar{x}$	Range	No.
		El Yunque 20°C.(1a)				El Yunque 20°C.(1b)			
	Body	5.77	0.11	5.25- 6.50	25				
Jan. 26	Tail	11.81	0.17	10.50-13.00	25				
	Body	6.88	0.23	5.50- 8.00	21	5.12	0.12	4.50- 5.50	15
Feb. 2	Tail	14.20	0.54	10.00-16.00	21	10.53	0.38	9.00-11.50	15
	Body	8.11	0.34	6.50-10.00	21	6.68	0.27	6.00- 7.50	14
Feb. 10	Tail	17.78	0.63	13.00-21.00	21	13.89	0.41	12.50-15.00	14
	Body	9.70	0.50	8.00-11.00	21	8.54	0.44	7.00- 9.50	14
Feb. 17	Tail	21.93	0.65	18.00-24.00	21	17.89	0.45	16.00-19.00	14
	Body	10.63	0.26	9.00-11.50	21	10.28	0.34	9.00-11.00	14
Feb. 24	Tail	26.25	0.75	22.00-27.00	21	20.85	0.75	18.00-23.00	14
	Bodv	12.89	0.44	10.50-14.00	20	12.23	0.28	11.50-13.00	14
Mar. 1	Tail	29.45	1.03	24.00-35.00	20	27.50	0.96	24.00-30.00	14
	Body	14.24	0.54	11.50-16.00	19	13.77	0.36	13.00-14.50	14
Mar. 8	Tail	32.76	1.16	27.00-37.00	19	30.30	1.04	27.00-33.00	14
	Body	15.03	0.48	12.50-16.50	19	14.69	0.38	13.50-15.50	14
	Tail	35.26	1.16	29.00-39.00	19	33.14	0.95	29.00-35.00	14
Mar. 15	Hindleg	0.16	0.22	0.00- 2.00	19	0.48	0.36	0.00- 1.50	14
	Body	15.64	0.53	12.75-17.00	19	15.19	0.37	13.75-16.00	14
	Tail	37.57	1.26	31.00-42.00	19	35.25	1.11	30.00-38.00	14
Mar. 21	Hindleg	1.63	0.70	0.00- 5.00	19	2.71	0.98	0.00- 6.00	14
	Body	15.92	0.48	13.00-1700	19	15.54	0.35	14.00-16.25	14
	Tail	39.26	1.34	32.00-43.00	19	36.25	1.29	30.00-40.00	14
Mar. 29	Hindleg	3.90	1.60	0.00-12.00	19	5.61	1.92	1.00-12.00	14
	Body	14.57	0.43	12.50-16.00	19	14.28	1.03	13.00-15.00	14
	Tail	38.10	2.02	30.00-44.00	19	34.92	1.37	30.00-39.00	14
	Hindleg	6.13	2.26	0.00-15.00	19	7.85	2.28	3.00-15.00	14
Apr. 6	Foreleg	0.31	0.62	0.00- 6.00	19				
	Body	15.03	0.40	12.50-16.00	19	14.60	0.33	13.00-15.00	14
	Tail	37.21	2.20	25.00-45.00	19	36.14	1.13	31.00-38.00	14
	Hindleg	10.42	3.20	0.00-22.00	19	12.78	3.16	4.00-23.00	14
Apr. 13	Foreleg	1.63	1.50	0.00- 9.00	19	0.93	1.26	0.00- 7.00	14
	Body	14.88	0.32	14.00-16.00	18	14.70	0.40	13.00-16.00	14
	Tail	31.11	4.78	1.00-43.00	18	31.00	1.69	5.00-38.00	14
	Hindleg	14.66	3.48	0.00-25.00	18	16.96	3.41	4.50-25.00	14
Apr. 20	Foreleg	3.78	2.12	0.00-11.00	18	4.89	2.40	0.00-11.00	14
	Body	14.61	0.36	14.00-16.50	18	14.61	0.69	12.00-18.00	14
	Tail	22.77	7.30	0.00-42.00	18	21.14	6.40	0.00-35.00	14
	Hindleg	18.64	3.78	0.00-27.00	18	19.30	3.44	4.50-24.00	14
Apr. 27	Foreleg	5.53	1.98	0.00-11.00	18	6.66	2.08	0.00-10.50	14
	Body	14.36	0.38	13.00-15.50	14	14.50	0.58	12.00-16.00	12
	Tail	18.86	7.86	0.00-41.00	14	14.42	8.20	0.00-34.00	12
	Hindleg	18.75	4.32	0.00-27.00	14	20.58	3.17	10.00-26.00	12
May 4	Foreleg	7.14	1.74	0.00-10.00	14	7.70	2.14	0.00-11.00	12
	Body	14.91	0.49	13.00-16.00	12	14.66	0.62	12.50-16.00	9
	Tail	6.92	7.00	0.00-32.00	12	3.11	4.04	0.00-18.00	9
	Hindleg	20.13	5.34	0.00-28.00	12	22.20	3.02	15.00-28.00	9
May 11	Foreleg	8.29	2.30	0.00-11.50	12	9.17	0.90	7.00-10.50	9
	Body	14.87	1.31	13.00-16.00	4	14.33	1.45	13.00-15.50	3
	Tail	7.50	15.00	0.00-30.00	4	0.00	0.00	0.00- 0.00	3
	Hindleg	16.13	8.63	3.50-23.00	4	20.66	2.96	18.50-23.50	3
May 18	Foreleg	7.00	4.66	0.00- 9.50	4	9.00	1.00	8.50-10.00	3
	Body	13.00			1				
	Tail	30.00			1				
	Hindleg	3.75			1				
May 25	Foreleg	0.00			1				

Figure 2.--Growth rate of two groups of montane El Yunque tadpoles (1a and 1b) cultured at 20°C. The horizontal line represents the mean of the sample; the vertical line, the range; and the box, plus and minus twice the standard error of the mean.


El Yunque 20°C. (1a)
Body
Tail
Hindleg
Foreleg
45
40
35
30
25
20
15
10
5
0
10 20 30 40 50 60 70 80 90 100 110 120
Days
Growth rate in mm.
El Yunque 20°C. (1b)
40
35
30
25
20
15
10
5
0
10 20 30 40 50 60 70 80 90 100 110 120
Days

increase in fore leg of 9% as compared to the lowland population (Table 3) cultured at the temperature approximating its environment (30°C.).

(2) The montane population (Table 4, Figure 3) cultured at 30°C. has an increase in body length of 4.2%; a decrease in tail length of 17.7%; an increase in hind leg length of 19.46%; and an increase in fore leg of 53.7% as compared when raised at the temperature approximating its evnironment (20°C.).

(3) The lowland population cultured at 20°C. (Tables 5 and 6, Figures 4 and 5) has a decrease in body length of 14.4%; a decrease in tail length of 17.8%; a decrease in hind leg length of 132%; and a decrease in fore leg length of 33.3% as compared when raised at the temperature approximating its environment (30°C.).

