RESTING METABOLIC RATE AND ITS ADAPTIVE SIGNIFICANCE IN THE COTTON RAT, *SIGMODON*

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ABSTRACT

RESTING METABOLIC RATE AND ITS ADAPTIVE SIGNIFICANCE IN THE COTTON RAT, *SIGMODON*.

by James R. Bowers

The resting metabolic rates were measured and analyzed from five species of cotton rats, *S. alleni*, *S. fulviventer*, *S. leucotis*, *S. ochrognathus* and *S. hispidus*. In all, 103 specimens were studied by means of open-circuit indirect calorimetry modified from Depocas and Hart (1957) and Brown (1968).

The measured resting metabolic rates were compared to determine the amount of individual variation (between individuals of the same species from a single locality), geographic variation (among samples of the same species from different localities), and interspecific variation (between samples of different species).

The resting metabolic rate of two laboratory populations, *S. h. toltecus* and *S. ochrognathus*, were statistically distinct from each other and all other laboratory populations. Those populations not statistically distinguishable, demonstrated a resting metabolic rate that was weight dependent in accordance with the work of Brody (1945) and Kleiber (1961).

Variation from the expected resting metabolic rate, that is observed in the xerophylic species, *S. ochrognathus*, follows expectations when environmental influence is considered. Low metabolism seems to

give this species a selective advantage by allowing it to maintain a lower body temperature, a reduction in energy necessary to maintain basal level, greater water preservation and a greater reproductive potential.

The hydrophylic subspecies, *S. h. toltecus*, due to excessive available energy in the form of food, reduced necessity for activity and proximity of water for intake and cooling is thought to demonstrate a high metabolism due to the lack of necessity for physiological control.

It is indicated that genetic differences between populations cause divergent standard energy production regardless of the immediate environmental conditions. Metabolism as an index, in some cases, seems to measure a local type adaptation, indicating that metabolism in the case of *Sigmodon* is an ecotypic phenomenon.

RESTING METABOLIC RATE AND ITS ADAPTIVE SIGNIFICANCE IN THE COTTON RAT, SIGMODON.

By

James R. Bowers

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I. INTRODUCTION

A. Purpose

Mammals respond in two ways in withstanding the stresses exerted upon them in their environments. The first response is behavioral, in which the animal may try to avoid the stress or perhaps seek a physical means to allay it. The second response to the stress is by concomitant changes in some or many functions of the animal's physiology. By choosing and studying one physiological function it should be possible to evaluate its adaptive significance and how it affects the survival of a particular animal population in its environment. Also it should be possible to compare and contrast particular populations of mammals (within and between species) subjected to varying environmental stresses, with respect to one physiological parameter.

Although a great deal of recent information is available concerning the adaptation of homeotherms to their environment, the bulk of this information deals with animals that have developed highly specialized mechanisms to allow them to survive in extreme environmental conditions. The less noticeable differences that occur between related populations occupying different habitats have been mostly unstudied. Such investigations have great potential not only in demonstrating how selective pressures in the environment act upon a species to produce an adapted phenotype but also in showing how the adaptations acquired by a species may allow them to live in diverse climatic zones.

Metabolic differences observed between congeneric groups of mammals have been given two kinds of explanations. According to the first explanation, genetic differences between species in the same genus will cause divergent standard energy production regardless of the immediate environmental conditions surrounding the experimental animals. The second explanation is that all quantitative differences in standard energy production are functions of the influence exerted on an individual and the population by the immediate environment. By measuring and comparing the metabolic rate (the integral portion of the standard energy production) of selected samples of cotton rats of the genus *Sigmodon*, this study will assist in demonstrating the validity of the initial hypothesis. By resting metabolic rate for the homeothermic cotton rat is meant its rate of metabolism within the region of thermoneutrality when the animal is quiet (following Brown, 1968, and modified from Scholander *et al*., 1950).

Cotton rats of the genus *Sigmodon* are excellent mammals to use in congeneric comparative experiments. The *Sigmodon fulviventer*-group has four species which are located in diverse habitat types in southwestern North America, while the *Sigmodon hispidus*-group has a single wide-ranging species, which occurs in many of the habitat types also occupied by representatives of the *S. fulviventer*-group (see Figure 1). This study compares representatives of five geographically-separated populations of *S. hispidus* and representatives of each of the four species belonging to the *S. fulviventer*-group with respect to resting metabolic rate (see Figure 1 and Figure 2).

B. Literature Review

Metabolism varies among species of small mammals as indicated by the work of Morrison (1948), Hatfield (1939), Cook and Hannon (1954), Benedict and Lee (1936), Lee (1939, 1940) and Benedict and Petrik (1930).

Figure 1. Geographic distribution of the two major groups of the cotton rat, *Sigmodon*.

S. *fulviventer*-group ----- ▨

S. *hispidus*-group -------- ▧

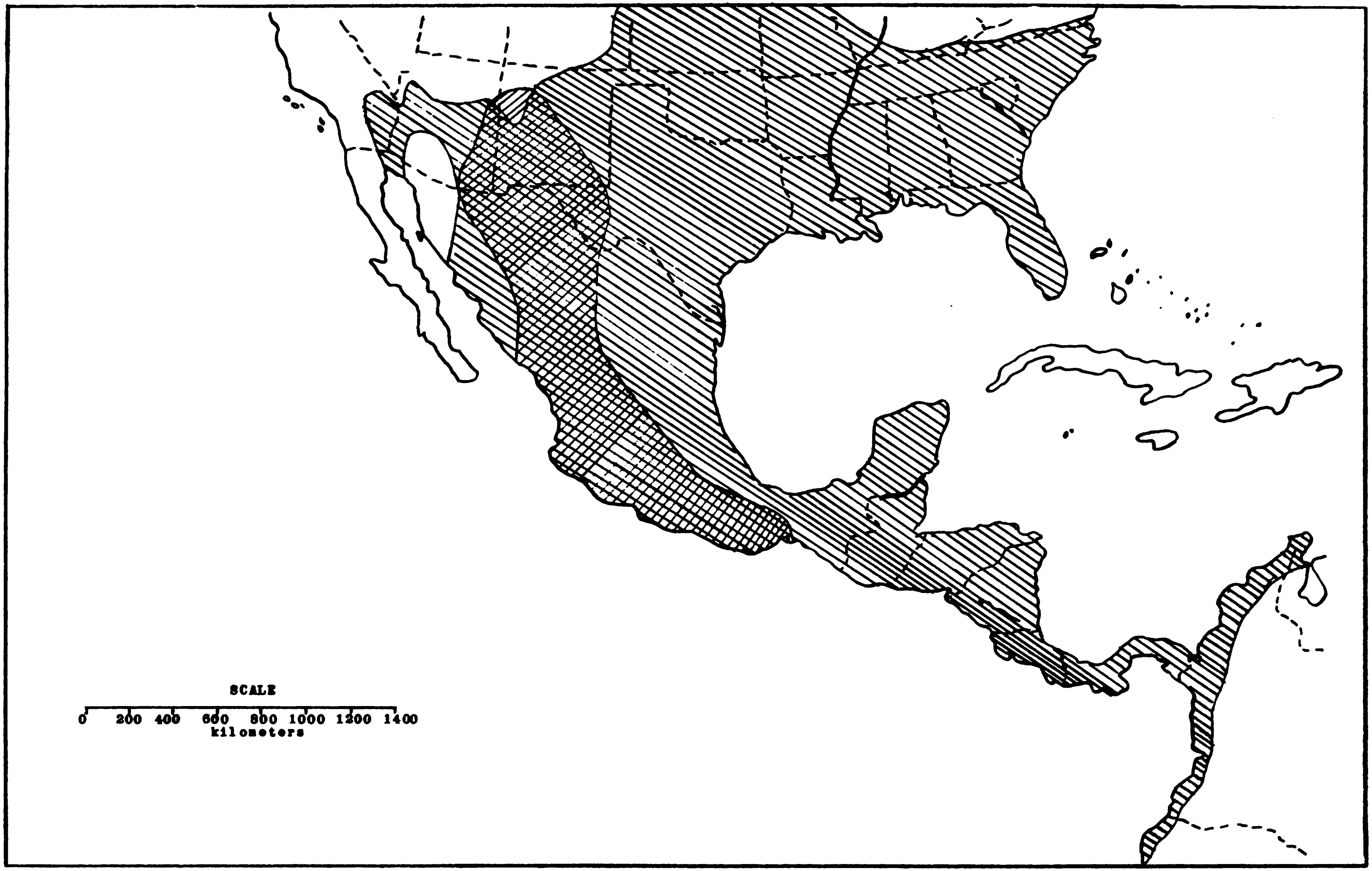

Figure 1.

Figure 2. Geographic distribution of species within the *Sigmodon fulviventer*-group.

