STUDIES ON MORPHOLOGY AND BIOLOGY OF COTTON RATS (SIGMODON HISPIDUS) FROM NORTHERN MEXICO TO SOUTHERN NEBRASKA

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Cleveland, Arthur G., Studies on Morphology and Biology of Cotton Rats (Sigmodon hispidus) from Northern Mexico to Southern Nebraska. Doctor of Philosophy (Biology), December, 1971, 83 pp., 12 tables, 16 illustrations, 90 titles.

This investigation was designed to evaluate the need for retaining both Sigmodon hispidus texianus and Sigmodon hispidus berlandieri as subspecific designations. An attempt was made to demonstrate bioclimatic variation and reproductive seasonality in cotton rats. The validity of applying the results of isolated studies of cotton rat populations to the species as a whole was examined.

Population studies of cotton rats were made in Kansas, Oklahoma, and Texas from 1967 through 1971. Museum specimens across the study area were also examined for morphological characteristics. Autopsies were performed on sixty-one specimens to determine parasitological variation.

A clinal effect was shown on a north-south line through three temperature isotherms in cotton rats. Litter size was shown to increase from southern to northern areas. Length of breeding season was shown to have an inverse relationship to litter size. Differences in sex ratios in cotton rats from northeastern Mexico to Kansas were shown not to be statistically significant. Results of population dynamics

studies and morphological examinations indicate restraint should be exercised in making applications of local studies to the species in general.

A quantitative comparison of cotton rat endoparasites revealed differences in the populations studied. The absence of filarid infection in the cotton rat specimens from the two northern study areas was demonstrated. A recommendation was made that the subspecific designation of *Sigmodon hispidus berlandieri* be placed in synonymy with *Sigmodon hispidus texianus*.

STUDIES ON MORPHOLOGY AND BIOLOGY OF COTTON RATS (*SIGMODON HISPIDUS*) FROM NORTHERN MEXICO TO SOUTHERN NEBRASKA

DISSERTATION

Presented to the Graduate Council of the
North Texas State University in Partial
Fulfillment of the Requirements

For the Degree of

Doctor of Philosophy

By

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Denton, Texas

December, 1971

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INTRODUCTION

General

Over the past century it has become increasingly clear that several mammalian species have expanded their ranges northward across the south-central United States. Among the most interesting of these species are the pigmy mouse (Baiomy taylori), the nine-banded armadillo (Dasypus novemcinctus), and the hispid cotton rat (Sigmodon hispidus). The pigmy mouse is continuing to expand its range in Texas (Packard, 1960; Baccus, Greer, Raun, 1971). The nine-banded armadillo has slowed its northward advance as evidenced by the latest study of its geographical distribution in the United States (Cleveland, 1970). The cotton rat appears to have reached a relatively stable northern distribution, periodically receding from the northern extremes reported by Jones (1960) and Genoways and Schlitter (1966). Of these three animals mentioned, only the cotton rat appears to have reached the northern limits of its distribution, at least for the present time.

Many investigators have studied the population dynamics and natural history (Inglis, 1955; Odum, 1955; Goertz, 1965) of the cotton rat. There is, however, a paucity of information on the species over a large geographical area. Most researchers have relied upon cotton rats from a single locality to produce information that they often applied to the species as a whole. Little has been done to correlate research on cotton rat morphology, natural history, parasitology, and reproduction in one locality with similar studies in a distant locality.

The cotton rat occurs from northern South America through-out Mexico and into the southern United States (Walker, 1964). Anthony (1928) stated that cotton rats are found in greatest numbers from Mexico to Peru. The geographic range has expanded between 1933 and 1947 from southern Kansas to northern Kansas (Cockrum ,1948). Jones (1960), Genoways and Schlitter (1966), and Choate and Genoways (1966) reported the cotton rat in southern Nebraska. Hall and Kelson (1959) recorded the cotton rat from southern California to southern Virginia. The species of Sigmodon have been elaborated on recently by Baker (1969) and Zimmermann (1970).

Bowers (1971) has summarized the habitat of the hispid cotton rat as being extremely varied. He noted local populations adapted to a variety of hot and cold, mesic and xeric, and grassy and brushy situations which vary in latitude and altitude. Specific studies on cotton rat habitats in various regions are outlined in Appendix I. Cotton rats are present in a majority of the climatic provinces of Thornthwaite (1931).

Taxonomy

A number of changes have been made in the taxonomy of Sigmodon hispidus since the original description in 1825 (Say and Ord). The names assigned this group were summerized by Coues (1877) and again by Bailey (1902). The present taxonomic situation in cotton rats appears to have evolved from early attempts by Coues (1877), Allen (1891), Mearns (1897) and Bailey (1902, 1905) to separate these animals at the subspecific level. Hall and Kelson (1959) designated thirty-three subspecies of Sigmodon hispidus. On a line from Veracruz to extreme northeastern Kansas, only two of these subspecies are encountered: S. h. texianus and S. h. berlandieri. The separation of these subspecies is shown in Figure 1 (adapted from Allen, 1905) and Figure 2 (adapted from Hall and Kelson, 1959). The validity of such a subspecific designation is of major concern in this study.

Bioclimatic Variation

During the past fifteen years, classical rules of climatic variation have undergone extensive discussion and evaluation. Particularly, Bergmann's and Allen's Rules (reviewed by Mayr, 1956) have caught the attention of evolutionists. These rules revolve around the concept that a species or group of related species undergo morphological and physiological changes with latitude and altitude. Not that altitude nor latitude themselves have any direct

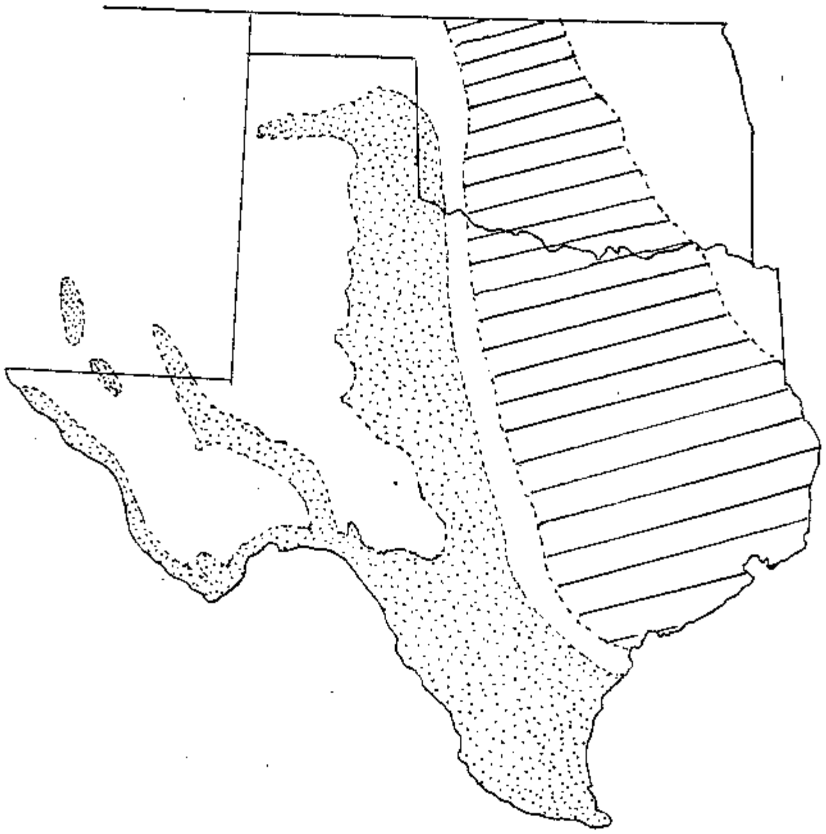

Fig. 1--Separation of subspecies of _Sigmodon hispidus_ by Allen (1905).