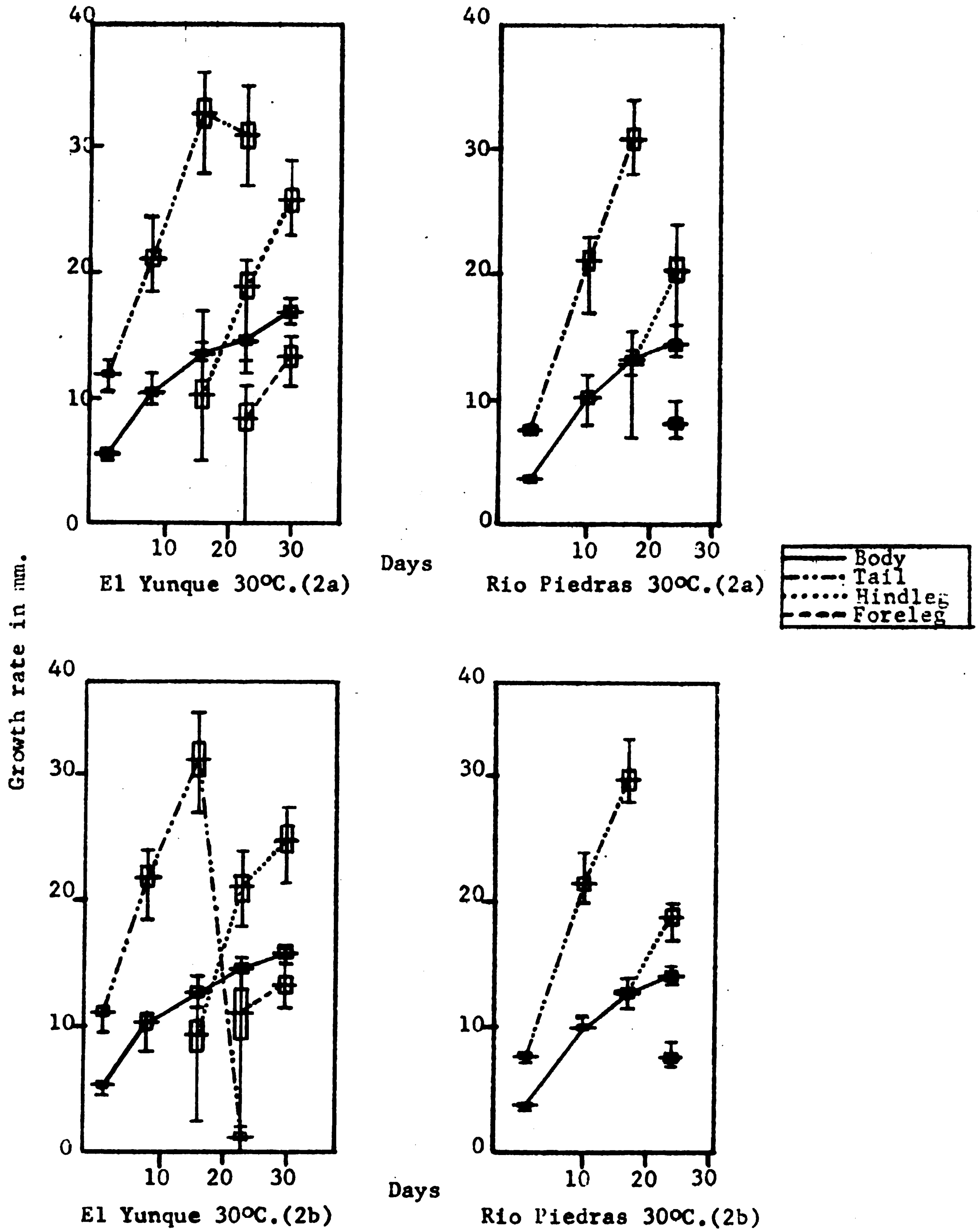
When both population samples are cultured at their native temperatures, the El Yunque population develops bigger body, tail, hind and fore legs. At reversed temperatures, the montane population continues to develop bigger body, hind and fore legs, whereas the lowland population develops much smaller body, tail, hind and fore legs.

It would seem that the montane population is more adaptable at both native and experimental temperature con-

TABLE 3.--Measurements of two groups (2a and 2b) of lowland Rio Piedras tadpoles cultured at 30°C.

Date		Rio Piedras 30°C.(2a)				Rio Piedras 30°C.(2b)			
		$\bar{x}$	$2S\bar{x}$	Range	No.	$\bar{x}$	$2S\bar{x}$	Range	No.
	Body	3.69	0.78	03.50- 4.00	25	3.83	0.11	3.50- 4.00	15
Mar. 28	Tail	7.65	0.11	07.25- 8.00	25	7.70	0.15	7.25- 8.00	15
	Body	10.25	0.32	08.00-12.00	25	10.25	0.17	10.00-11.00	15
Apr. 6	Tail	21.18	0.60	17.00-23.00	25	21.56	0.51	20.00-24.00	15
	Body	13.30	0.24	12.00-14.00	24	12.83	0.32	11.50-14.00	15
	Tail	30.80	0.64	28.00-34.00	24	29.70	0.77	28.00-33.00	15
Apr. 13	Hindleg	12.85	0.65	7.00-15.50	24	13.00	0.49	11.50-14.00	15
	Body	14.53	0.27	13.50-16.00	24	14.36	0.33	13.50-15.00	15
	Tail	0.00	0.00	0.00- 0.00	24	0.00	0.00	0.00- 0.00	15
	Hindleg	20.42	0.83	14.00-24.00	24	18.86	0.60	17.00-20.00	15
Apr. 20	Foreleg	8.20	0.37	7.00-10.00	24	7.82	0.36	7.00- 9.00	15

Figure 3.--Growth rate of two groups (1a and 2b) of montane El Yunque tadpoles and two groups (1a and 2b) of lowland Rio Piedras tadpoles cultured at 30°C. The horizontal line represents the mean of the sample; the vertical line, the range; and the box, plus and minus twice the standard error of the mean.



Growth rate in mm.
Days
El Yunque 30°C.(2a)
Rio Piedras 30°C.(2a)
Body
Tail
Hindleg
Foreleg
El Yunque 30°C.(2b)
Rio Piedras 30°C.(2b)

TABLE 4.--Measurements of two groups (2a and 2b) of montane El Yunque tadpoles cultured at 30°C.