S. *fulviventer* ------ ▧

S. *leucotis* --------- ▨

S. *alleni* ----------- ▤

S. *ochrognathus* ----- ░

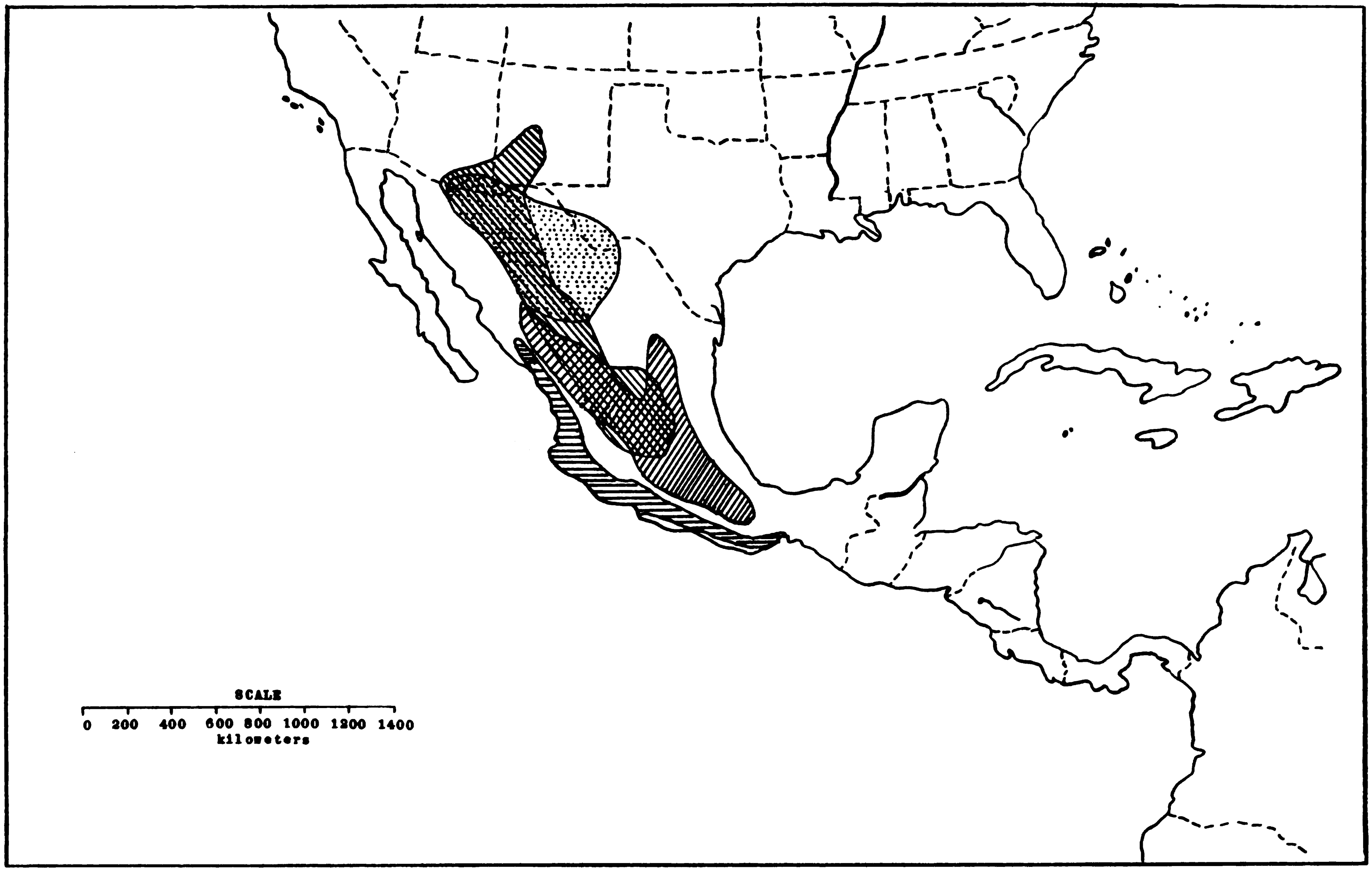

Figure 2.

Pearson (1947, 1948) noted that among animals of different species but of the same weight range there was wide variation in metabolic rate, and thus felt metabolism was not closely associated with taxonomic, ecological or anatomical factors. Cook and Hannon (1954) found that metabolic variations within a species could be identified when the species was segregated according to geographical subspecies.

The rate of oxygen consumption is influenced by activity, temperature, nutrition, body size, season and time of day as well as previous oxygen experience and genetic background (Prosser and Brown, 1962). Keeping other variables constant, Brody (1945) suggests the use of a power function of body weight, BMR (Cal/day)= $70.5 W^{0.7}$ (W = body weight in Kg), as a general reference for making inter- and intraspecific comparisons of basal metabolic rate. It has been shown by Morrison (1948) that this relation pertains to rodents. Kleiber (1961) also suggests the use of a power function of body weight, BMR (Cal/day) = $70 W^{0.75}$ (W = body weight in Kg), to make the same general reference.

Variables inherant in the differential laboratory treatment of experimental animals may affect their metabolism. For instance, the ingestion of protein may elevate the expenditure of energy from the basal level of a mammal by 15-40 percent, while the specific dynamic action for fat is about 12 percent basal elevation and for carbohydrate it is about 5 percent (Hoar, 1966).

In some instances acclimatization to different altitudes has been thought to alter metabolism. In mammals gradual acclimatization at high altitude results in increased oxygen capacity of the blood due to increase in the number of circulating erythrocytes, increased myoglobin and an increased cardiac output (Murie, 1961; Mitchell and Edman, 1951).

However, either no metabolic changes or only a slightly reduced oxygen consumption has been found in tissues from animals acclimated to high altitudes (Ullrich, 1956).

The environmental temperature of an animal would affect the animal directly, only by changing the body temperature in accordance with the environment, if it were outside the thermoneutral zone of the animal. A change in body temperature arising in this way would alter the metabolism of the animal. It would be expected that an animal from an area with high environmental mean temperature has a lower metabolic rate than an animal from an area with low environmental mean temperature (Sullivan and Mullin, 1954).

Metabolic studies on small birds and mammals have produced conflicting results concerning temperature's effect on metabolism. When measured at temperatures below thermoneutrality, rats (Gelineo, 1934), hibernators during summer (Gelineo, 1939 and Kayser, 1939), and rabbits (Gelineo, 1949) demonstrate that a decrease in acclimation temperature results in higher heat production at the same exposure temperature. However, differences in thermal history neither affected oxygen consumption in rats (Adolph, 1950 and Sellers _et al_., 1951) or or hamsters (Adolph, 1951) at the same low temperature nor affected that of the white-footed mouse at any temperature (Hart, 1953). According to Hart (1953), the demonstration that differences in thermal history do not affect oxygen consumption at the same exposure temperature indicates that white-footed mice acclimate to changes in temperature only by changes in heat production. There is no evidence in the case of white-footed mice that there is an increase in overall body insulation with acclimation to decreased temperatures, comparable to that found in larger mammals (Hart, 1953).

Scholander (1950), observing tropical mammals found many of them are well furred and are thus adapted to maintain body temperature by lowering the body-to-air gradient through insulation. He also found they either protect themselves against heat by sweating and panting, avoid the sun by seeking shade, remain inactive during the heat of the day or resort to water for cooling.

Water availability in the environment appears to be an important determinant in the adaptation of an animal to its environment. If an animal functions optimally at a low resting metabolic rate; this low rate of metabolism may be considered to be adaptive, if the animal normally inhabits an area of low water availability. In decreasing its metabolism an animal may decrease its insensible water loss by lowering the volume of air passing into its lungs and through its respiratory passages, thus decreasing the amount of water lost as vapor through evaporation (Murie, 1961). An even greater evaporation modification may be found when considering the skin. While studying <u>Peromyscus maniculatus sonoriensis</u>, Chew (1955) found that excitement, which is accompanied by a rise in metabolic rate, increases evaporation from the skin. The physiological control for this phenomenon is not known. Physiological control of either or both of these areas of insensible water loss would give a selective advantage to animals occupying environments of low vapor pressure and minimal water availability (Murie, 1961). Chew (1957) and Lindeborg (1955) have shown that some rodent species do differ in insensible water loss. Correlated with lower metabolic rate is the reduction in caloric requirements. The reduction in necessary energy requirements might be reflected in the size of an animal's foraging range, the population density and the availability of food in different seasons (Murie, 1961).

Adaptations such as those mentioned above may seem unimportant when considering the ability of some rodents to survive on below normal water intake (Lindeborg, 1952; French, 1956; Chew and Hinegardner, 1957) or to achieve a constant water intake on changed diets (Williams, 1959). However, survival tests give no direct evidence of reproductive ability and it is a reasonable assumption that those animals having optimal food and water intake will be the animals with the greatest reproductive success (Murie, 1961).

Traits such as those mentioned above, although subtle, may have tremendous selective consequence and must be considered for their effects in any study of metabolism.

II. EXPERIMENTAL

A. Animals

A total of 103 animals containing representatives of all five species included in the genus Sigmodon (see Baker, 1969, in press), were used in this study. Wild parental stocks of these rodents in the M. S. U. Museum Live Animal Laboratory were obtained mostly by field trips to México under the direction of Rollin H. Baker with financial support from the National Science Foundation (GB-2227). Other animals were contributed through the kind cooperation of Ronald Gaertner (Arkansas), Robert Packard and Daniel Womochel (Texas) and Merle Kuns (Panamá). When animals subjected to the metabolic tests were descendants of these wild-caught stocks, they are marked as such with asterisks in the following listing. Also, listed with the names of the species (and subspecies) studied is a number which corresponds to the approximate collecting locality on Figure 3, the locality of capture and the number of individuals used. As shown below in most cases ten animals from each population sample were used.

Sigmodon hispidus

The wide-ranging hispid cotton rat occurs from Nebraska southward to Perú (see Figure 1), and local populations are adapted to a variety of hot and cold, mesic and xeric, grassy and brushy, and latitudinal and altitudinal variable situations. Representatives of this species used are from five localities:

Sigmodon hispidus texianus (Audubon and Bachman)

1. Arkansas: Benton Co., 6 km. E Rogers	10*

Figure 3. Approximate geographical location of the studied populations of the cotton rat, _Sigmodon_. For population and locality key refer to experimental animal section.