▨ _S. hispidus texianus_

░ _S. hispidus berlandieri_

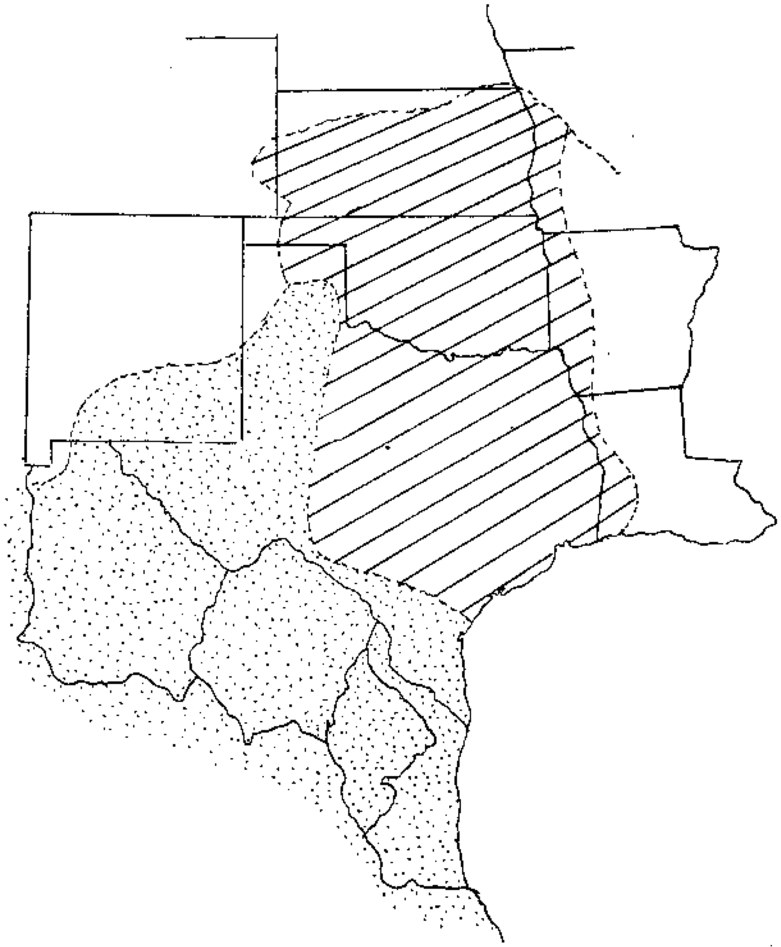

Fig. 2--Separation of subspecies of *Sigmodon hispidus* by Hall and Kelson (1959).

▨ *S. hispidus texianus*

░ *S. hispidus berlandieri*

influence upon the animal, but that these parameters reflect climatic changes which occur as a species expands its range from a tropical to a temperate to an arctic environment. Basically, Bergmann's Rule states that endothermal animals tend to be smaller in size in tropical areas and hence have more surface area in proportion to body size than populations in cooler regions. This phenomenon is usually interpreted as being a manifestation of heat conservation in the north and heat radiation in the warmer regions of the south. Bergmann's rule has been most recently demonstrated by Brown and Lee (1969) in _Neotoma_ of western North America and by Judd (1970) in _Peromyscus maniculatus_ across New Mexico and the panhandle of Texas. According to Allen's Rule, endothermal animals in northern climates will have shorter extremities than their relatives in temperate and tropical areas, resulting in more heat radiation from the larger ears and tails in warm climates, and less heat dissipation in cooler climates. Neither of these rules have previously been demonstrated in cotton rats.

Population Dynamics

Cotton rat populations are subject to extreme fluctuations in density somewhat comparable to the population cycles of certain rabbits and rodents of more northern regions of North America. Goertz (1964) has reviewed the literature relative to these fluctuations in numbers of cotton rats in the United States. Except for the possible regulatory factors discussed in his paper, causes for these dramatic changes remain unknown. Largely because of these unexplained fluctuations, the population dynamics of Sigmodon have been widely studied over the past thirty to forty years. Many of these studies were unpublished theses. Unfortunately, upon examination, some of these documents failed to indicate the location (even the state) of the study area (e.g., Provo, 1962). This complicated the analysis of such works. Of special value, however, were local studies presented by Abegg (1939), Louisiana; Schendel (1940), Oklahoma; Clayton (1952), Kansas; Boatwright (1955), Kansas; Inglis (1955), central Texas; Odum (1955), Georgia; Raun and Wilks (1964), south Texas; Goertz (1965), Oklahoma; and Arnwine (1966), Oklahoma. These studies provided only limited considerations of sex ratios, litter size and maximum longevity. Sex ratios usually were determined for fewer than a dozen animals (e.g., Boatwright, 1955). Often these ratios produced results that were not easily explainable, other than small sample size. Maximum longevity for individual cotton rats was generally expressed as "...less than six months..." (Odum, 1955; Goertz, 1965). Most studies were only one or two seasons in length (e.g. , Clayton, 1952) thus not providing recaptures for an extended period of time. Distance moved by individual cotton rats has been noted by most researchers in field studies (e.g., Inglis, 1955; Goertz, 1965; Arnwine, 1966). Great variability in these distances is noted.

Litter size in *Sigmodon* has been reviewed by Goertz (1965) and examined specifically in terms of effects of northward dispersal by Kilgore (1970). Unfortunately, Goertz (1964) records no information on litter size above southern Oklahoma or south of the United States border. Therefore, he was unable to make any substantial comparisons. Likewise, Kilgore (1970) failed to take his southern sample far enough south of his northern sample to fully appreciate the extent to which litter size may vary in the cotton rat. The current study will present additional data and attempt to substantiate regional differences relative to the theories and examples of Lord's (1960) review and studies by Hoffman (1958); Moore (1961); Barkalow (1962); Jackson (1965); Keith, *et al*. (1966); and Smith and McGinnis (1968).

Body Temperature

Body temperature affects behavior and chemical reactions so profoundly in virtually all organisms that Bartholomew (1968) has termed it one of the major parameters in biology. Despite its importance, investigations on this subject in many mammalian species are relatively few in number when compared to other topics in the biological sciences (Johansen and Krog, 1960). Furthermore, investigations of body temperature have been generally confined to one or a few individuals per study reportedly due to a lack of facilities or time on the part of the researcher. Laboratory studies by several authors (Hart and Heroux, 1953; Bartholomew and Cade, 1957; Bartholomew and MacMillan, 1961; Hudson and Bartholomew, 1964; Hart, Pohl, and Tenner, 1965; Hainsworth, 1967; Getz, 1968; and Sealander and Guess, 1970) have contributed methodology and data on a number of mammalian species. Field studies, even fewer in number, which contribute to our knowledge of temperature regulation in small mammals, have been reviewed by Cleveland (1968).