Date		El Yunque 30°C.(2a)				El Yunque 30°C.(2b)			
		$\bar{x}$	$2S\bar{x}$	Range	No.	$\bar{x}$	$2S\bar{x}$	Range	No.
	Body	5.65	0.14	5.00- 6.00	25				
Jan. 26	Tail	11.93	0.22	10.50-13.00	25				
	Body	10.48	0.33	9.50-12.00	20	5.12	0.14	4.50- 5.50	15
Feb. 2	Tail	21.20	0.62	18.50-24.50	20	10.56	0.36	9.50-11.50	15
	Body	13.70	0.22	13.00-14.60	20	10.23	0.73	8.00-11.00	13
	Tail	32.87	1.04	28.00-36.00	20	21.90	0.87	18.50-24.00	13
Feb. 10	Hindleg	10.08	1.35	5.00-17.00	20	0.00	0.00	0.00- 0.00	13
	Body	14.56	0.31	13.00-15.00	20	12.80	0.46	11.50-14.00	13
	Tail	31.00	1.00	27.00-35.00	20	31.30	1.53	27.00-35.00	13
	Hindleg	18.90	0.97	12.00-21.00	20	9.42	1.80	2.50-14.00	13
Feb. 17	Foreleg	8.55	1.08	0.00-11.00	20	0.00	0.00	0.00- 0.00	13
	Body	16.88	0.39	16.00-18.00	18	14.58	0.38	13.00-15.50	13
	Tail	0.00	0.00	0.00- 0.00	18	1.30	0.32	1.00- 2.00	13
	Hindleg	25.80	0.70	23.00-29.00	18	21.30	1.08	18.00-24.00	13
Feb. 24	Foreleg	13.44	0.67	11.00-15.00	18	11.08	1.96	0.00-14.00	13
	Body					15.87	0.33	15.00-16.50	13
	Tail					0.00	0.00	0.00- 0.00	13
	Hindleg					24.73	0.99	21.50-27.50	13
Mar. 1	Foreleg					13.40	0.56	11.50-15.50	13

TABLE 5.--Measurements of one group (1a) of lowland Rio Piedras tadpoles cultured at 20°C. $\bar{x}$ refers to the mean length and $2S\bar{x}$ denotes plus and minus twice the standard error of the mean.

Rio Piedras 20°C.(1a)

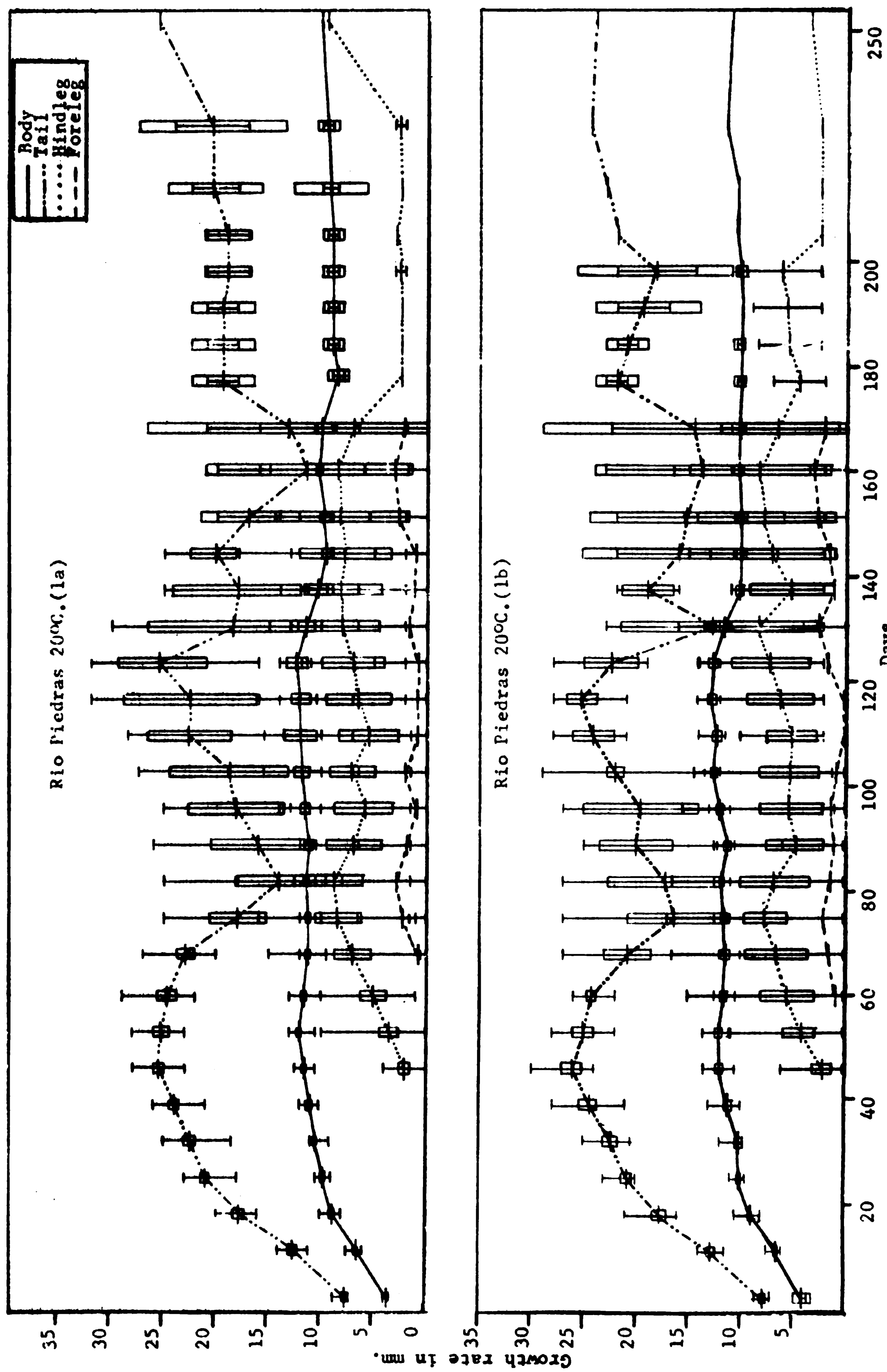
Date		$\bar{x}$	$2S_{\bar{x}}$	Range	No.	Date		$\bar{x}$	$2S_{\bar{x}}$	Range	No.
	Body	3.65	0.76	3.50- 4.00	25		Body	12.43	0.94	11.00-14.00	7
Mar. 28	**Tail**	7.64	0.15	7.25- 8.75	25		Tail	25.28	4.11	16.00-32.00	7
	Body	6.52	0.18	6.00- 7.50	25		Hindleg	6.96	3.04	2.00-12.00	7
Apr. 6	**Tail**	12.38	0.27	11.25-14.00	25	Jul. 28	Foreleg	0.71	1.42	0.00- 5.00	7
	Body	8.81	0.22	8.00-10.00	25		Body	11.50	0.84	10.00-13.00	7
Apr. 13	**Tail**	17.86	0.42	16.00-20.00	25		Tail	18.55	8.20	0.00-30.00	7
	Body	9.85	0.17	9.00-10.50	25		Hindleg	8.00	3.55	2.00-15.00	7
Apr.20	**Tail**	21.08	0.43	18.00-23.00	25	Aug.4	Foreleg	1.64	2.14	0.00- 6.50	7
	Body	10.50	0.17	9.25-11.00	25		Body	10.25	1.02	9.00-12.00	6
Apr. 27	**Tail**	22.42	0.54	18.50-25.00	25		Tail	18.00	6.16	0.00-25.00	6
	Body	10.95	0.22	10.25-12.00	25		Hindleg	8.12	3.78	2.00-14.00	6
May 4	**Tail**	23.94	0.50	21.00-26.00	25	Aug. 11	Foreleg	1.08	2.16	0.00- 6.50	6
	Body	11.68	0.24	10.50-12.50	25		Body	9.65	0.44	9.00-10.00	5
May 11	**Tail**	25.48	0.55	23.00-28.00	25		Tail	20.20	2.50	18.00-25.00	5
	Hindleg	2.07	0.44	0.00- 4.00	25		Hindleg	7.85	4.45	2.00-13.00	5