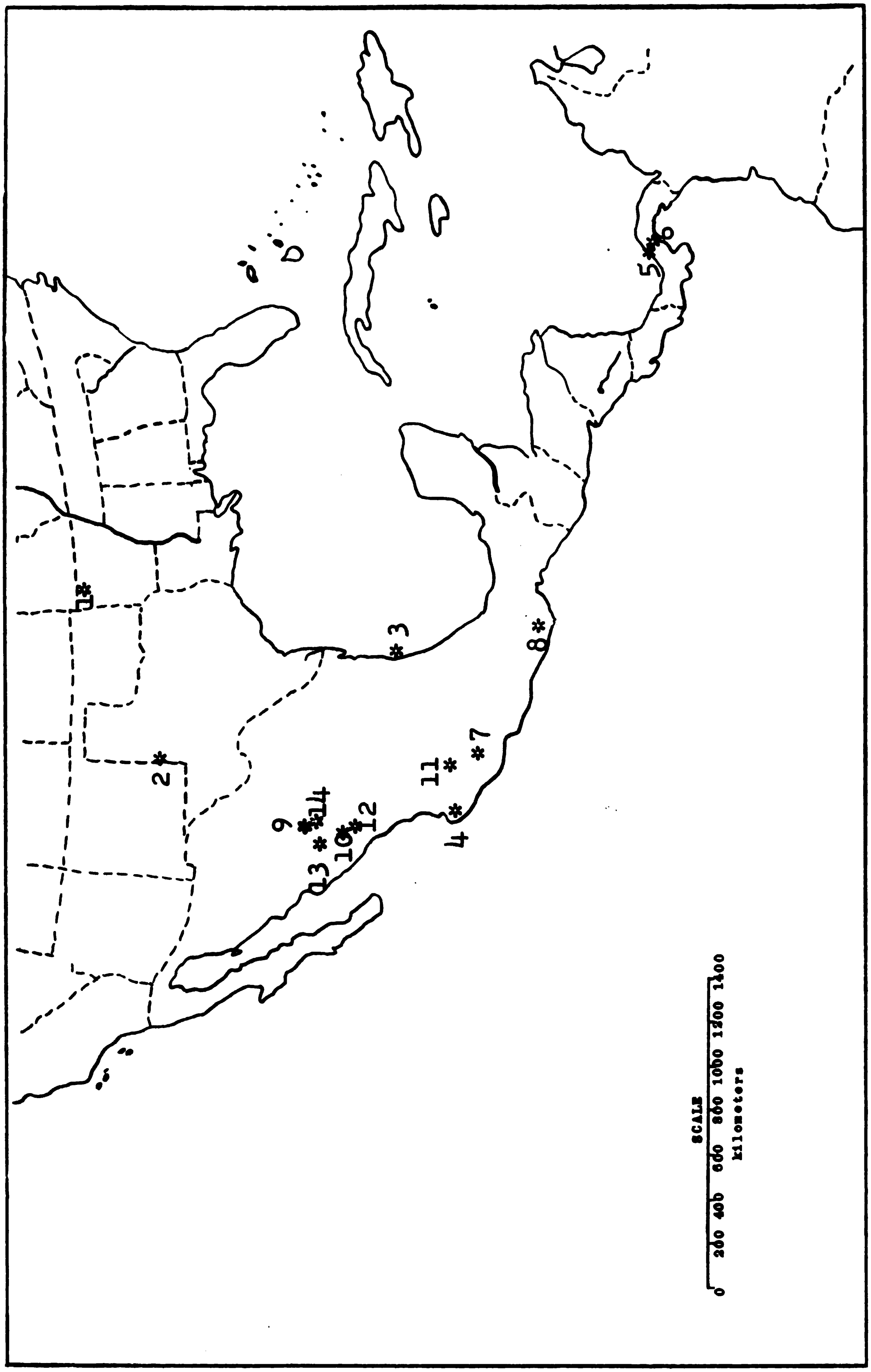
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Figure 3.

Environmental characteristics: cool winters and hot summers, mesic, 36° 30' N lat, 422 m elevation, luxuriant grass and brush.

Sigmodon hispidus berlandieri Baird

2.	Texas: Lubbock Co., Lubbock.	10*

Environmental characteristics: cold winters and hot summers, moderately xeric, 33° 40' N lat, 988 m elevation, sparse grass and brush.

Sigmodon hispidus toltecus (Saussure)

3.	Veracruz: Isla del Toro	10*

Environmental characteristics: hot, mesic, 22° 30' N lat, 6 m elevation, luxuriant coastal grass.

Sigmodon hispidus mascotensis J. A. Allen

4.	Jalisco: 10 km. SW Autlán	10*

Environmental characteristics: warm, mesic, 19° 30' N lat, 1342 m elevation, luxuriant grass, brush and montane tropical forest.

Sigmodon hispidus chiriquensis J. A. Allen

5.	Canal Zone: Chiva Chiva Road	3
6.	Canal Zone: France Field	7

Environmental characteristics: hot, mesic, 9° N lat, 100 m elevation, luxuriant grass and brush.

Sigmodon alleni

The brown cotton rat lives along the Pacific slope and coastal plain in southwestern México from Sinaloa to Oaxaca. It ranges from sea level in tropical areas to as high in elevation as 3050 m on sub-boreal mountain sides (see Figure 2). Representatives of this species studied are from two localities (also see Baker, 1969, in press):

Sigmodon alleni vulcani V. Bailey

7. Michoacán: 10 km. W Capácuaro 5 + 2*

Environmental characteristics: cool, mesic, 21° N lat, 2059 m elevation, brush, some grass, forest.

Sigmodon alleni planifrons (Nelson and Goldman)

8. Oaxaca: 13 km. SSW Juchatengo 6*

Environmental characteristics: cool mesic, 19° N lat, 1921 m elevation, brush, some grass, mixed boreal-tropical forest.

Sigmodon fulviventer

The buff-bellied cotton rat is an inhabitant of elevated grasslands on the eastern slopes of the Sierra Madre Occidental from southern Arizona and New Mexico southward to Michoacán (see Figure 2). Representatives of this species are from three localities (also see Baker, 1969, in press):

Sigmodon fulviventer minimus J. A. Allen

9. Durango: 11 km. NNE Boquilla 1*

Environmental characteristics: cool winters and warm summers, moderately xeric, 26° 20' N lat, 1952 m elevation, dry bunch grass, mixed cactus, acacia, mesquite, some juniper and oak.

Sigmodon fulviventer fulviventer J. A. Allen

10. Durango: Hda. Coyotes 9*

Environmental characteristics: cold winters and cool summers, mesic, 24° 40' N lat, 2475 m elevation, moist bunch grass in meadow surrounded by pine-oak forest.

Sigmodon fulviventer melanotis (V. Bailey)

11. Jalisco: 2 km. NW La Barca $2 + 8^{*}$

Environmental characteristics: cool winters and warm summers, moderately mesic, 20° 30' N lat, 1525 m elevation, mixed grass and weeds in fallow fields.

Sigmodon leucotis

The white-eared cotton rat is an inhabitant of openings covered with mixed bunch grass and brush surrounded by pine-oak forest in the higher mountains of central and southern México (see Figure 2). Representatives of this species were from one locality (also see Baker, 1969, in press):

Sigmodon leucotis V. Bailey

12. Durango: Hda. Coyotes $4 + 6^{*}$

Environmental characteristics: cold winters and warm summers, mesic, 24° 40' N lat, 2475 m altitude, moist shrub with rocky substrate at edge of pine-oak forest.

Sigmodon ochrognathus

The yellow-nosed cotton rat is an inhabitant of the arid mountains of the extreme southwestern parts of Texas, New Mexico and Arizona southward into Coahuila, Chihuahua and Durango (see Figure 2). Representatives of this species are from two localities (also see Baker, 1969, in press):

Sigmodon ochrognathus baileyi J. A. Allen

13. Durango: 3 km. NE Boquilla 8^{*}
14. Durango: 11 km. NE Boquilla 2^{*}

Environmental characteristics: cool winters and warm summers, moderately xeric, 26° 20' N lat, 1952 m elevation, sparse bunch grass, mixed cactus, acacia, mesquite, some juniper and oak on dry rocky hillsides.

General Comments

The animals used for experimentation were kept in groups of 2-5 individuals, in large galvanized steel and hardware cloth cages (20.5" X 13.75" X 12") and given a diet of Purina Mouse Breeder Chow and water (*ad libidum*). The ambient temperature and the relative humidity of the quarters in which the animals were confined were maintained at approximately 20-23° C and 30 percent, respectively.

The wild-caught animals were allowed to acclimate to laboratory conditions for at least 90 days, while the laboratory-raised individuals were allowed to attain adult weight prior to study. Only healthy-appearing adult animals (males and non-pregnant females) were used for experimentation. Animals were judged to be adults by the following criteria: (a) If they weighed 64 grams or more (see Table 1) and (b) when laboratory-reared, if they ranged in age from 90 to 200 days. The two sexes were used together in all calculations since no general sex-specific differences in oxygen uptake were discerned. Similar observations for *Peromyscus* have been reported by Hayward (1965) and Musser and Shoemaker (1965). The experiments were performed during a period from January to December, 1968.