One aspect of temperature regulation in mammals, production of torpor, has been investigated in a few species, particularly in the genus Perognathus (Bartholomew and Cade, 1957; Tucker, 1962). No such phenonomen has been yet demonstrated in Sigmodon. Knowledge of whether this condition can actually occur in the cotton rat could be helpful in explaining temperature problems apparently faced by Sigmodon in cold weather (Dunaway and Kaye, 1961; Goertz, 1964; Cleveland, 1968). Low body temperatures could be explained by this entry of cotton rats into torpor. Lack of the ability to enter torpor favors alternative explanations proposed by Cleveland (1968). As used here, torpor is defined as the physiological condition achieved by certain animals to minimize loss of energy by slowing down the body processes. This condition is further characterized by a sluggish or inactive individual whose body temperature drops, usually rapidly, to one or two degrees above ambient. Tucker (1962) reported that torpidity can be induced in pocket mice (*Perognathus californicus*) by reducing the amount of food provided. Similar studies of *Perognathus longimembrus* (Bartholomew and Cade, 1957) indicated that periods of torpor lasting several days resulted when the availability of food was reduced. Hudson and Bartholomew (1964) reported that *Citellus* (=*Spermophilus*) *tereticaudus* became torpid when deprived of food and water. Bartholomew (1968) postulated that similar conditions could cause a wide variety of other small mammals to become torpid. However, reports of food and water deprivation effects on body temperatures of many species (including *Sigmodon*) are not presently available. Dr. J. E. Brower of Northern Illinois University has recently completed work on a number of species of the genus *Perognathus* and suggested that *Sigmodon hispidus* could probably be forced into torpor within twenty-four hours by water and food deprivation (personal communication). Work in this present study was undertaken to determine what effect, if any, food and water deprivation and lowered ambient temperature has upon maintaining endothermy in trapped cotton rats, encountering similar conditions.

Considerable lability has been shown in the body temperatures of Sigmodon hispidus in southern Oklahoma (Cleveland, 1968) when measured in the field over four seasons. In order to better understand the role of this lability in the life of Sigmodon, this present study additionally involved the measurement of such temperatures in northern (Kansas) and southern (south Texas) regions.

Parasitology

Parasites have been suggested as a possible factor in large-scale population reduction in cotton rats as early as 1940 (Schendel). In such a population "crash" in Oklahoma, cotton rats were known to have had a variety of ectoparasites, encysted cestodes, and visceral trematodes, cestodes and nematodes. These parasites, however, were not considered to be causative factors in the population reduction since these parasites had also been observed when "stable" population numbers had been present. Unfortunately, neither quantitative data nor species identification were presented (Goertz, 1964). A review of helminths from the cotton rat was reported by Melvin and Chandler (1950). Subsequently, endoparasite surveys of cotton rats have been made in Brazos County, Texas (Hugghins, 1951) and Haskell County, Texas (Kimbrough, 1970). Other parasitological examinations of cotton rats have been concerned with ectoparasites (review in preparation by J. O. Whitaker, personal communication), applications of cotton rat filarial infections to medical research (reviewed by Bertram ,1966), and presentation of new species of endoparasites (Schell, 1952; Melvin, 1952; Smith, 1954). A study of blood parasites of southwest Texas rodents included examination of 400 cotton rats (Eads and Hightower, 1952). The filarial worm, _Litomosoides carinii_, has been reported from cotton rats in Florida (Williams, 1948), "southern states" (Bertram, 1966), south Texas (Westbrook and Scott, 1955) and southwestern Texas (Eads and Hightower, 1952). Hugghins (1951) noted his inability to recover a single filarid in his study in east-central Texas. Although filarids were not specifically mentioned in the north Texas study of Kimbrough (1970), he indicated their complete absence from the 397 specimens examined (personal communication). Neither quantitative data nor species identification of cotton rat endoparasites from Oklahoma or Kansas has been reported.

Objectives

A primary objective of this study was to evaluate the need for retaining both _S. h. texianus_ and _S. h. berlandieri_ as subspecific designations. At the same time, an attempt was made to demonstrate bioclimatic variation in cotton rats to support Bergmann's and Allen's rules.

Another objective was to show regional variation in litter size and reproductive seasonality in cotton rats. An attempt was made to determine the validity of applying the results of isolated studies of cotton rat population dynamics (sex ratios, maximum distance traveled, and maximum recorded longevity) to the species as a whole.

In order to better understand maintenance of endothermy in trapped cotton rats, one objective was to determine whether they would enter torpor as a result of food and water deprivation and lowered ambient temperature. Such a demonstration would aid in the interpretation of field studies on cotton rat body temperatures. Additionally, an attempt was made to show seasonal rectal temperature variation in three different isothermal regions.

Finally, an objective of this study was to provide a quantitative comparison of cotton rat endoparasites from three regions to include the first such studies reported from Oklahoma and Kansas.

METHODS

In 1967, cotton rat field investigations of population dynamics and endothermy were initiated in southern Oklahoma, one-half mile west of the University of Oklahoma Biological Station, just north of Lake Texoma at Willis, Marshall County. Research was continued at this site when additional study areas were established in south Texas, nine miles northeast of Sinton, San Patricio County, and in central Kansas, three miles west of Americus, Chase County.

Animals were live-trapped and their rectal temperatures routinely recorded. Sherman live-traps were used. Rectal temperatures were taken with a Schulthesis cloacal thermometer. Weights were recorded, and body length and hind foot length noted. Sex determinations were made, and reproductive status recorded, when possible. Each animal was toe-clipped as described by Blair (1941) for future identification and then released at the point of capture. Subsequent captures were noted and measurements taken again. Young born in traps were removed to the laboratory until weaning, and then released at the site of capture along with the mother. All were toe-clipped. Each study area was set up in a grid system similar to that described by Cleveland (1968).

Museum specimens were examined from the University of Kansas, University of Oklahoma, University of Oklahoma

Biological Station, University of Texas at Arlington, Texas A & I University, University of Texas at Austin, North Texas State University, Texas A & M University, Welder Wildlife Foundation Museum, and Angelo State University. Specimens were examined for general appearance, standard measurements, sex, location, and embryos present. Skulls were measured for length of nasal, total length, length of alveolar tooth row, interorbital breadth, and distance between auditory bullae. Only those specimens identified as adults based upon the criterion of Chipman (1965) for weight and nasal length were used.

Cotton rats from areas adjacent to the study areas were examined for endoparasites. Autopsies included examination of pleural cavity, liver, kidneys, stomach, intestine, caecum, and urinary bladder. Endoparasites were relaxed in physiological saline for 20-30 minutes, fixed in AFA (alcohol-formalin-acetic acid) and transferred to 70% isopropyl alcohol for identification. To insure that all adult filarids were removed, the pleural cavity was washed with saline as described by Westbrook and Scott (1955) to achieve "virtually 100% recovery of these worms."

The laboratory investigations of effects of food and water deprivation upon rectal temperature involved cotton rats trapped in Wise County, Texas. All were adults by weight (Chipman, 1965). Animals were acclimated to laboratory conditions for one week prior to initiation of tests. Ambient temperature was 25°C. ± 1°C. A constant photoperiod of LD 9:15 centered at 12:30 was maintained. Animals were housed in individual cages to prevent huddling. Prior to initiation of tests, rolled oats, Purina rabbit pellets, and water were available *ad libitum*. All rectal temperatures were taken with a Schulthesis cloacal thermometer.

Seven cotton rats (three male, four female) were deprived of food for six days. Water was available *ad libitum*. Rectal temperatures were recorded daily. Five cotton rats (two males, three females) were used as controls. Controls had food and water *ad libitum*. All animals in this test were at an ambient temperature of 25°C. ± 1°C..

Following the first test, the seven cotton rats were deprived of food and water until death occurred. Autopsies were performed within three hours after the death of each rat.

In a second temperature test, five cotton rats (three females, two males) and a control group of five cotton rats (two males, three females) were both acclimated for two days to an ambient temperature of 18°C. ± 1°C.. Food and water were removed from the test group. The controls had food and water *ad libitum*.

Morphological data and litter sizes were pooled by isothermic regions for comparison since temperature has already been pointed to as the paramount environmental factor for *Sigmodon*. The major study areas were located in three different ten-degree isothermic regions affording an excellent means for comparison of samples (Figure 3).

Skeletal materials, mammal skins, and parasitological specimens prepared in the course of this study are deposited in the North Texas State University Museum of Zoology and the Texas Wesleyan College Museum of Zoology. Determination of means and standard errors was made with the assistance of a General Electric Mark I computer.