	Body	11.98	0.26	10.50-13.00	25	Aug. 18	Foreleg	1.00	2.00	0.00- 5.00	5
	Tail	25.20	0.62	23.00-28.00	25		Body	9.69	0.47	9.00-10.00	4
May 18	**Hindleg**	3.48	0.88	0.00-10.00	25		Tail	17.00	4.76	10.00-20.00	4
	Body	11.71	0.25	10.00-13.00	25		Hindleg	8.19	6.32	2.00-14.00	4
	Tail	24.78	0.78	22.00-29.00	25	Aug. 25	Foreleg	2.63	3.04	0.00- 5.50	4
May 25	**Hindleg**	4.98	1.27	1.00-13.00	25		Body	10.25	0.50	10.00-11.00	4
	Body	11.43	0.25	9.50-12.00	24		Tail	11.50	9.66	0.00-20.00	4
	Tail	22.95	0.72	20.00-27.00	24		Hindleg	8.50	6.94	2.00-15.00	4
	Hindleg	7.02	1.78	0.50-15.00	24	Sep. 3	Foreleg	6.00	0.00	6.00- 6.00	4
Jun. 2	**Foreleg**	0.51	0.70	0.00- 7.00	24		Body	10.00	1.14	9.00-11.00	3
	Body	11.43	0.20	10.00-12.00	24		Tail	13.33	13.42	0.00-21.00	3
	Tail	18.00	2.72	1.50-25.00	24		Hindleg	7.00	9.00	2.00-16.00	3
	Hindleg	8.23	2.18	1.00-16.00	24	Sep. 11	Foreleg	2.17	4.32	0.00- 6.50	3
Jun. 9	**Foreleg**	2.30	1.14	0.00- 6.50	24		Body	8.50	1.00	8.00- 9.00	2
	Body	11.46	0.25	10.50-12.50	21		Tail	19.50	3.00	18.00-21.00	2
	Tail	13.90	4.32	0.00-25.00	21		Hindleg	2.50	0.00	2.50- 2.50	2
	Hindleg	8.56	2.53	1.50-18.00	21	Sep. 20	Foreleg	0.00	0.00	0.00- 0.00	2
Jun. 16	**Foreleg**	2.86	1.48	0.00- 8.00	21		Body	9.00	1.00	8.50- 9.50	2
	Body	11.30	0.29	10.50-12.00	15		Tail	19.50	3.00	18.00-21.00	2
	Tail	16.06	4.58	0.00-26.00	15	Sep. 27	Hindleg	2.50	0.00	2.50- 2.50	2
	Hindleg	6.92	2.64	1.50-16.00	15		Body	9.00	1.00	8.50- 9.50	2
Jun. 23	**Foreleg**	1.90	1.44	0.00- 6.50	15		Tail	19.50	3.00	18.00-21.00	2
	Body	11.54	0.48	10.00-13.00	12	Oct. 4	Hindleg	2.50	0.00	2.50- 2.50	2
	Tail	18.13	4.51	1.00-25.00	12		Body	9.00	1.00	8.50- 9.50	2
	Hindleg	5.96	2.74	1.50-14.00	12		Tail	19.00	2.22	17.00-21.00	2
Jun. 30	**Foreleg**	0.96	1.28	0.00- 6.00	12	Oct. 11	Hindleg	2.75	0.50	2.50- 3.00	2
	Body	11.83	0.62	10.00-13.25	12		Body	9.00	1.00	8.50- 9.50	2
	Tail	18.75	5.80	0.00-27.50	12		Tail	19.00	2.22	17.00-21.00	2
	Hindleg	7.12	2.26	1.50-15.50	12	Oct. 18	Hindleg	3.00	0.00	3.00- 3.00	2
Jul. 7	**Foreleg**	2.04	1.74	0.00- 6.50	12		Body	9.25	3.50	8.50-10.00	2
	Body	11.95	1.58	10.00-13.50	9		Tail	20.25	4.50	18.00-22.50	2
	Tail	22.72	3.94	12.00-28.50	9	Oct. 27	Hindleg	2.50	0.00	2.50- 2.50	2
	Hindleg	5.55	2.84	1.50-15.50	9		Body	9.50	1.00	9.00-10.00	2
Jul. 14	**Foreleg**	0.77	1.54	0.00- 7.00	9		Tail	20.50	7.00	17.00-24.00	2
	Body	12.17	0.90	10.50-14.00	9	Nov. 9	Hindleg	2.75	0.50	2.50-3.00	2
	Tail	22.66	6.34	0.00-32.00	9		Body	10.00			1
	Hindleg	6.56	3.09	2.00-16.00	9		Tail	25.50			1
Jul. 21	**Foreleg**	0.77	1.54	0.00- 7.00	9	Dec. 2	Hindleg	9.50			1