B. Methods

The resting metabolic rate of the cotton rats was estimated by

Table 1: Individual Weights of Population Samples of Cotton Rats

Subspecies	Location	Weight (grams) mean	Weight (grams) range
S. h. texianus	Arkansas: vic. Rogers	191.6	(170.6-227.5)
S. h. berlandieri	Texas: vic. Lubbock	190.9	(152.9-221.9)
S. h. toltecus	Veracruz: Isla del Toro	87.8	(70.1-103.5)
S. h. mascotensis	Jalisco: vic. Autlán	116.2	(70.8-135.0)
S. h. chiriquensis	Canal Zone: vic. Chiva Chiva Road and France Field	109.8	(64.4-143.8)
S. a. vulcani	Michoacán: vic. Capácuaro	120.1	(83.6-214.0)
S. a. planifrons	Oaxaca: vic. Juchatengo	155.6	(128.9-176.6)
S. f. minimus	Durango: vic. Boquilla	161.8	(161.8)
S. f. fulviventer	Durango: vic. Coyotes	166.4	(133.2-197.7)
S. f. melanotis	Jalisco: vic. La Barca	109.3	(76.1-187.5)
S. leucotis	Durango: vic. Coyotes	128.6	(94.8-155.5)
S. ochrognathus	Durango: vic. Boquilla	115.1	(99.7-142.4)

measuring oxygen consumption, in an individual monitoring system in which the oxygen uptake was recorded at intervals of 15 minutes. During each experiment a pre-weighed adult animal was kept in a black plexiglass chamber (see Figure 4). Cotton was placed in the chamber to allow the animal to build a nest in an effort to quiet it. The chamber contained a centigrade thermometer for internal heat measurements and was fitted with a "periscope" to allow for observation of the animals at any time during measurement (see Figure 4-C). In the back of the chamber was a 2" by 1/4" vertical translucent plate which allowed light into the chamber, for observations, using the periscope. The chamber was fitted with an air inlet T-tube and an air outlet T-tube placed directly opposite and at 90^{o} angles to each other, to assure maximum mixing of chamber air (see Figure 4-A). Tygon tubing was used for all connections in the air line. Air, fed to the chamber, flowed from a low pressure pump at a rate of approximately 500 cc/minute through a tube containing a water absorbant (Drierite) then into the animal chamber (see Figure 5). The air leaving the chamber flowed first through a rotameter for measuring flow rate, then into a moisture-absorbing train containing more Drierite, before entering a Beckman Oxygen Analyzer (Model E2).

Metabolic measurements were taken between the hours of 9:00 A. M. and 9:00 P. M., when the captive rats appeared to be the least active. Each animal was allowed to remain for one hour in the chamber, to become adjusted to this environment, prior to having its oxygen uptake recorded at 15 minute intervals. Measurement of oxygen uptake was continued until two successive 15-minute-interval measurements demonstrated that minimal oxygen uptake was reached. Usually, two similar readings, with a 15-

Figure 4-A. Diagram of metabolic chamber illustrating air inlet T tube (A), vertical translucent plate (B), and air outlet T tube (C).

Figure 4-B. Diagram of top of metabolic chamber illustrating position of periscope (A), transparent plexiglass (B), chamber insert gasket (C), and thermometer position (D).

Figure 4-C. Side view of top of metabolic chamber illustrating chamber insert gasket (A), periscope (B), light repelling flap (C), and centigrade thermometer (D).

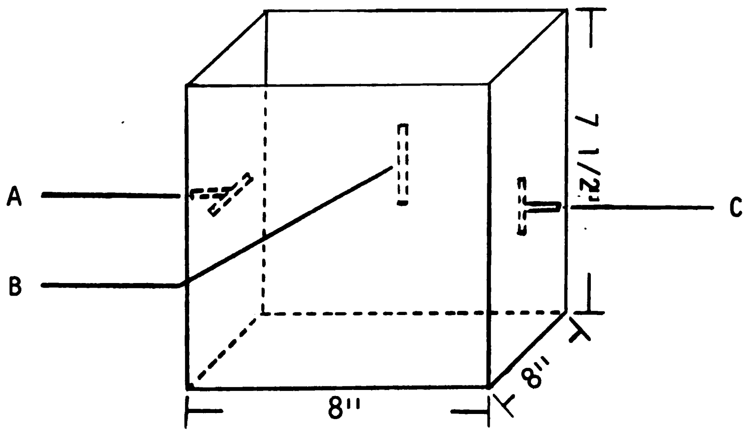

Figure 4-A

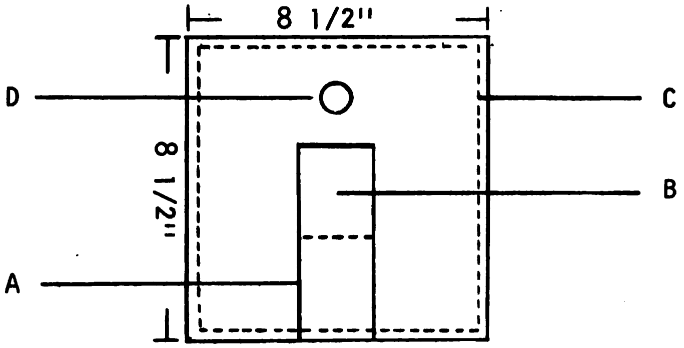

Figure 4-B

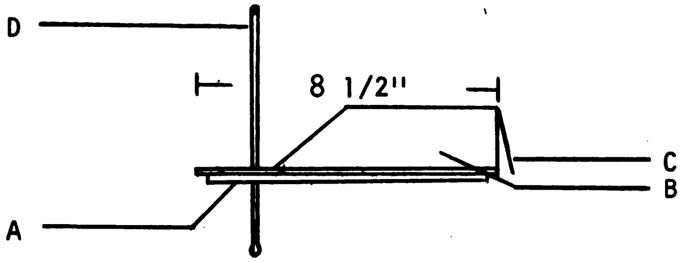

Figure 4-C

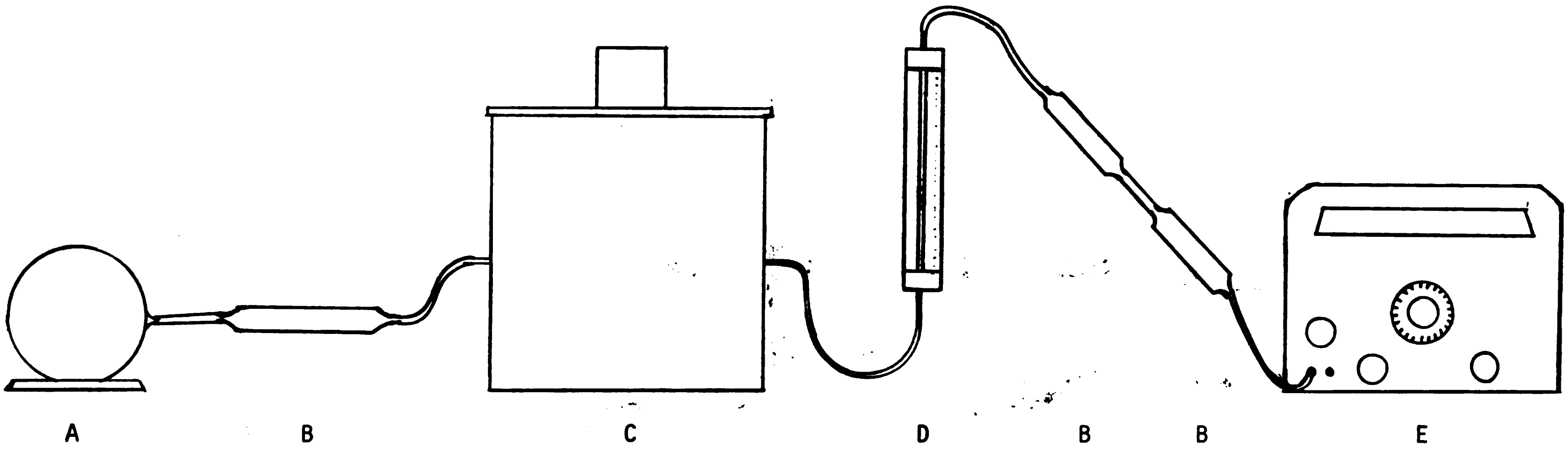

Figure 5. Diagram illustrating the flow of air through the oxygen monitoring system. Letters indicate low pressure air pump (A), Drierite absorbing tubes (B), metabolic chamber (C), rotameter (D), and the Beckman Oxygen Analyzer (E).

minute interval separating readings, were obtained for an individual animal within a two hour period, although for some highly "active" animals as long as five hours were required.

From the minimal oxygen uptake and the rate of gas flow, oxygen consumption (volume of dry gas at standard temperature and pressure) was calculated using the applicable formula modified from Depocas and Hart (1957). The weight of the cotton rats prior to the experimental run was used for calculation of all weight-specific, resting metabolic rates.

Since cotton rats starved in advance for 12 hours became highly active in the metabolic chamber, it was decided to not deprive them of normal amounts of food prior to experimentation. However, the animals received no food during the period of measurement. Brown (1968) found that Neotoma maintained similar metabolic rates while being deprived of food for as long as seven hours, during which time the animals became postabsorptive. He suggested that specific dynamic action is not an important variable in metabolic studies such as his own. Assuming that the metabolism of other small rodents may be somewhat similar to that of Neotoma, starving the experimental cotton rats was not thought to be a necessity.

The weights of the studied populations (see Table 1) did not demonstrate variance homogeneity, thus were analyzed using the non-parametric Kruskal-Wallace one-way Analysis of Variance (Siegel, 1956). Using this test it was determined that the weights of three populations (S. h. berlandieri, S. h. texianus, and S. h. toltecus) differed significantly from the other eight populations. Due to the above variation the three differing populations could not be included in an analysis of variance concerning metabolism. Since only one sample was measured of _S_. _fulviventer_ _minimus_ from Boquilla, Durango, it is excluded from various statistical analyses. The Newman-Keuls method (Winer, 1962), a modified q statistic, was used to evaluate the differences found between the eight populations that could be analyzed. The above mentioned eight experimental populations were used in determining linear relationships demonstrated through linear regression analysis (Li, 1964). The three populations that differed from the eight used in analysis were added to the linear plots after the relationships were determined.

III. RESULTS

The resting metabolic rates for the five population samples of S. hispidus, the two of S. alleni, the two of S. fulviventer, and one each of S. leucotis and S. ochrognathus, respectively, are listed in Table 2 and charted in Figure 6.

Variation of resting metabolic rate within population samples is shown to be extensive in certain populations (see Figure 6). This is due to variation in weights of animals within each experimental population (see Table 1), which was caused by limited choice of experimental animals.