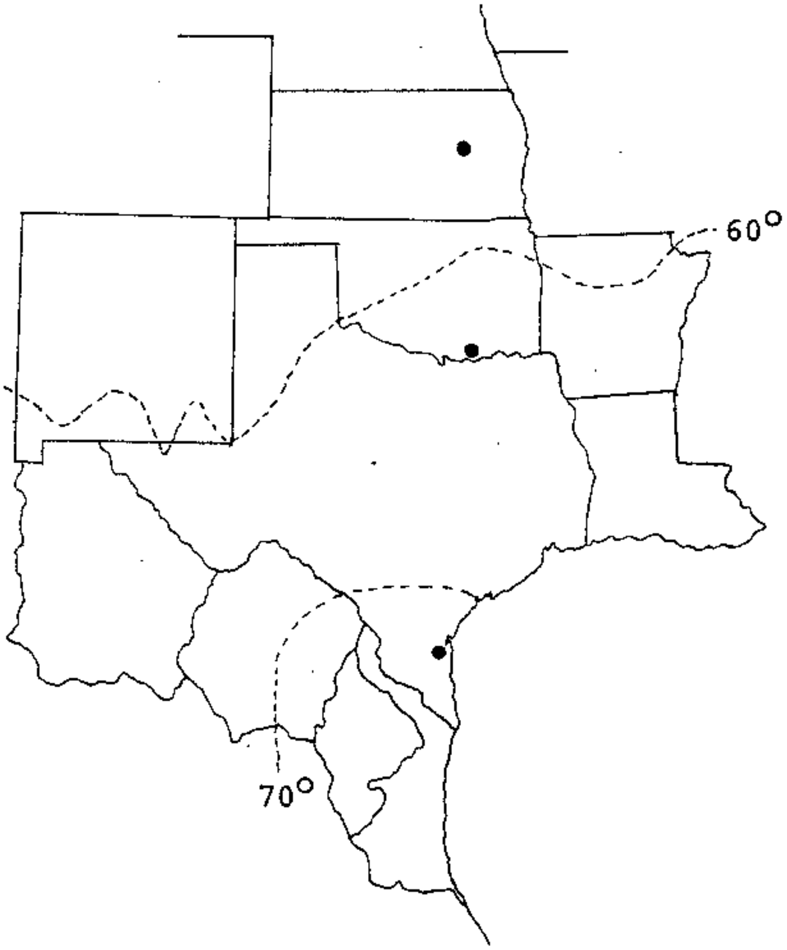

Fig. 3--Geographic area of this study. Dotted lines indicate normal annual temperature isotherms in degrees Fahrenheit. Circles mark study plot locations.

RESULTS

A total of 1310 cotton rats was live-trapped over a five-year period (1967-1971) from fifteen counties in three states in the United states and Tamaulipas, Mexico. Live-trapping in eleven other counties in five states yielded no cotton rats. This represented a total of 10,087 trap-nights (number of traps set multiplied by the number of nights trapped) in the field. In addition, 649 museum specimens were examined from 133 counties from eight states in the United States. Also, fifty-four specimens were examined from eleven localities in three states in Mexico.

It is of particular interest that extensive trapping for over a week in southern Iowa, northwestern Missouri, extreme northeastern Kansas, and southern Nebraska failed to produce any Sigmodon. Trapping in southern Nebraska was attempted at five sites, including the same locality as reported by Jones (1960) for the state (Appendix II).

Cotton rats were trapped across the study region from local populations ranging from very high to very low relative densities. Diverse habitats were occupied by the rats with no single "type" habitat predominating. Well-drained habitats with abundant cover vegetation were generally preferred. Since railroad right-of-ways usually meet these requirements, these areas were frequently found to have abundant numbers of cotton rats. The vegetation types for the different trapping sites from Mexico to Kansas are shown in Table I. Six of the twenty-four areas (thirty-seven percent) where cotton rats were located, were along railroad right-of-ways. Adjacent areas with similar vegetation frequently would be without cotton rat populations. The types of predominant vegetation where cotton rats were trapped confirm their ability to adapt to diverse habitat areas.

The weights of cotton rats taken during the field study are shown in Figure 4. Included in these weights are the weights from Payne County, Oklahoma. A total of 562 cotton rats weights was measured. A general increase in weights from south Texas to central Kansas was evident. The leveling off in central Kansas might have resulted from the small sample size. The upper extremes of weights from three other localities are higher. However, the mean of the Kansan weights shows a measureable (thirty-seven percent) increase over the south Texas mean. The variation in body weights from museum specimens is less dramatic, but consistent with the trend in field weights (Figure 5). The sample is smaller, but contains only cotton rats whose weight exceeds 120 grams. Sixty-five adult museum specimens with weights were available.

TABLE I

VEGETATION TYPES IN TRAP SITES

State	County	Vegetation Type
Kansas	Lyon	(1) Bluestem, locust, sumac (2) Ragweed, bluestem
Kansas	Chase	Bluestem, sunflower, dewberry (RR)*
Oklahoma	Marshall	(1) Broomweed clumps (2) Bluestem, dewberry, briar (3) Bermuda grass, dewberry
Texas	Bee	Ironweed clumps
Texas	Childress	Mesquite, juniper, short grass
Texas	Cottle	Leaf cactus, short grass, weeds (RR)
Texas	Kenedy	Bluestem, mesquite (RR)
Texas	Kleburg	Short grass, weeds (RR)
Texas	Nueces	(1) Bluestem, weeds (2) Weeds, trash (RR)
Texas	Randall	Mesquite, weeds
Texas	Refugio	Johnson grass, weeds (RR)
Texas	San Patricio	(1) Cactus, broomweed, mesquite (2) Bluestem, weeds (3) Short grass, weeds, mesquite

TABLE I --Continued

State	County	Vegetation Type
Texas	Shelby	Bermuda clumps
Texas	Tarrant	Hackberry, Johnson grass
Texas	Wise	(1) Dense bluestem (2) Cactus, bluestem (3) Weeds (dumpground)
Chihuahua	- - -	Tamarix , bermuda grass