TABLE 6.--Measurements of one group (1b) of lowland Rio Piedras tadpoles cultured at 20°C. $\bar{x}$ refers to the mean length and $2S\bar{x}$ denotes plus and minus twice the standard error of the mean.

Rio Piedras 20°C. (1b)

Date		$\bar{x}$	$2S\bar{x}$	Range	No.	Date		$\bar{x}$	$2S\bar{x}$	Range	No.
	Body	3.90	0.80	3.50- 4.00	15		Body	11.67	0.56	11.00-12.50	6
Mar. 28	Tail	7.77	0.21	7.00- 8.50	15		Tail	12.85	8.80	0.00-23.00	6
	Body	6.52	0.20	6.00- 7.50	15		Hindleg	8.38	5.15	2.00-16.00	6
Apr. 6	Tail	12.87	0.32	11.50-14.00	15	Aug. 4	Foreleg	2.25	2.90	0.00- 7.00	6
	Body	8.82	0.33	8.00-10.50	15		Body	10.25	0.50	10.00-11.00	4
Apr. 13	Tail	17.80	0.61	16.00-21.00	15		Tail	19.00	2.50	16.00-22.00	4
	Body	10.03	0.23	9.50-11.00	15		Hindleg	5.13	4.13	2.00-11.00	4
Apr. 20	Tail	20.70	0.53	20.00-23.00	15	Aug. 11	Foreleg	1.00	2.00	0.00- 4.00	4
	Body	10.07	0.33	9.75-12.00	15		Body	10.13	0.25	10.00-10.50	4
Apr. 27	Tail	22.43	0.72	20.50-25.00	15		Tail	16.00	9.40	2.00-22.00	4
	Body	11.18	0.38	10.00-13.00	15		Hindleg	7.00	6.10	2.00-15.00	4
May 4	Tail	24.40	0.90	21.00-28.00	15	Aug.18	Foreleg	1.50	3.00	0.00- 6.00	4
	Body	11.86	0.37	10.50-13.50	15		Body	10.06	0.51	9.50-10.75	4
	Tail	26.00	0.97	24.00-30.00	15		Tail	15.25	9.20	0.00-22.00	4
May 11	Hindleg	1.96	0.92	0.00- 6.00	15		Hindleg	7.75	6.61	2.00-15.50	4
	Body	12.03	0.38	11.00-13.50	15	Aug.25	Foreleg	2.63	3.20	0.00- 6.50	4
	Tail	25.06	0.94	22.00-28.00	15		Body	10.38	0.48	10.00-11.00	4
May 18	Hindleg	3.95	1.84	0.00-11.00	15		Tail	13.75	10.26	0.00-23.00	4
	Body	11.70	0.28	10.50-12.50	15		Hindleg	8.25	6.76	2.00-16.50	4
	Tail	24.33	0.70	22.00-26.00	15	Sep. 3	Foreleg	6.00	0.00	5.00- 7.00	4
	Hindleg	5.42	2.60	0.00-15.00	15		Body	10.33	0.66	10.00-11.00	3
May 25	Foreleg	0.33	0.66	0.00- 5.00	15		Tail	14.50	14.52	0.00-22.50	3
	Body	11.42	0.46	10.00-12.00	15		Hindleg	6.50	5.80	2.00-12.00	3
	Tail	20.76	2.28	10.00-27.00	15	Sept. 11	Foreleg	2.00	4.00	0.00- 6.00	3
	Hindleg	6.53	3.06	0.00-16.50	15		Body	10.25	0.50	10.00-10.50	2
Jun. 2	Foreleg	1.55	1.38	0.00- 7.00	15		Tail	22.00	2.00	21.00-23.00	2
	Body	11.66	0.23	11.00-12.50	15	Sept. 20	Hindleg	4.50	5.00	2.00- 7.00	2
	Tail	16.43	4.96	0.00-27.00	15		Body	10.25	0.50	10.00-10.50	2
	Hindleg	7.62	2.14	0.00-17.00	15		Tail	21.00	2.00	20.00-22.00	2
Jun. 9	Foreleg	1.90	1.54	0.00- 7.00	15	Sept. 27	Hindleg	5.50	6.00	2.50- 8.50	2
	Body	11.75	0.26	11.00-12.50	13		Body	10.00	0.00	10.00-10.00	2
	Tail	17.15	5.54	0.00-27.00	13		Tail	19.50	5.00	17.00-22.00	2
	Hindleg	6.71	3.40	0.00-16.50	13	Oct. 4	Hindleg	5.75	6.50	2.50- 9.00	2
Jun. 16	Forelge	1.38	1.46	0.00- 7.00	13		Body	10.25	0.50	10.00-10.50	2
	Body	11.43	0.35	10.50-12.25	10		Tail	18.25	7.50	14.50-22.00	2
	Tail	19.95	3.50	6.00-25.00	10	Oct. 11	Hindleg	6.25	7.50	2.50-10.00	2
	Hindleg	4.70	2.72	0.00-12.50	10		Body	10.50			1
Jun. 23	Foreleg	1.05	1.40	0.00- 5.25	10		Tail	22.00			1
	Body	12.15	0.45	11.00-13.00	10	Oct. 18	Hindleg	2.50			1
	Tail	19.50	5.52	0.00-27.00	10		Body	10.50			1
	Hindleg	5.38	3.24	1.00-15.50	10		Tail	23.00			1
Jun. 30	Foreleg	1.30	1.74	0.00- 7.00	10	Oct. 27	Hindleg	2.50			1
	Body	12.59	0.46	12.00-13.50	8		Body	11.50			1
	Tail	22.00	6.60	0.00-29.00	8		Tail	24.50			1
	Hindleg	5.25	3.00	1.25-14.50	8	Nov. 9	Hindleg	2.50			1
Jul. 7	Foreleg	0.81	1.62	0.00- 6.50	8		Body	11.00			1
Jul. 7	Body	12.43	0.63	11.50-14.00	7		Tail	24.00			1
	Tail	24.14	2.11	21.00-28.00	7	Dec. 2	Hindleg	3.50			1
Jul. 14	Hindleg	5.14	2.46	2.00-10.00	7		Body	10.50			1
	Body	12.82	0.58	12.00-14.25	7		Tail	24.00			1
	Tail	25.28	1.73	21.00-28.00	7	Dec. 16	Hindleg	6.00			1
Jul. 21	Hindleg	6.21	3.25	2.00-13.00	7						
	Body	12.68	0.66	12.00-14.25	7						
	Tail	22.43	2.68	19.00-28.00	7						
	Hindleg	7.18	3.72	2.00-14.00	7						
Jul. 28	Foreleg	1.70	2.20	0.00- 6.00	7						

Figure 4.--Growth rate of two groups (1a and 1b) of lowland Rio Piedras tadpoles cultured at 20°C. The horizontal line represents the mean of the sample; the vertical line, the range; and the box, plus and minus twice the standard error of the mean.


Rio Piedras 20°C.(1a)
Rio Piedras 20°C.(1b)
Body
Tail
Hindleg
Foreleg
Growth rate in mm.
Days
35
30
25
20
15
10
5
0
20
40
60
80
100
120
140
160
180
200
250

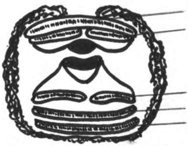


Figure 5. Tooth morphology of *Leptodactylus albilabris* tadpole.

ditions and the lowland population is affected at the reduced temperature.

Relationship of Appendage Growth to Body Length.--Table 7 expresses the differential changes that developed between the body and its appendages; namely, the tail, hind legs and fore legs. These data were derived by dividing the maximum weekly mean body length into the maximum weekly mean length of the appendage being measured, in an effort to ascertain any differences thatmay have developed between the populations during the developmental period. The data, thusly treated, revealed the following information.

(1) In their natural environmental temperature conditions, the lowland population indicated a ratio of tail-length to body-length 0.32 lower than that of the montane population.

(2) The lowland population maintained a more or less constant proportion between body and tail-lengths at both temperatures.

(3) The montane population decreased its proportion of tail to body-lengths by 0.44 when cultured at 30°C.

(4) The length of the hind leg to that of the body-length of both the montane population and the lowland population at their native temperature conditions share a common ratio of 1.35.

(5) The ratio of hind leg and body-lengths of the lowland population, at reversed temperature (20°C.), is reduced by one-half.

TABLE 7.--A comparison of the maximum weekly growths between body-lengths and appendage-lengths of *Leptodactylus albilabris* tadpoles from El Yunque and Rio Piedras when reared at 20°C. and 30°C.