The relationship between body weight and metabolism (O_2 consumed cc/g/hr) is demonstrated in Figure 7. The slope and intercept of the regression line were calculated using the mean metabolism (O_2 consumed cc/g/hr) of S. ochrognathus, S. alleni planifrons, S. alleni vulcani, S. leucotis, S. h. chiriquensis, S. h. mascotensis, S. f. fulviventer and S. f. melanotis.

Table 2. Resting Metabolic Rates of sample populations of *Sigmodon*

Subspecies	Location	Average and consumption	Extreme oxygen (cc/g/hr)
S. h. texianus	Arkansas: vic. Rogers	1.31	(.96-1.56)
S. h. berlandieri	Texas: vic. Lubbock	1.33	(1.02-1.75)
S. h. toltecus	Veracruz: Isla del Toro	2.42	(2.11-2.89)
S. h. mascotensis	Jalisco: Vic. Autlán	1.53	(1.23-1.57)
S. h. chiriquensis	Canal Zone: vic. France Field and Chiva Chiva Road	1.68	(1.10-2.35)
S. a. vulcani	Michoacán: vic. Capácuaro	1.62	(1.33-1.95)
S. a. planifrons	Oaxaca: vic. Juchatengo	1.33	(1.10-1.58)
S. f. fulviventer	Durango: vic. Coyotes	1.47	(1.22-1.85)
S. f. melanotis	Jalisco: vic. La Barca	1.54	(1.14-1.81)
S. leucotis	Durango: vic. Coyotes	1.45	(1.38-1.54)
S. ochrognathus	Durango: vic. Boquilla	1.34	(1.15-2.01)

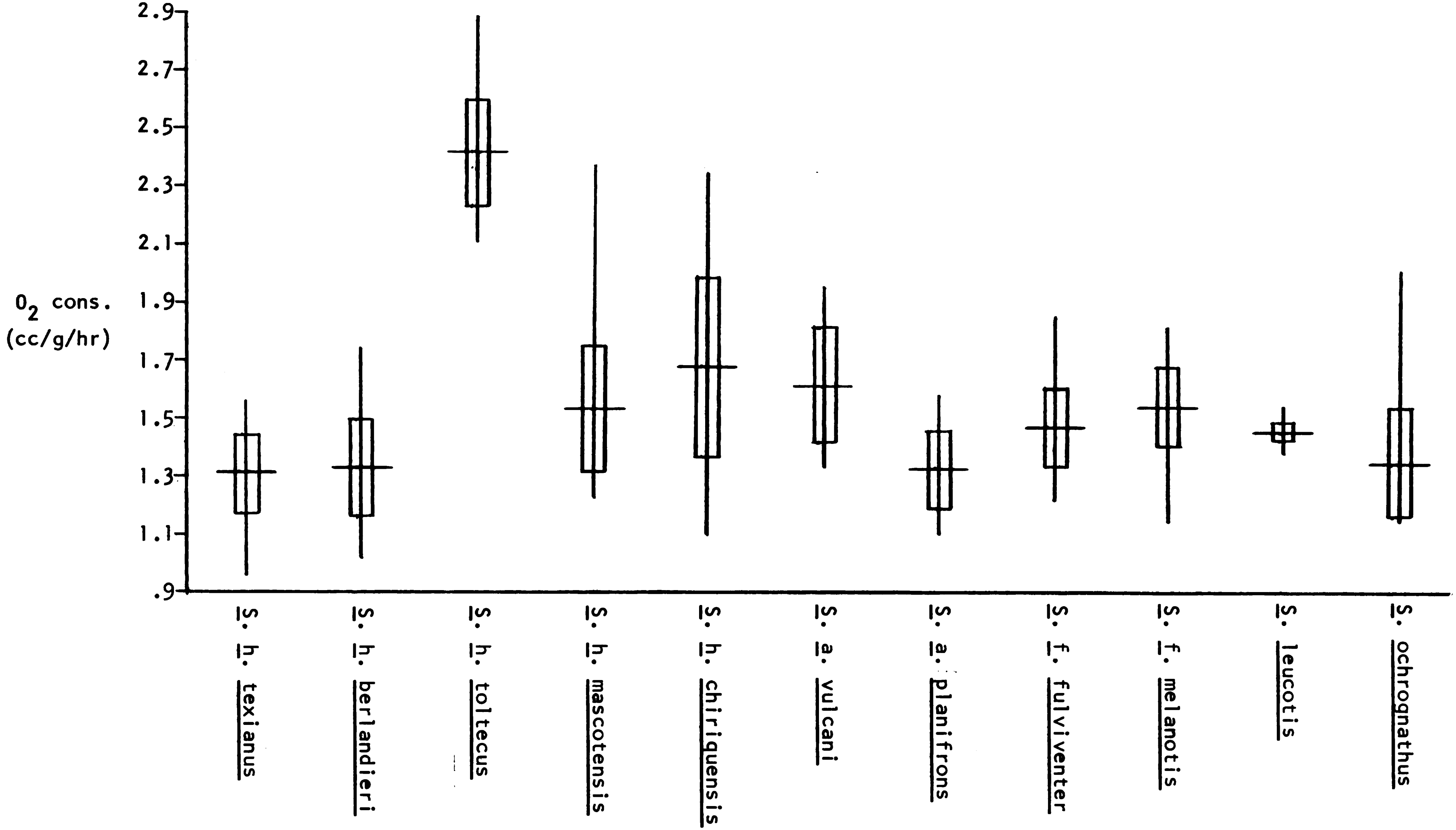

Figure 6. Resting metabolic rates for the studied populations of *Sigmodon*. The vertical line indicates range, the horizontal line indicates the population mean, and the vertical bar indicates 95 percent confidence intervals $(\bar{X} \pm t_{.05} \frac{S_x}{\sqrt{N}})$.

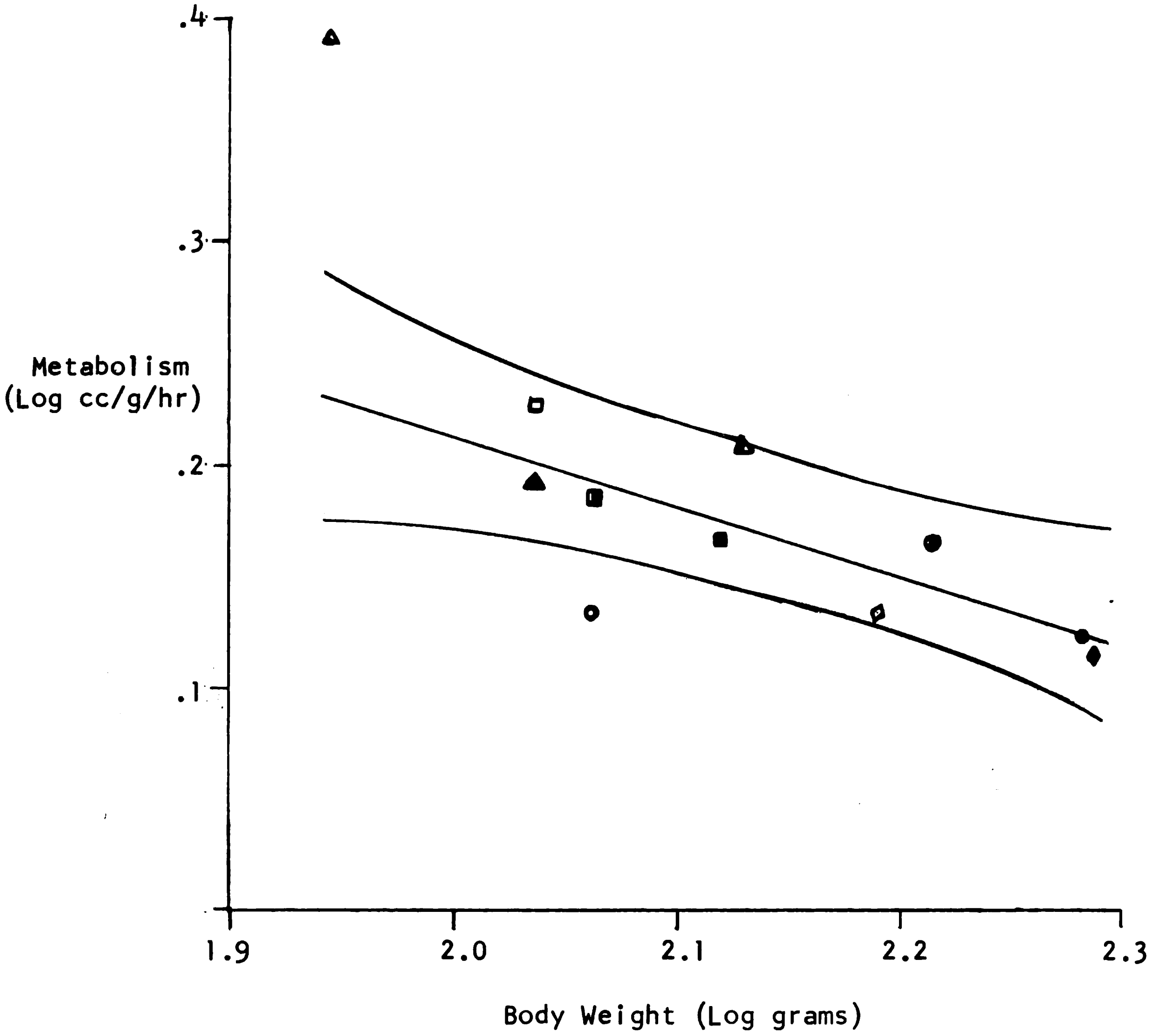

Figure 7. Regression of metabolism (Oxygen consumption cc/g/hr) on body weight (grams) for all studied populations of *Sigmodon.*

Key:

◆ *S. h. texianus*
● *S. h. berlandieri*
△ *S. h. toltecus*
◧ *S. h. mascotensis*
▢ *S. h. chiriquensis*
▲ *S. a. vulcani*
◇ *S. a. planifrons*
◐ *S. f. fulviventer*
▲ *S. f. melanotis*
■ *S. leucotis*
○ *S. ochrognathus*

IV. DISCUSSION

A. Individual Variation

Using as many as 10 animals from each population for testing (see Methods), it was found that individual variation was often considerable (see Table II). Maximum range of variation in resting metabolic rates were found for the sample of *S. hispidus chiriquensis* (1.25). Minimum range was found in *S. leucotis* (.16). The remaining nine populations measured have ranges between .35 and .86.