* RR denotes habitat along railroad right-of-way

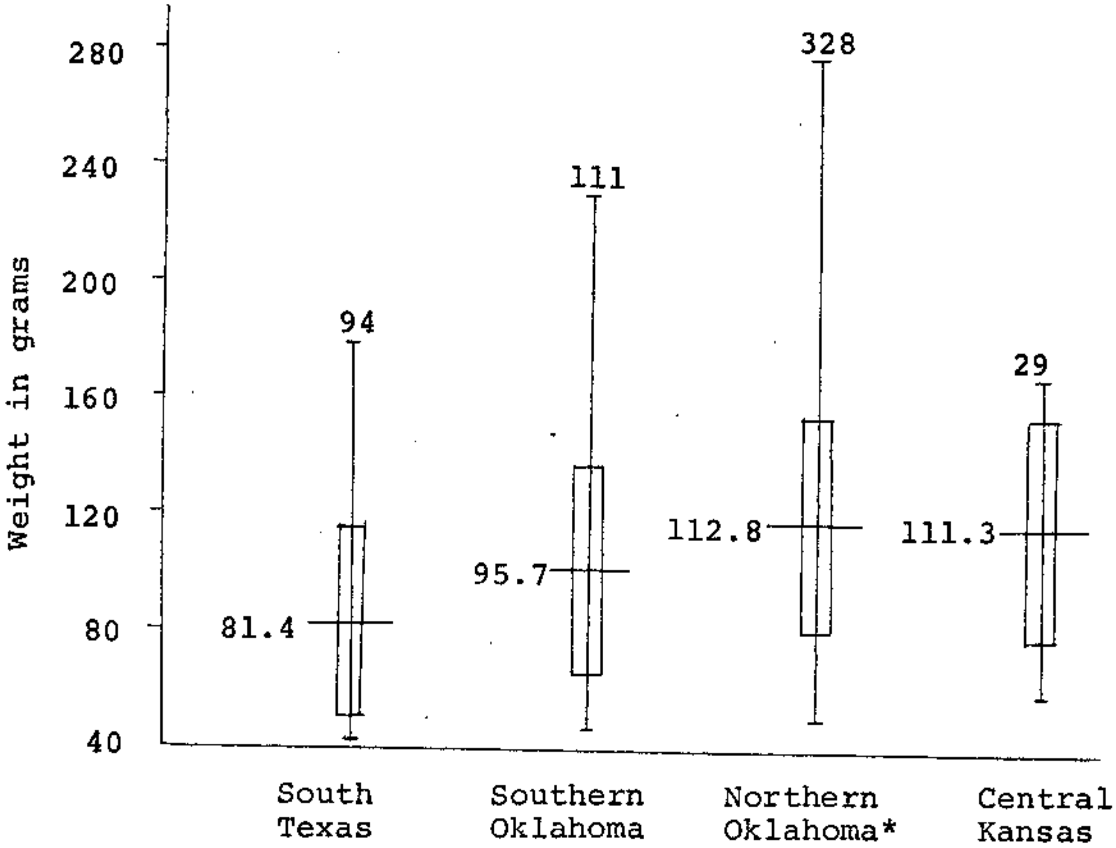

Fig. 4--Field weights of Sigmodon over forty grams. Vertical lines represent the range, horizontal lines the mean, and rectangles twice the standard error. Numbers above the vertical lines indicate sample size.

*From Hepworth data

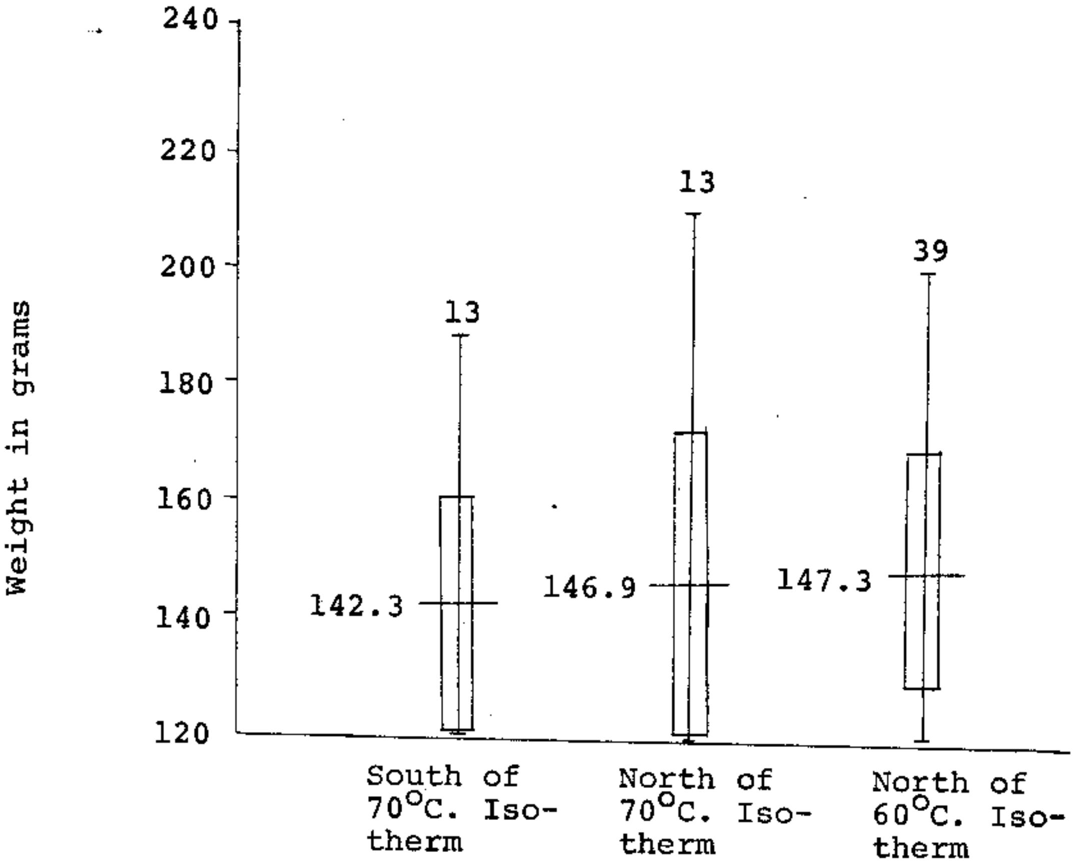

Fig. 5--Variation in body weights for Sigmodon above 120 grams. See Fig. 4 for explanation.

An increase in total skull length of cotton rats may be seen in Figure 6. These measurements represent variations in adult skull length along a south to north line from Faumare, Mexico, to McPherson County, Kansas. The clinal character of the means is similar to that already shown (Figures 4,5). Body lengths are presented for museum specimens in Figure 7. These 634 measurements show a slight clinal trend with shorter-bodied cotton rats in the warmer southern isotherm. Examination of the auditory bullae revealed regional differences in the distances between these structures. These measurements, shown in Figure 8, present a clear clinal trend toward greater skull breadth. The mean and both extremes show great uniformity in regional variation. Together, Figures 4 through 8 reveal an increase in overall body size for cotton rats and provide the first application of Bergmann's Rule to this species.

Allen's Rule is demonstrated in cotton rats in the tail length measurements shown in Figure 9. The longer tails of warm, southern region rats show a decrease in length toward the cooler, northern isotherms. A total of 622 tail measurements was made from the three isotherms to provide evidence of this clinal character in Sigmodon.

A curious phenomonon in Sigmodon molar tooth row length is shown in Figure 10. An apparent increase in this