Location			Maximum weekly mean	$2S\bar{x}$	Range	No.	Maximum length	Appendage/ Body ratio	Char.
El Yunque	20°C.	(1a)	15.92	0.48	13.00-17.00	19	17.80		
El Yunque	20°C.	(1b)	15.54	0.35	14.00-16.25	14	18.00		
Rio Piedras	30°C.	(2a)	14.53	0.27	13.50-16.00	24	16.00		
Rio Piedras	30°C.	(2b)	14.36	0.33	13.50-15.00	15	15.00		
									Body
El Yunque	30°C.	(2a)	16.88	0.39	16.00-18.00	18	18.00		
El Yunque	30°C.	(2b)	15.87	0.33	15.00-16.50	13	16.50		
Rio Piedras	20°C.	(1a)	12.43	0.94	11.00-14.00	7	14.00		
Rio Piedras	20°C.	(1b)	12.82	0.58	12.00-14.25	7	14.25		
El Yunque	20°C.	(1a)	39.26	1.34	32.00-43.00	19	45.00		
El Yunque	20°C.	(1b)	36.25	1.29	30.00-40.00	14	40.00	2.40	
Rio Piedras	30°C.	(2a)	30.80	0.64	28.00-34.00	24	34.00		
Rio Piedras	30°C.	(2b)	29.70	0.77	28.00-33.00	15	33.00	2.08	
									Tail
El Yunque	30°C.	(2a)	32.87	1.04	28.00-36.00	20	36.00		
El Yunque	30°C.	(2b)	31.30	1.53	27.00-35.00	13	35.00	1.96	
Rio Piedras	20°C.	(1a)	25.48	0.55	23.00-28.00	28	32.00		
Rio Piedras	20°C.	(1b)	26.00	0.97	24.00-30.00	15	30.00	2.04	
El Yunque	20°C.	(1a)	20.13	5.34	0.00-28.00	12	28.00		
El Yunque	20°C.	(1b)	22.20	3.02	15.00-28.00	9	28.00	1.35	
Rio Piedras	30°C.	(2a)	20.42	0.83	14.00-24.00	24	24.00		
Rio Piedras	30°C.	(2b)	18.86	0.60	17.00-20.00	15	20.00	1.35	
									Hindleg
El Yunque	30°C.	(2a)	25.80	0.70	23.00-29.00	18	29.00		
El Yunque	30°C.	(2b)	24.73	0.99	21.50-27.50	13	27.50	1.56	
Rio Piedras	20°C.	(1a)	8.56	2.53	1.50-18.00	21	18.00		
Rio Piedras	20°C.	(1b)	8.38	5.15	2.00-16.00	6	17.00	0.67	
El Yunque	20°C.	(1a)	8.29	2.30	0.00-11.50	12	11.50		
El Yunque	20°C.	(1b)	9.17	0.90	7.00-10.50	9	11.00	0.55	
Rio Piedras	30°C.	(2a)	8.20	0.37	7.00-10.00	24	10.00		
Rio Piedras	30°C.	(2b)	7.82	0.36	7.00- 9.00	15	9.00	0.55	
									Foreleg
El Yunque	30°C.	(2a)	13.44	0.67	11.00-15.00	18	15.00		
El Yunque	30°C.	(2b)	13.40	0.56	11.50-15.50	13	15.50	0.82	
Rio Piedras	20°C.	(1a)	6.00	0.00	6.00- 6.00	4	8.00		
Rio Piedraw	20°C.	(1b)	6.00	0.00	5.00- 7.00	4	7.00	0.48	

(6) At reversed temperature (30°C.), the El Yunque population increases its proportion of hind leg-length to body-length by 0.21.

(7) When these two populations are cultured at reverse temperature conditions, the ratios of hind leg to body-lengths and foreleg to body-lengths of the lowland population is approximately one-half that of the montane population.

(8) The length of the foreleg to that of the body-length of both the montane population and the lowland population share a common ratio of 0.55.

(9) At reversed temperature (30°C.), the El Yunque population increases its proportion of foreleg to body-length by 0.27.

(10) At reversed temperature (20°C.), the lowland population decreases its proportion of foreleg to body-length by 0.07.

Allen's Rule states that protruding body parts, such as tail, ears, bill extremities, and so forth, are relatively shorter in the cooler parts of the range of a species than in the warmer parts. The data, when subjected to this interpretation, indicates that the Rule is maintained by four of the ratios measured. Specifically, they are:

(1) Increased hindleg to body proportion of the montane population cultured at 30°C.

(2) Reduced hindleg to body proportion of the lowland population cultured at 20°C.

(3) Increased foreleg to body proportion of the montane population cultured at 30°C.

(4) Reduced foreleg to body proportion of the lowland population cultured at 20°C.

On the other hand, Allen's Rule is not maintained with respect to the larger tail to body proportion of the montane population as compared to that of the lowland population. Futhermore, the Rule appeared to be inconsequential when comparing the hindleg to body proportion and foreleg to body proportion when both populations are cultured at their native temperature conditions.

Comparison of Developmental Stages

Gosner (1960) charted the developmental stages of larval development on the basis of the presence or absence of conspicuous features in varying degrees of noticeable changes. The criteria utilized by Gosner (*op. cit.*) were employed during this study to compare the growth patterns of the lowland and highland populations of *Leptodactylus albilabris* larvae. The stages, used herein, are listed below with their associated distinguishing features.

Stages 17-21: based on the development of the oral suckers.

Stage 22: tail fins become transparent and circulation begins.

Stage 23: oral disc and labial tooth-rows begin to differentiate.

Stages 23-25: development of operculum and consequent disappearance of external gills.

Stage 25: spiracle present on left side.

Stages 26-30: length/diameter relationship of the developing limb-bud.

Stages 31-37: development of toes.

Stages 38-40: proportional changes in the length of individual toes and the appearance of metatarsal and subarticular tubercles.

Stage 41: disappearance of cloacal tail piece.

Stage 42: appearance of forelimbs.

Stages 43-46: identified by metamorphosis of the head indicated by changes in the mouth.

Samples selected at random from each population were examined and their stages ascertained (Table 8). The following are some observations that were made:

(1) At stage 26, the montane population is 1.97 times larger in body and 2.3 times larger in tail length than the lowland.

(2) At stage 27, the montane population is 1.75 times larger in body and 2.07 times larger in tail length than the lowland.

(3) At stage 31, the montane population is 1.50 times larger in body and 1.75 times larger in tail length than the lowland.

(4) At stage 36, the montane population is 1.45 times larger in body and 1.79 times larger in tail length than the lowland.

TABLE 8.--A comparison of measurements at similar larval stages of Leptodactylus albrilabris collected from Rio Piedras and El Yunque.