Variation in these values in the ubiquitious *S. hispidus* (from .35 to 1.25) may reflect their greater tolerance to climatic conditions while the more ecologically-restricted *S. leucotis* (.16), *S. alleni* (.48 and .62), *S. ochrognathus* (.86), and *S. fulviventer* (.57 and .63) show a lesser amount of variation.

B. Intraspecific Metabolic Variation

Sigmodon hispidus

Population samples of the hispid cotton rat were purposely chosen to include representatives from various habitats in which this ubiquitious species occurs. As would be expected (see Prosser and Brown, 1962), population samples with a higher mean body weight, which were found in the more northern localities, have resting metabolic rates averaging lower than those of samples of the smaller-sized animals taken from the more southern and warmer climates (see Table 2 and Figure 6). The sample from Isla del Toro in Veracruz (*S. h. toltecus*) has the highest average metabolic rate. Assuming that this average of 2.42 cc/g/hr of oxygen consumed is normal for this population, I would guess that this high figure might be the result of a combination of influences: its small size, its insular isolation, and its mesic, tropical savanna-grass habitat. As shown in Figure 7, the resting metabolic rates of all of these populations, except for the Veracruz animals, are not significantly different at the 95 percent confidence level.

Sigmodon alleni

The two population samples came from somewhat similar, cool, montane areas, at the junction between the higher pine-oak forest and the lower humid tropical forest, although, as shown in Table I, the Oaxacan population sample (*S. a. planifrons*) averaged 35 g per individual heavier than those animals in the Michoacán population sample (*S. a. vulcani*). The heavier weight may account for the lower average resting metabolic rate determined for the former sample (see Table 2).

Sigmodon fulviventer

The resting metabolic rates of the population samples from the northern part (Durango) and the southern part (Jalisco) of the Mexican Plateau are essentially the same (see Table 2). Any variation observed for these population samples seemed to be in direct correlation with the mean weight of the animals studied. The major environmental differences between habitats of these populations are in altitude and temperature, the Durangan locality being substantially higher and colder.

C. *Interspecific Geographic Variation*

Sigmodon fulviventer and *Sigmodon ochrognathus*

S. f. minimus and *S. ochrognathus* occured in the same locality near Boquilla, Durango. *S. f. minimus* was found occupying the flat, grassy areas, while *S. ochrognathus* occupied the dry, rocky hillsides. The resting metabolic rate of *S. ochrognathus*, due to body size, would be expected to be higher than that of *S. fulviventer* of the same area (see Table 1 and Figure 7). However, the former's metabolic rate was statistically lower than that of the one specimen of *S. fulviventer* measured. A low resting metabolic rate may give *S. ochrognathus* of this xeric area a selective advantage by allowing it to maintain a lower body temperature, a reduction in the quantity of energy necessary to maintain basal level, greater water preservation and a greater reproductive potential.

Sigmodon fulviventer and *Sigmodon leucotis*

S. f. fulviventer and *S. leucotis* occurred in the same locality near Coyotes, Durango. However, *S. f. fulviventer* occupied the moist bunch grasses and meadows of the area while *S. leucotis* was found in the moist shruby and rocky areas. When statistically analyzed with 95 percent confidence, these two species were found not to vary in oxygen consumption (see Figures 6 and 7) indicating an ecotypic adaptation occurs in these cotton rats.

Sigmodon hispidus and *Sigmodon alleni*

The *S. hispidus* population taken from near Autlán, Jalisco and the two S. alleni populations from Michoacán and Oaxaca, respectively, occupied somewhat similar habitats. As would be expected, their resting metabolic rates do not differ significantly (see Figure 7).

D. Factors Influencing Metabolic Rate

Disease or Adverse Endocrine Condition

According to Newburgh (1945) and Gaertner (1963) any abnormal condition such as disease or adverse endocrine control will have an effect on the oxidative rate. An adverse endocrine condition, although not superficially noticeable, might be directly demonstrated in the failure of a population to reproduce. Due to the above considerations ten individuals measured from a S. a. planifrons population, which was slowly dying out in the laboratory, were eliminated from inter- and intraspecific comparisons. In their place the measured values for six S. a. planifrons, made using a modification of closed circuit indirect calorimetry, taken by Ostrander (unpublished, 1966) were used. The other wild-caught or laboratory-reared animals used in this study appeared normal outwardly, from the standpoint of health.

Weight

Linear regression analysis was used to determine the linear relationships between S. leucotis, S. ochrognathus, S. f. fulviventer, S. f. melanotis, S. a. vulcani, S. h. mascotensis and S. h. chiriquensis. Confidence limits at the 95 percent level were fitted and plotted for this line (see Figure 7). Plotting the other five studied populations on this regression graph illustrates that S. h. texianus, S. a. planifrons and _S_. _h_. _berlandieri_ readily fit within the confidence intervals. Because these latter three fit within the confidence intervals they can be considered, with 95 percent confidence, to demonstrate similar correlation of metabolism with body weight. Thus, Figure 7, a linear regression of metabolism on body weight has been based on the nine pertinent populations.

Using an analysis such as the above has compensated for one of the two variables present in this study, that of weight variation. Any further variation observed in metabolic values must be due to variation in genetic character of the studied subspecies (see Figure 6).

Brody (1945) and Kleiber (1961) suggested the use of a power function of body weight as a general reference for making inter- and intraspecific comparisons of basal metabolic rate (see Figure 8). Morrison (1948) demonstrated that the relationship suggested by Brody and Kleiber applies to small rodents as well as larger mammals. The values expected for Brody's or Kleiber's approximation (see Figure 8) are for basal metabolic rates and would be expected to be lower than resting metabolic values, since the non-postabsorptive condition of _Sigmodon_ while being measured may raise the expenditure of energy from the basal level by 5-40 percent (Hoar, 1966), due to specific dynamic action. As is demonstrated by Figure 8, although the energy expenditure is elevated by the non-postabsorptive state, the slope of the regression of energy production on body weight would remain constant.

It has been demonstrated that variations from the supposed normal metabolic values of _Sigmodon_, which are found in comparing metabolism and weight must be due to factors other than immediate environmental influence. Also, the resting metabolic rates recorded for the

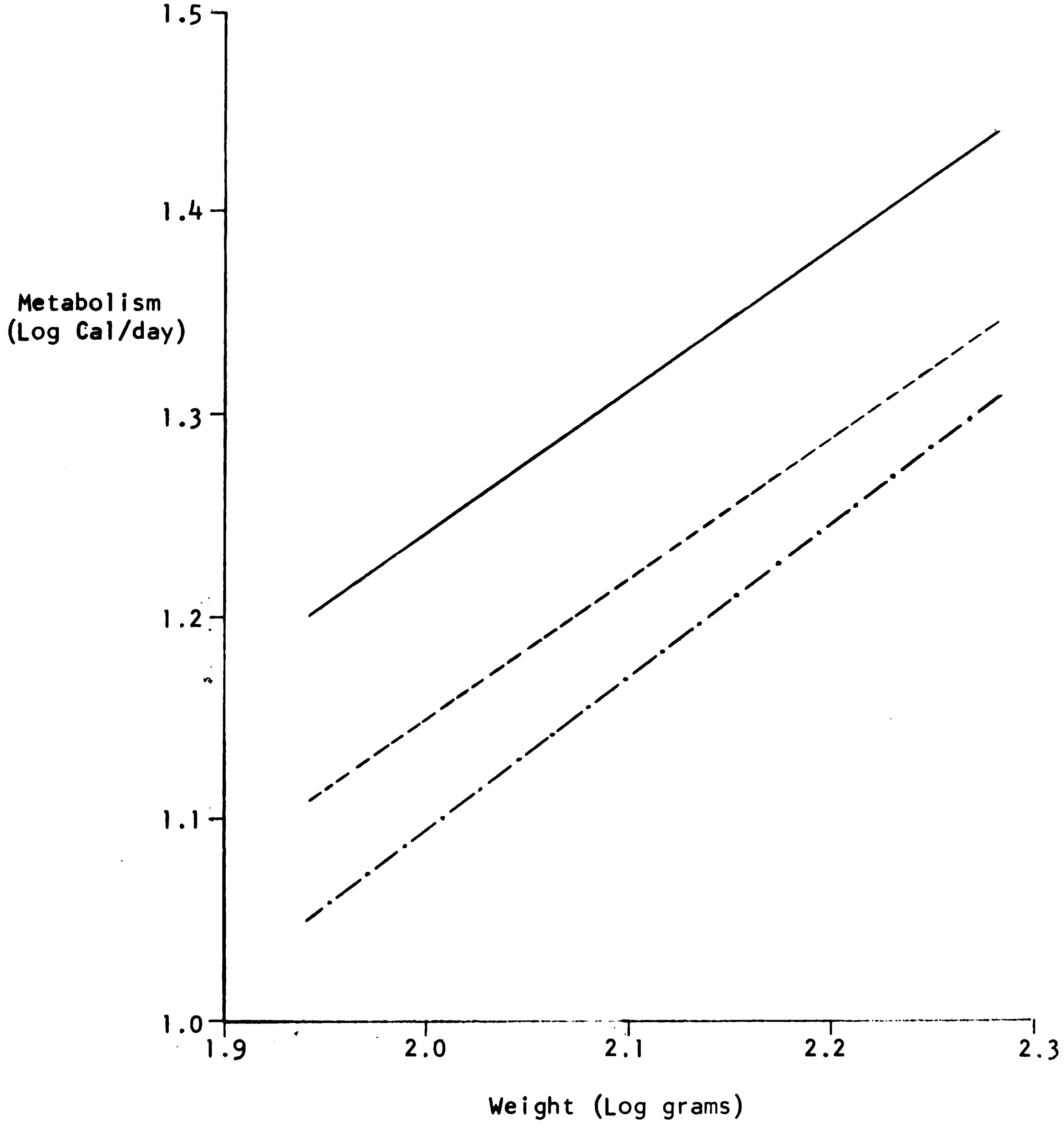

Figure 8. Regression of metabolism (Cal/day) on weight (grams).