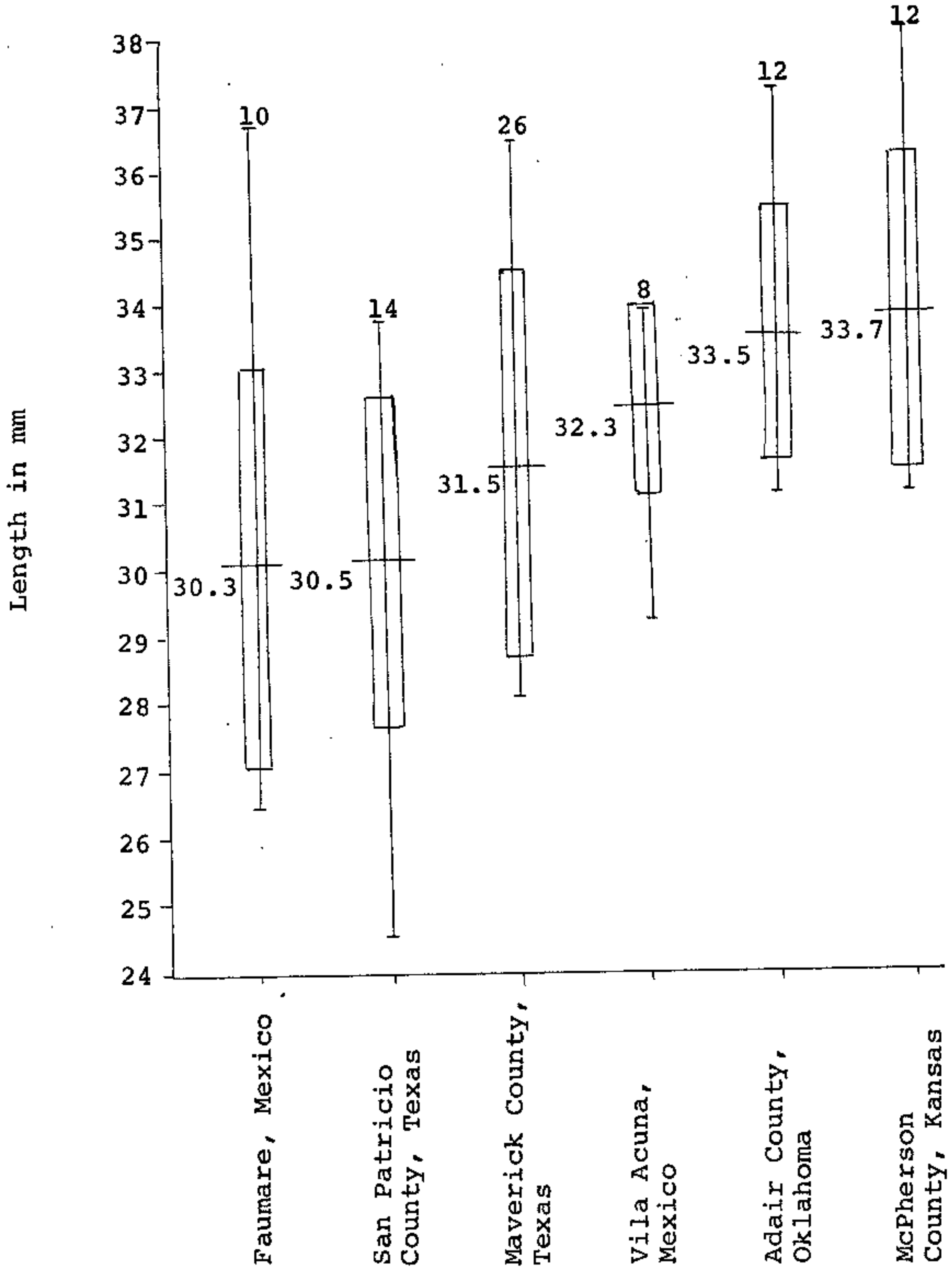

Fig. 6--Variation in total skull length of adult Sigmodon hispidus along a south to north line. See Fig. 4 for explanation.

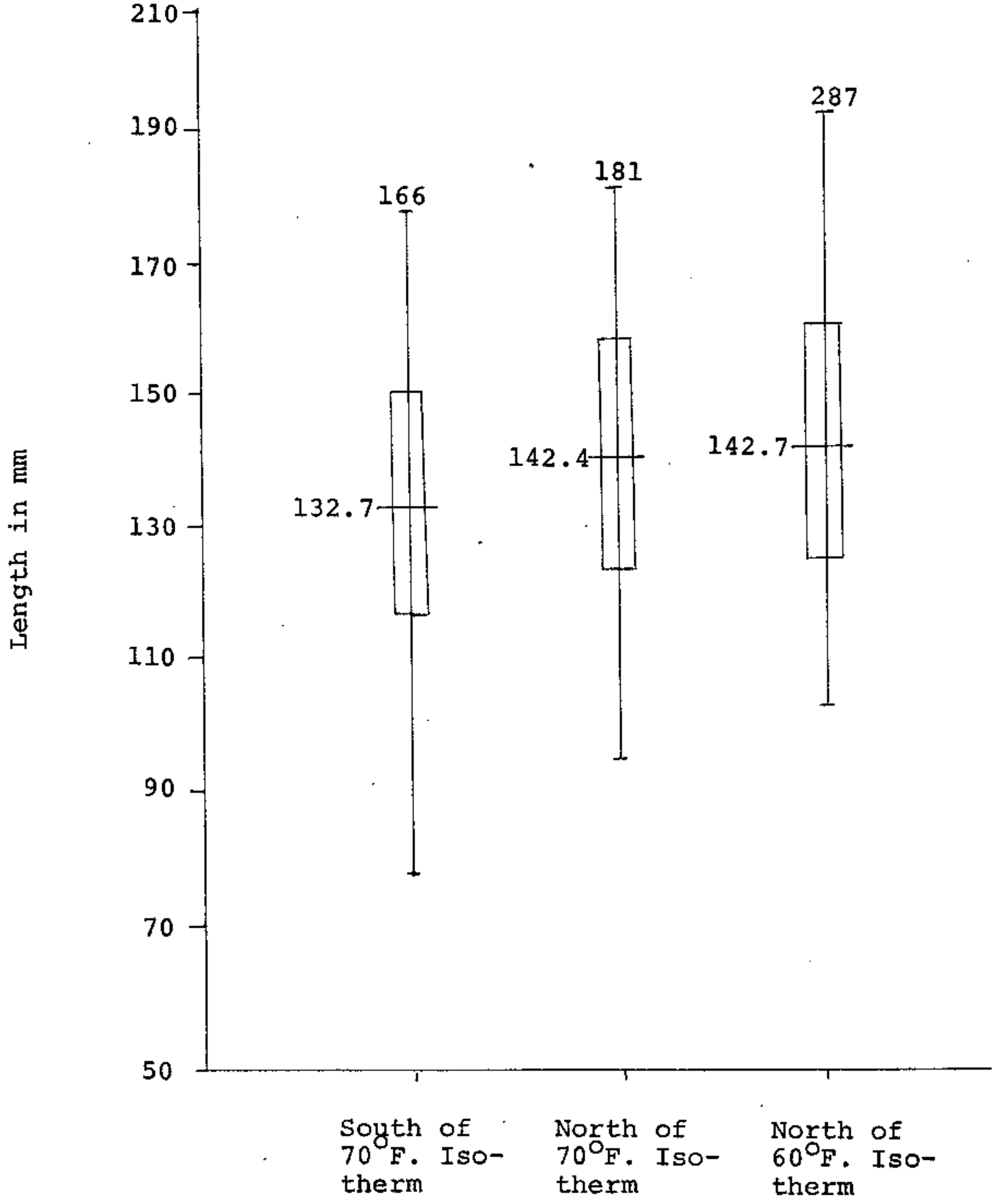

Fig. 7--Variation in body length of <u>Sigmodon hispidus</u>. See Fig. 4 for explanation.