Stage	Body Length $\bar{x}$	Body Length range	Tail Length $\bar{x}$	Tail Length range	Total Length $\bar{x}$	Total Length range	No.
			El Yunque				
24	6.31	5.50- 8.00	10.44	9.75-11.50	16.75	15.25-19.50	4
25	7.81	6.50- 9.50	12.25	9.00-20.00	20.06	16.00-19.50	12
26	11.10	8.25-13.25	17.67	11.00-22.00	28.77	20.00-35.00	35
27	11.54	8.50-14.50	18.40	12.50-23.00	29.94	21.00-44.75	60
28	12.35	7.50-16.00	19.96	14.00-28.50	32.31	23.00-44.50	51
29	13.27	11.50-14.75	21.30	15.00-25.00	34.57	25.50-37.50	10
20	13.12	12.50-14.00	22.08	21.00-23.00	35.20	34.00-37.00	6
31	13.17	12.50-15.00	21.33	20.00-23.00	34.50	32.50-37.00	9
32	13.37	13.00-13.75	21.50	20.00-23.00	34.87	33.00-36.75	2
33	13.19	12.50-14.00	21.17	18.50-23.50	34.36	31.00-37.25	9
34	13.25	13.25	21.50	21.50	34.75	34.75	1
35	13.75	13.75	24.25	24.25	38.00	38.00	1
36	13.75	10.00-15.00	23.66	22.00-25.00	37.41	33.00-40.00	6
37	14.50	14.00-15.00	24.87	24.75-25.00	39.37	39.00-39.75	2
38	15.12	14.75-15.50	24.75	24.50-25.00	39.87	39.75-40.00	2
39	14.87	14.00-16.00	23.75	17.50-29.00	38.62	33.00-44.50	16
40	14.10	13.00-15.00	24.00	22.00-27.00	38.10	35.00-41.00	13
41	13.80	11.50-16.00	24.20	21.50-26.00	38.00	34.00-42.00	5
42	13.62	13.00-14.25	27.00	27.00-27.00	40.62	40.00-41.25	2
43	13.87	13.00-15.00	24.87	22.00-28.50	38.74	35.00-42.00	4
			Rio Piedras				
26	5.63	5.00- 5.50	7.61	7.00-10.00	13.24	12.00-16.25	11
27	6.60	5.75- 8.25	8.88	7.00-11.50	15.48	12.50-21.25	44
28	7.45	6.00- 8.25	10.20	8.00-12.50	17.65	14.50-20.25	23
29	8.40	7.00- 9.00	11.58	9.50-13.00	19.98	16.50-22.00	20
30	8.50	8.00- 9.50	11.60	10.00-13.50	20.10	17.50-22.50	12
31	8.70	7.50- 9.50	12.19	10.00-14.00	20.89	17.50-23.50	8
32	8.80	8.00-10.00	11.90	10.00-15.00	20.70	18.00-25.00	8
33	8.85	8.00- 9.50	12.20	10.50-13.50	21.05	19.50-23.00	10
34	9.21	8.25-10.25	12.96	11.50-15.25	22.17	20.00-25.25	6
35	9.30	8.75-10.75	12.00	10.00-14.25	21.30	18.00-25.00	5
36	9.46	8.00-11.50	13.20	11.00-16.50	22.66	19.00-28.00	13
37	10.00	10.00	16.00	16.00	26.00	26.00	1
38	10.44	9.25-12.00	15.00	13.00-17.00	25.44	24.00-29.00	4
39	11.60	11.00-12.00	17.20	14.50-19.00	28.80	26.00-30.75	9
40	13.00	13.00	14.00	14.00	27.00	27.00	1

(5) At stage 39, the montane population is 1.28 times larger in body and 1.37 times larger in tail length than the lowland.

(6) At stage 40, total length diminishes through resorption of the tail, and larval mouth parts begin to break down.

On the basis of these comparisons, at comparable stages, the montane tadpoles are longer in both body and tail measurements than those from the lowland habitat.

Comparison of Tooth Morphology

A tadpole acquires rows of teeth during its period of early development and loses them during the period of metamorphosis.

The standard tooth morphology of the *Leptodactylus albilabris* tadpole (Figure 6) exhibits two upper tooth rows (1 and 2) with a median space on the second upper row, and three tooth rows (3, 4, and 5) below the mandibles with a smaller median space on the first lower row.

Table 9 summarizes the conditions of tooth row numbers at the various developmental stages within the two populations of larvae studied.

A "typical" tooth row is one with a continuous series of teeth present; "poorly developed" refers to the presence of a ridge or part of it with labial teeth discontinuous; and "absent" denotes no ridge or labial teeth.

samples of Rio Piedras and El Yunque populations of *Leptodactylus albilabris* tadpoles.

TABLE 9.--A comparison of the relationship of tooth morphology to developmental stages of samples of Rio Piedras and El Yunque populations of _Leptodactylus albilabris_ tadpoles.

Tooth row no.	Condition	Loc.	Stages 24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1	Typical	R.P.	--	--	7	42	17	17	10	5	7	9	5	4	10	1	3	8	1	--	--	--
		E.Y.	0	6	34	54	48	10	6	9	2	6	1	1	5	2	2	13	6	2	0	0
	Poorly dev.	R.P.	--	--	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	--	--	--
		E.Y.	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	3	1	1	1
	Absent	R.P.	--	--	4	2	6	3	2	3	1	1	1	1	3	0	1	1	0	--	--	--
		E.Y.	4	5	1	5	1	0	0	0	0	3	0	0	1	0	0	3	4	2	1	3
2	Typical	R.P.	--	--	9	42	20	17	11	6	7	9	5	5	13	1	3	9	1	--	--	--
		E.Y.	0	10	35	58	51	10	6	9	2	6	1	1	6	2	2	15	9	3	0	1
	Poorly dev.	R.P.	--	--	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	--	--	--
		E.Y.	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
	Absent	R.P.	--	--	1	1	2	2	1	2	1	1	1	1	0	0	1	0	0	--	--	--
		E.Y.	4	0	0	1	0	0	0	0	0	3	0	0	0	0	0	1	3	2	1	3
3	Typical	R.P.	--	--	10	44	23	19	12	7	8	10	6	5	13	1	4	9	1	--	--	--
		E.Y.	1	12	35	59	51	10	6	9	2	6	1	1	6	2	2	16	10	3	0	1
	Poorly dev.	R.P.	--	--	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	--	--	--
		E.Y.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
	Absent	R.P.	--	--	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	--	--	--
		E.Y.	3	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	2	2	1	3
4	Typical	R.P.	--	--	7	43	20	19	12	6	8	10	6	4	12	1	4	9	1	--	--	--
		E.Y.	0	8	35	56	50	10	6	9	2	6	1	1	6	2	2	15	7	3	0	0
	Poorly dev.	R.P.	-	-	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	--	--	--
		E.Y.	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0
	Absent	R.P.	--	--	4	1	1	1	0	1	0	0	0	1	1	0	0	0	0	--	--	--
		E.Y.	3	3	0	3	0	0	0	0	0	3	0	0	0	0	0	1	2	2	1	4
5	Typical	R.P.	--	--	6	41	21	18	12	7	8	10	6	4	11	1	4	8	1	--	--	--
		E.Y.	0	4	34	54	48	9	6	9	2	6	1	1	5	2	2	13	5	3	0	0
	Poorly dev.	R.P.	--	--	1	0	2	0	0	0	0	0	0	0	1	0	0	1	0	--	--	--
		E.Y.	0	3	0	3	2	0	0	0	0	0	0	0	1	0	0	2	5	0	1	0
	Absent	R.P.	--	--	4	3	0	2	0	1	0	0	0	1	1	0	0	0	0	--	--	--
		E.Y.	4	5	1	3	1	1	0	0	0	3	0	0	0	0	0	0	1	2	1	4
Total no. examined		R.P.	0	0	11	44	23	20	12	8	8	10	6	5	13	1	4	9	1	0	0	0
		E.Y.	4	12	35	60	51	10	6	9	2	9	1	1	6	2	2	16	13	5	2	4

The pattern of tooth rows and mandibles in the montane population is essentially the same as those in the lowland. However, abnormalities of labial teeth as illustrated by "poorly developed" and "absent" develop more frequently by the lowland sample in the earlier stages of development. For instance, at stage 26 the lowland tadpoles have 27% abnormal conditions as compared to the 3% exhibited by the montane group, whereas, at stage 39 the montane tadpoles have a slightly larger tooth abnormality (19%) as compared to the lowland group with 14%.