(Kleiber, 1961) -·-·-·-·-·-·-·-·-·-·-·-·-·-

(Brody, 1945) - - - - - - - - - - - - - - - -

Sigmodon ————————————

experimental animals, although elevated above predicted values, would be expected due to specific dynamic action. It remains to attempt to determine those factors present in the previous environment of the animals that might influence their metabolic rate.

Altitude

Altitude has apparently exercised no effect on the resting metabolic rate of *Sigmodon* (see specimen listing and Figure 9). This may be the result of the distribution of *Sigmodon* in nature. Small mammals such as the cotton rat could not withstand the thermal stress to which they would have to submit, if passing into an area having an oxygen tension differing from their own enough to affect them. It has been reported that in mammals, gradual acclimatization at high altitude results in many physiological changes which are beneficial to oxygen utilization, but either no metabolic changes or only a slightly reduced oxygen consumption have been found (Murie, 1961; Mitchell and Edman, 1951; Ullrich, 1956).

Environmental Temperature

Environmental temperature apparently has directly exercised no effect on the metabolic rate of *Sigmodon*.(see Figure 10). The environmental temperature of *Sigmodon* would affect the animal directly, only by changing the body temperature in accordance with the environment, if the temperature were outside the thermoneutral zone of the genus. According to Sullivan and Mullin (1954) one would expect that an animal from an area with high environmental mean temperature has a lower

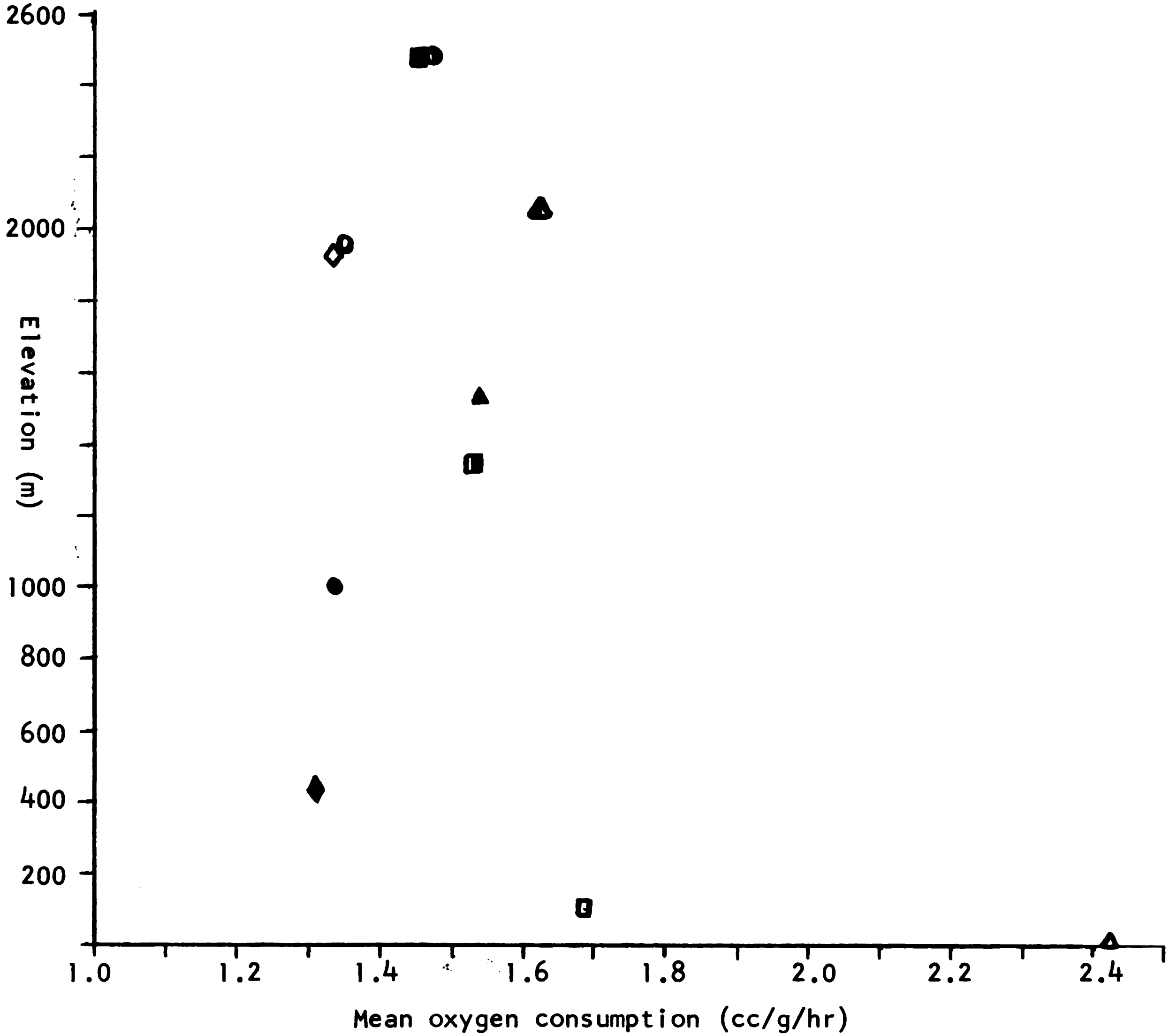

Figure 9. Comparison of mean oxygen consumption with altitude of trapping locality of populations of *Sigmodon*. Symbols are identified in key below.

◆ *S. h. texianus*
● *S. h. berlandieri*
△ *S. h. toltecus*
◘ *S. h. mascotensis*
▢ *S. h. chiriquensis*
▲ *S. a. vulcani*
◇ *S. a. planifrons*
◐ *S. f. fulviventer*
▲ *S. f. melanotis*
■ *S. leucotis*
◯ *S. ochrognathus*

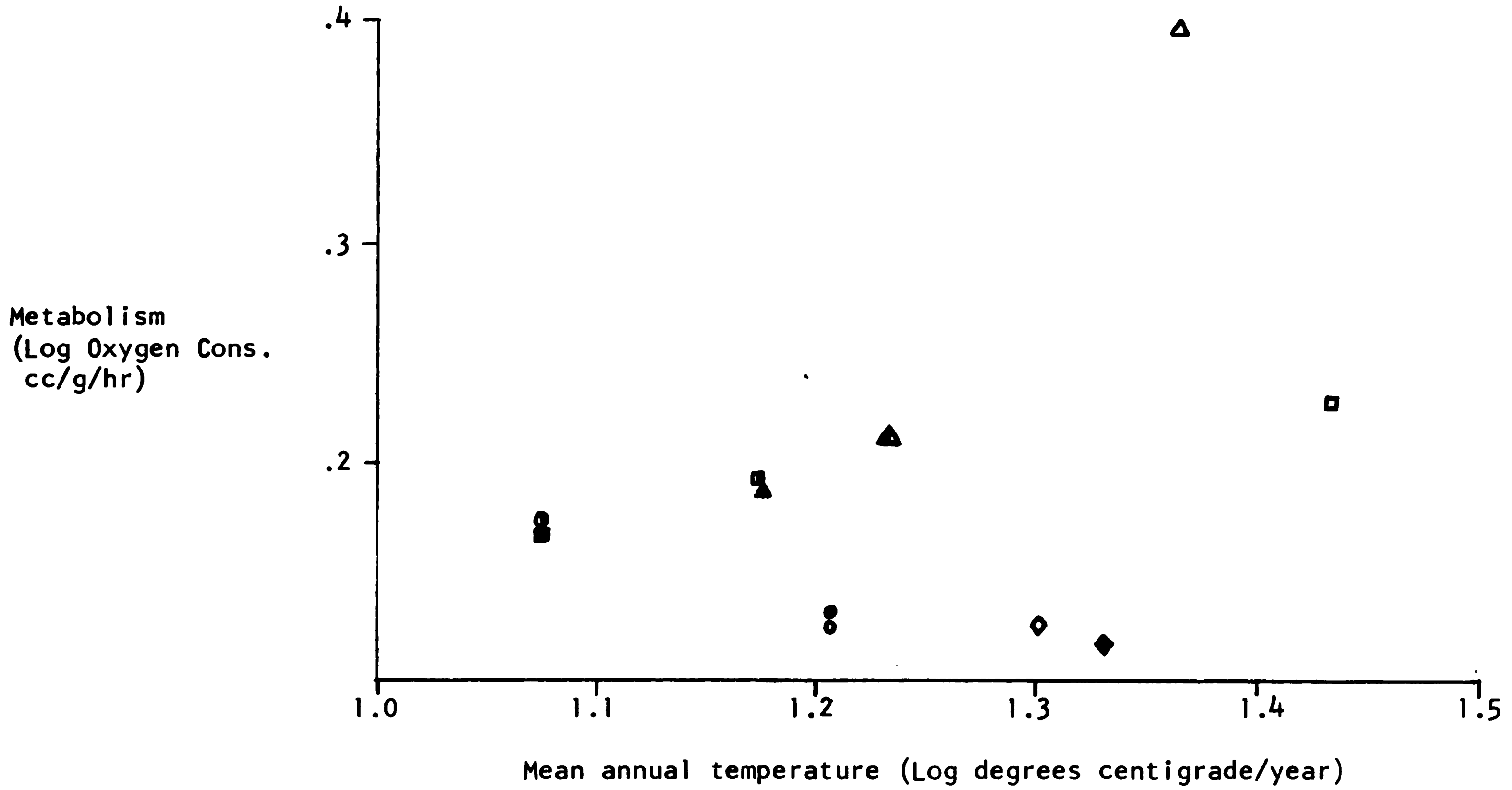

Figure 10. Regression of metabolism on mean annual temperature. For identification of symbols refer to key below.