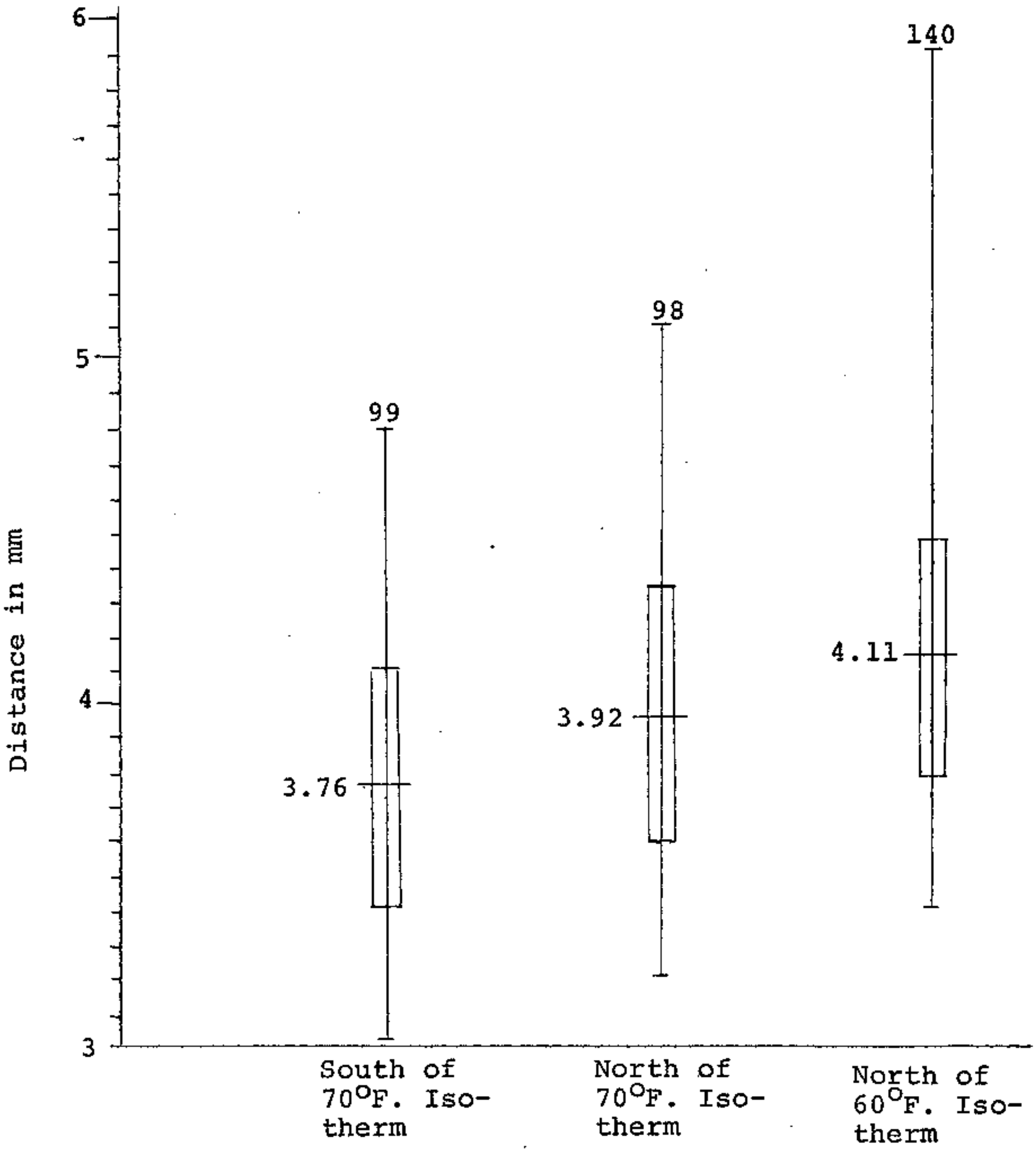

Fig. 8--Variation in inter-auditory bullae distances of <u>Sigmodon hispidus</u>. See Fig. 4 for explanation.

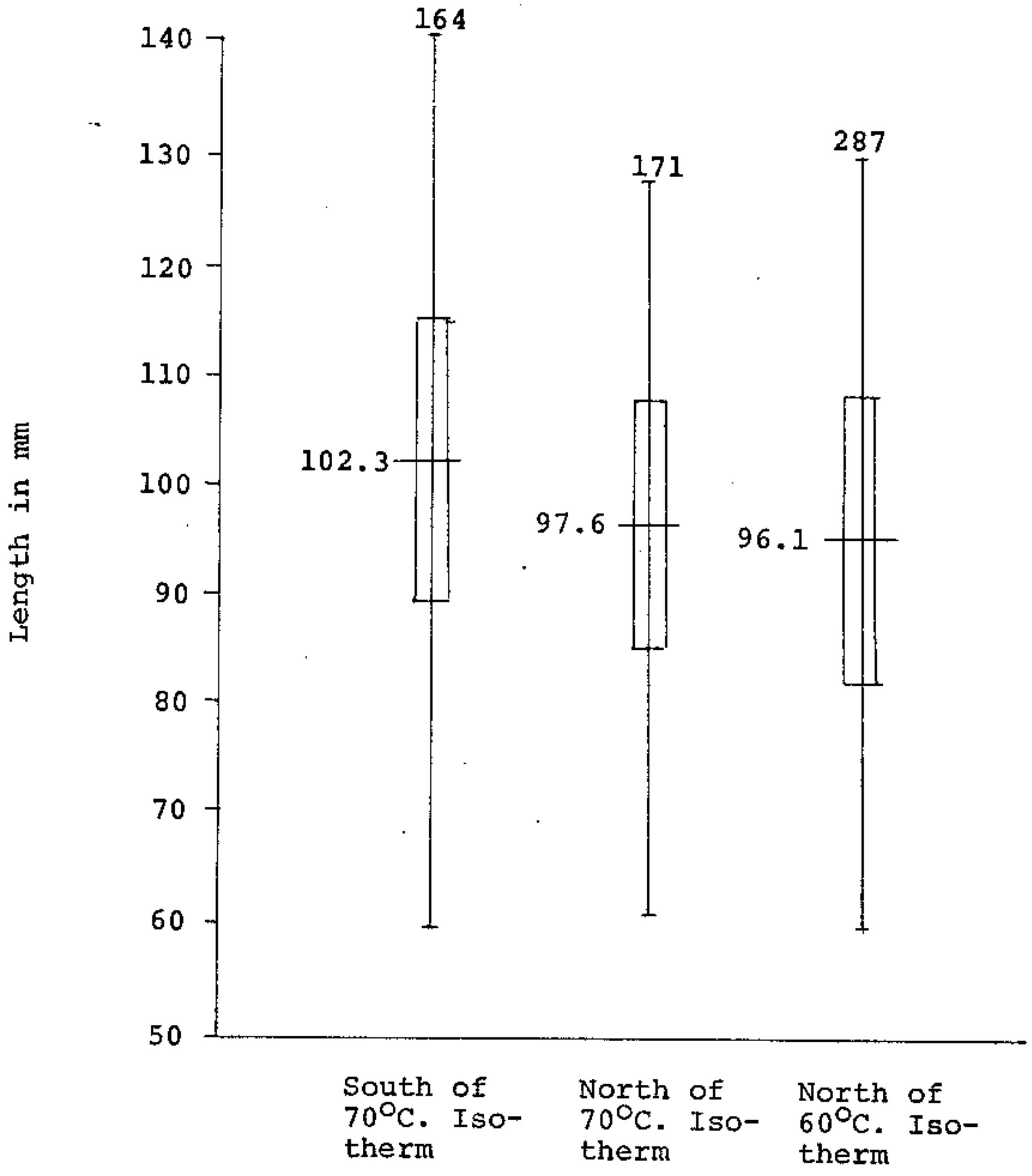

Fig. 9--Variation in tail length of *Sigmodon hispidus*. See Fig. 4 for explanation.