The early abnormality of the lowland tadpoles may be due to a combination of rapid growth and ease of injury to the smaller teeth as compared to the montane adaptation of larger teeth for swift running streams and a longer tadpole phase.

DISCUSSION

An important phase of adaptation is the development of morphological or physiological adjustments of animals to meet new environments. These adaptations have a hereditary basis and are subject to selection.

The constancy of some obviously important features are maintained by these adjustments of the organism. More generally, however, the adaptations increase the likelihood of survival for the individual in question; the adaptive adjustments necessary for survival may bring about marked alterations in the appearance of the individual or in physiological processes vital for its continued survival.

The genetic changes that comprise the fundamental adaptive responses of a population are not always easily visualized. The anatomical adaptations and growth rates of the two populations of *Leptodactylus albilabris* illustrate the fact that adaptation to a cooler temperature and higher altitude is accomplished by the modification of existing structures and difference in growth rate.

The montane tadpoles developed larger and less abnormal teeth, possibly an adjustment for feeding in swift streams. Futhermore, they expressed a more rapid rate of development at experimental temperatures approximating that of their environment that did the lowland population at the same low experimental temperature. The montane population sample developed very rapidly and transformed a few days later than the lowland population sample at the temperature approximating that of the lowland.

Burgess (1950) studied the development of Spade-foot toad larvae (Scaphiopus hammondii) under laboratory conditions and found an acceleration of growth due to higher temperature. Volpe (1958) proposed a hypothesis that the relatively rapid rates of embryonic development in toads are correlated with the limited period of time available for larval growth in temporary pools. However, temperature apparently plays an important role in affecting growth rates as indicated by the data obtained in this study.

Temperature has a fundamental effect on size and growth as suggested by the fact that most poikilotherms grow larger when raised at low temperatures than at higher temperatures and populations of the same species are larger from colder environments.

MacArthur and Baillie (1929), Imai (1937), and Ryan (1941) studied the response of animals to temperature and suggested that there is a shift in the anabolic-catabolic balance at different temperatures. Bullock (1955) and Prosser (1955) found that northern species maintain a higher metabolic rate at low temperatures than do related southern species. Wimpenny (1940), Newell (1949), and Dunbar (1953) described this size-temperature relationship as "delayed ontogeny."

Bergmann's and Allen's Rules are closely related to size and temperature. According to Mayr (1942), Bergmann's Rule states "the smaller-sized geographic races of a species are found in the warmer parts of the range, the larger sized races in the cooler districts."

Bergmann's principle is expressed by the lowland and highland populations cultured at their respective temperatures approximating their environment (Table 7). The montane population showed an increase in body length of 8.86% over the lowland population. At reversed temperature, the montane population body-length is increased by 4.2% and the body-length of the lowland group is reduced by 14.4%.

Carter (1961) has suggested that, probably, the most important general advantage of large over small size is the greater independence from the external environment which larger size allows. Protoplasm characteristically requires uniform maintenance of internal conditions unlike those of the exterior. The surface-volume ratio is less in large bodies than in similar smaller ones; hence, the proportion of living tissues in contact with the external environment is less in larger than in smaller animals.

The montane population showed superior survival characteristics as compared with the lowland population when the two groups were reared under reversed temperature conditons. The upland animals acquired a larger body in disregard to Bergmann's Rule and also developed longer appendages, contrary to expectation in keeping with Allen's Rule. The single apparent exception to this phenomenon was expressed by the tail reduction of the montane population. The data indicate, therefore, that the battle for survival in the more hazardous montane ecological location was advantageous to developing a population better equipped than the lowland population. The ratios of appendages to body-lengths were constant for both populations at their natural environmental temperatures.

The total larval developmental period, when compared at normal and experimental temperatures, revealed additional substantiary data. The montane population approximated favourably the length of the developmental period of the lowland population when the culture temperatures were reversed. On the other hand, the lowland population at 20°C. (the montane temperature) did not respond in a similar fashion. The survival inferiority of this population, perhaps, did not make for easy adaptation.

SUMMARY AND CONCLUSIONS

(1) Larvae from both lowland Rio Piedras and montane El Yunque populations of *Leptodactylus albilabris* were subjected to normal and experimental temperatures.

(2) Field collections of both population larvae supplement the study of tooth morphology and measurements at similar stages.

(3) Comparison of the normal developmental rate of larvae from the lowland at 30°C. and montane at 20°C. reveals that the latter developed much slower and transformation took place in about 111 days as compared to the lowland at 25 days.

(4) At reverse temperatures, the montane population takes 30.5 days, whereas the lowland population takes 252 days to transform into adult.

(5) At normal temperatures, the montane population develops longer body, tail, hind and forelegs than the lowland population.

(6) At reverse temperatures, the montane population continues to develop longer body, hind and forelegs, whereas there is a decrease in body, tail, hind and forelegs of the lowland population.

(7) Field collections reveal that at similar stages, the montane population is bigger in body, tail, hind and forelegs.

(8) The pattern of tooth rows and mandible in the montane population is essentially the same as those of the lowland population.

The analysis of the data, presented herein, provides the basis for the following conclusions:

(1) At normal temperatures, the lowland population develops more rapidly due to the higher temperature which occurs there as compared to the lower temperature condition of the montane population.

(2) A rise in temperature is followed by hastened metamorphosis, whereas a decrease in temperature has a retarding effect on metamorphosis.

(3) The rate of development of tadpoles from the montane region is less affected by a change in temperature than that of the lowland population.

(4) Selection for increasing size may be inferred to be the result of the statistical advantage that slightly superior bulk gives the montane population a wider range of temperature conditions.

(5) The conspicuous difference in growth rate is highly interesting in that is suggests an adaptation of the montane population for the lower temperature which occurs there.

(6) From the standpoint of evolution, this adaptive change is accumulative in the sense that it may not appear until the montane population has been subjected to the existing lower temperature for several generations.

(7) The pattern of tooth rows and mandible is essentially the same for both populations.

(8) Experimentation has provided evidence which does not point convincingly towards recognizing the two populations as distinct subspecies.

(9) Both populations are members of the same species. Some time ago, rather recently in terms of evolutionary chronology, migration occurred and the montane population developed peculiar morphological characteristics in the process of adaption to the new habitat. Should isolation continue it is feasible that speciation would occur.

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