◆ *S. h. texianus*
● *S. h. berlandieri*
◭ *S. h. toltecus*
◧ *S. h. mascotensis*

□ *S. h. chiriquensis*
◭ *S. a. vulcani*
◇ *S. a. planifrons*
◐ *S. f. fulviventer*

▲ *S. f. melanotis*
■ *S. leucotis*
○ *S. ochrognathus*

metabolic rate than an animal from an area with low environmental mean temperature. However, Hart (1953) studying the white-footed mouse found that differences in thermal history do not affect oxygen consumption at the same exposure temperature. The results found for *Sigmodon* tend to corroborate the results of Hart (1953) when statistically considered (see Figure 10). However, it must be pointed out that to ascertain the true relationship that exists between *Sigmodon* and its environmental temperature requires a study of the body-to-air gradient, behavior and insensible water loss.

Precipitation

The thermoregulatory resources of *Sigmodon* are expected to be limited in any environmental temperature range above thermoneutrality. Any use of body water by a rodent would be a detriment if the animal were in an environment with little water available. If an animal functions optimally at a low resting metabolic rate, this low rate of metabolism may be considered to be adaptive, if the animal normally inhabits an area of low water availability. According to Murie (1961), the decrease of metabolism found in some mammals may cause decrease in insensible water loss through the respiratory passages. An even greater modification of water loss was found by Chew (1955); he noted that excitement, which is accompanied by a rise in metabolic rate, increases evaporation from the skin. Physiological control of either or both of the above areas of insensible water loss would give a selective advantage to animals occupying environments of low vapor pressure and minimal water availability (Murie, 1961).

The availability of environmental water and its physiological affect on Sigmodon are demonstrated in this study (see Figure 11). The most xerophytic species of the genus, *S. ochrognathus*, shows a resting metabolic rate that is lower than the population expectation for that species by 12.9 percent (see Figure 6). Although further study is needed to demonstrate its validity, perhaps this reduction in metabolism is a selective advantage. The advantages of low metabolism attributable in this instance may be lower body temperature, reduction in quantity of energy necessary to maintain basal level, water preservation and greater species reproductive potential. On the other hand, *S. h. toltecus*, the most hydrophylic population studied, demonstrates a resting metabolic rate 42 percent above that expected for this subspecies. Perhaps excessive available energy in the form of food, reduced necessity for activity, and the proximity of much water for both bodily intake and cooling allow the excessive metabolism demonstrated for this subspecies of *S. hispidus*. Perhaps no physiological determinants of metabolism are active here; rather, the metabolic rate for this subspecies may be the function of the lack of necessity for physiological control.

It is clearly indicated that genetic differences between species will cause divergent standard energy production regardless of the immediate environmental conditions. The genetic differences between populations not necessarily being limited only to those factors that control metabolic balance, but also those concerning all behavioral and physiological processes. Metabolism as an index, seems simply to measure a local type of adaptation. It is an ecotypic parameter, not a phylogenetic phenomenon.

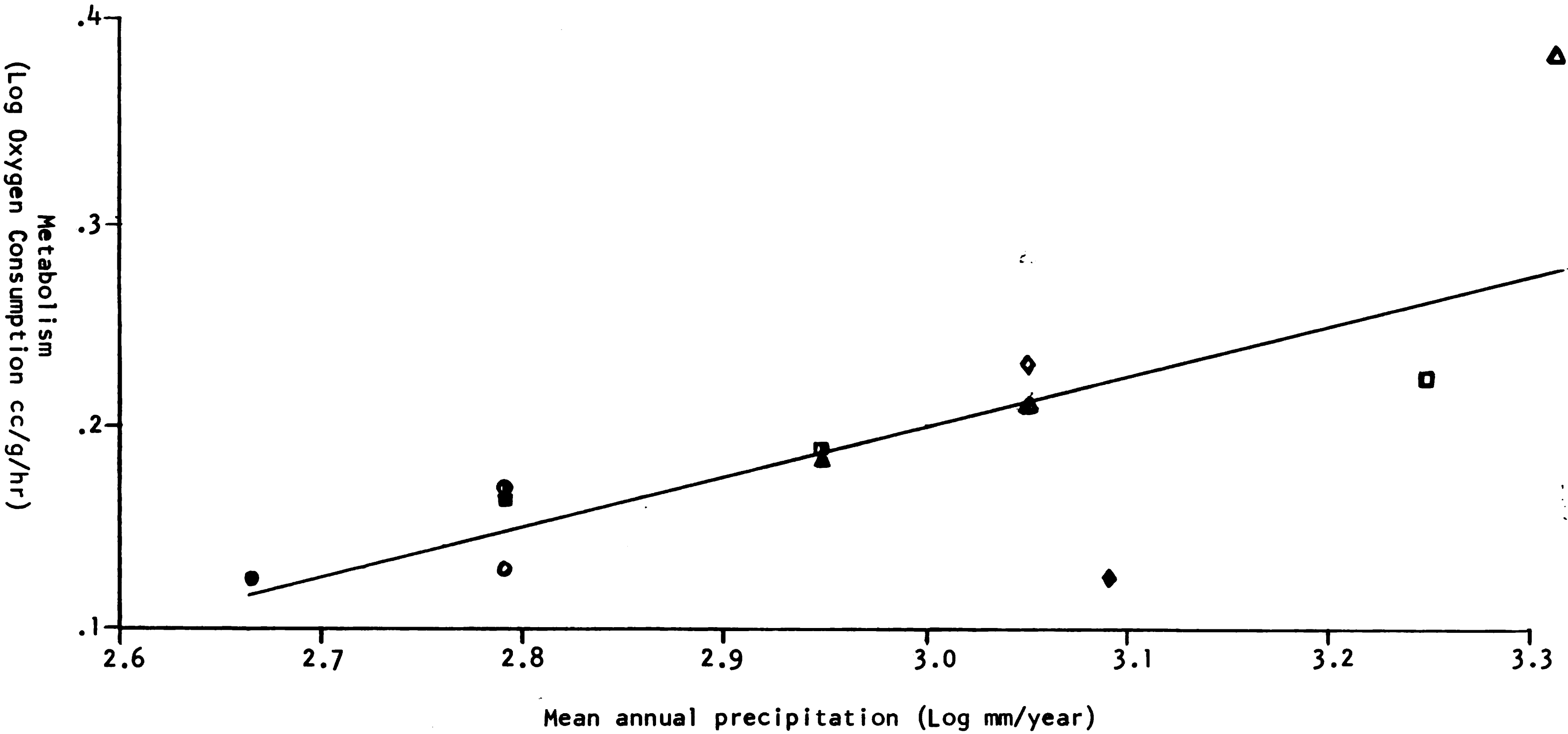

Figure 11. Regression of metabolism on mean annual precipitation. For identification of symbols refer to key below.

◆ *S. h. texianus*
● *S. h. berlandieri*
▲ *S. h. toltecus*
⬢ *S. h. mascotensis*
▢ *S. h. chiriquensis*

▲ *S. a. vulcani*
◊ *S. a. planifrons*
● *S. f. fulviventer*
▲ *S. f. melanotis*
■ *S. leucotis*
○ *S. ochrognathus*

V. SUMMARY

Resting metabolic rates were measured for five species of laboratory acclimated cotton rats, Sigmodon, from the United States, México and Panamá. The measurements were made by open-circuit indirect calorimetry modified from Brown, (1968). The resting metabolic rates of the studied populations were analyzed to determine variation within population samples, between geographically-separated population samples of the same species, and between species.

It was found that individual variation was often considerable. The maximum range of variation in resting metabolic rate was found in the ubiquitious species, S. hispidus, possibly reflecting this species greater tolerance for a wide range of climatic conditions. The more ecologically restricted S. leucotis, S. ochrognathus, S. alleni and S. fulviventer demonstrated less variation.

The resting metabolic rate of two laboratory populations, S. h. toltecus and S. ochrognathus were statistically distinct from each other and all other experimental populations. The populations that were not statistically distinguishable from the other populations, demonstrated a metabolic rate that was for the most part weight dependent in accordance with the work of Brody (1945) and Kleiber (1961).

Variation from the expected resting metabolic rate observed in S. ochrognathus follows directly its expectations when the influence exerted upon this species by its environment is considered. A low metabolic rate may give this species a selective advantage in its xeric environment by allowing it to have a lower body temperature, a reduction in the quantity of energy necessary to maintain basal level, greater water preservation and a greater reproductive potential.

S. *h*. *toltecus* may vary from the expected resting metabolic rate due to the lack of necessity for physiological controls. Excessive available energy in the form of food, reduced necessity for activity and proximity of water for intake and cooling, may allow high metabolic rates such as those observed for this population.

This study indicates that genetic differences between populations will cause divergent standard energy production regardless of the immediate environmental conditions. Also, metabolism as an index, in some cases, seems simply to measure a local type adaptation, indicating that metabolism, in the case of *Sigmodon*, is an ecotypic phenomenon.

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