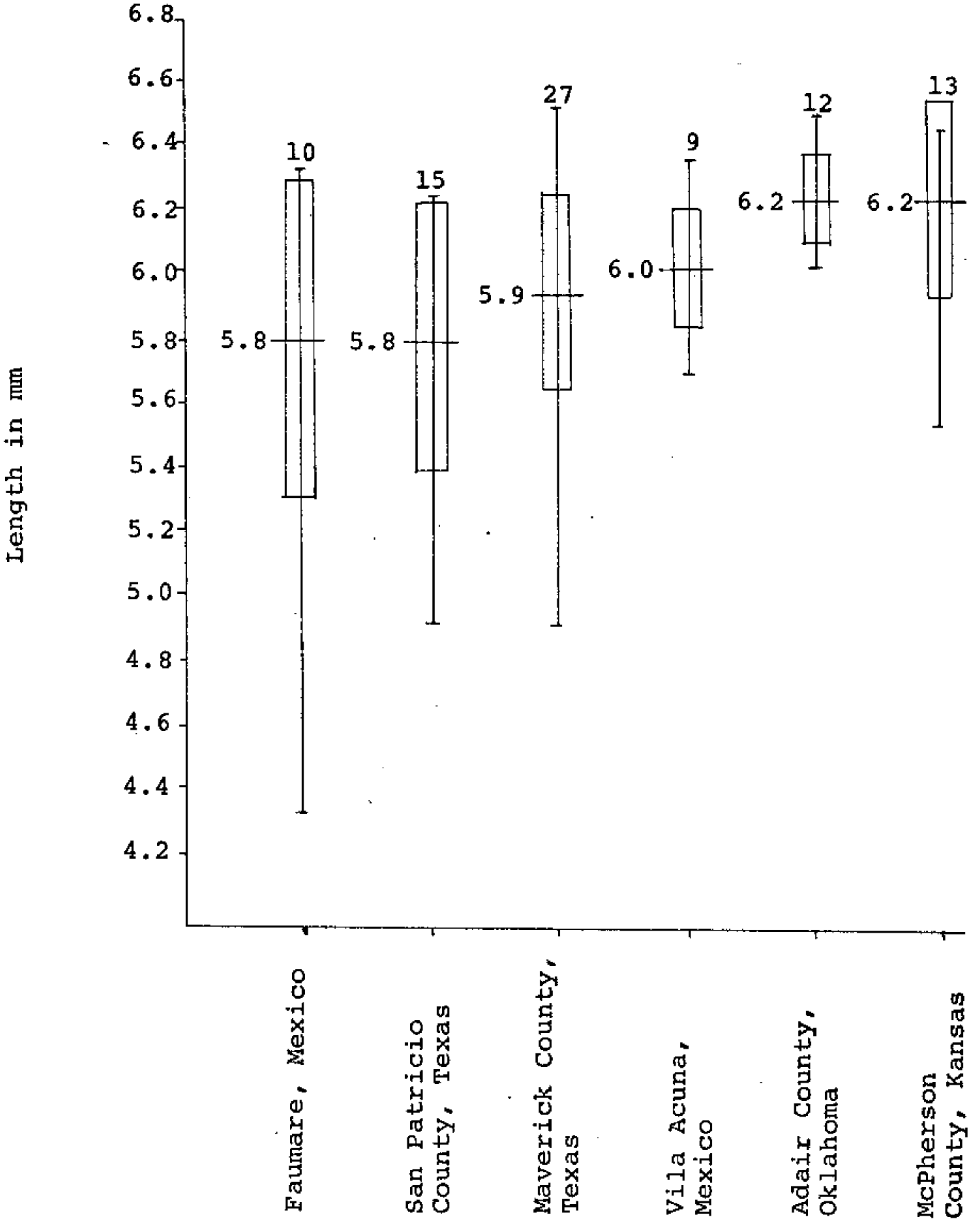

Fig. 10--Molar tooth row variations of <u>Sigmodon hispidus</u> along a south to north line. See Fig. 4 for explanation.

length became evident during analysis of measurements. This increase in length appears to be correlated with an increase in skull size. Additionally, teeth from southern cotton rats unexplainably tended to be worn to a higher degree than those from the northern areas.

Litter size variations are summarized in Figure 11. These represent a total of 95 records across the study area. The individual litter sizes and sources of data are shown in Table II. Regional pooling into three isotherms provides a definite demonstration of variation in litter size. Northern isotherm cotton rat litters are larger. Southern litters are noticeably smaller. A clear clinal effect is evident. All of the largest litters (ten or above) are in the two more northern isotherms. Thirty-nine percent of the southern litters are three or under in number. Only nine percent of the litters born north of the 60°F. isotherm are three or under in number (Table II).

Periods of the year during which cotton rats were observed to be sexually active are indicated in Figure 12. Severe winters were encountered in the northern areas during which snow was still on the ground one year until April 1. Reproductive activity in the northern cotton rat populations appears limited to less than six months of each year. An increase to ten months out of twelve in the Oklahoma population is evident. South Texas cotton rats

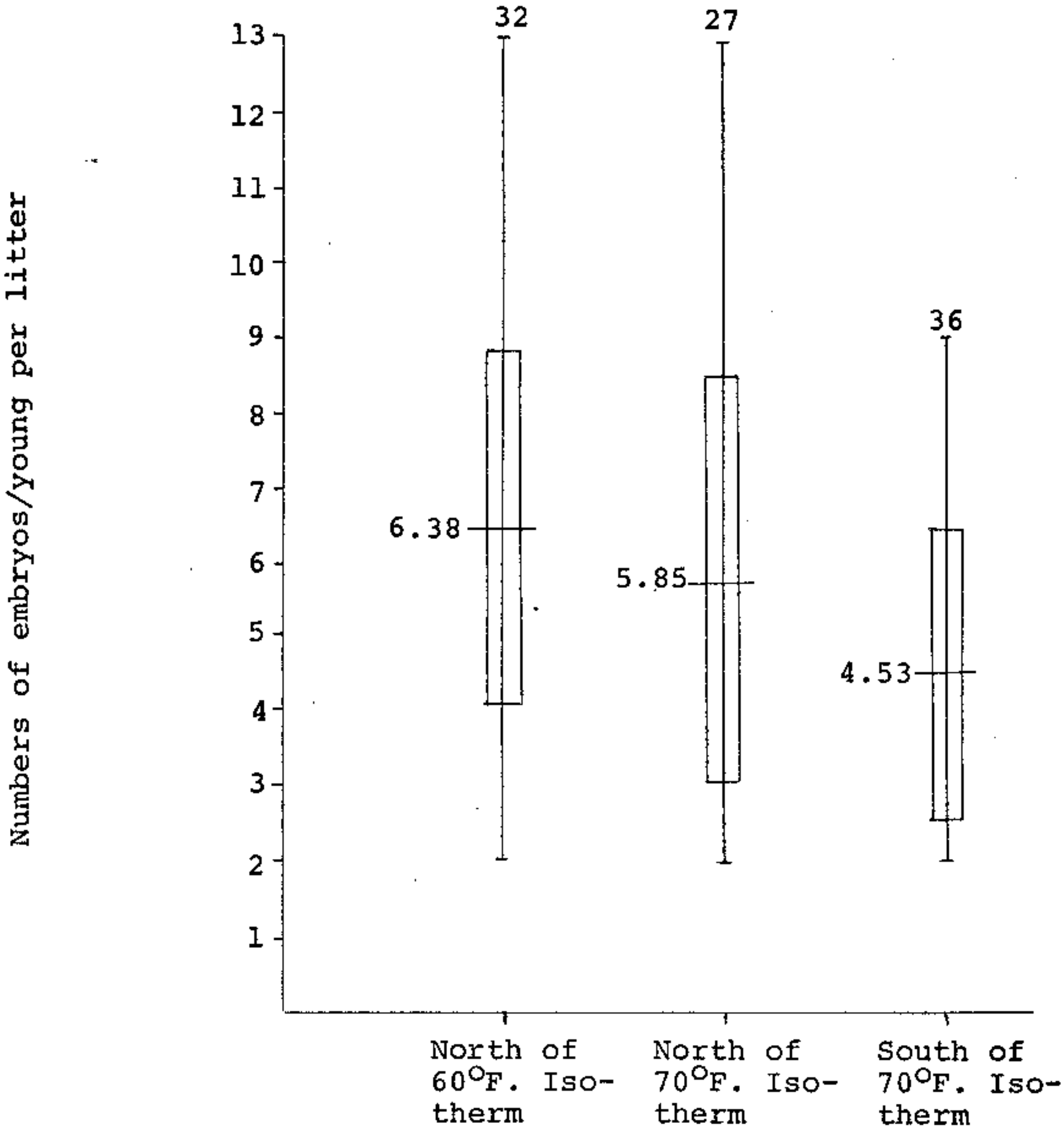

Fig. 11--Variation in the litter size of <u>Sigmodon hispidus</u> across three 10°F. Isotherms. See Fig. 4 for explanation.

TABLE II

INDIVIDUAL LITTER SIZES FROM THREE ISOTHERMS

Location	Litter size records	Source
North of 60°F. isotherm	2, 5, 5, 6, 6, 6, 7	This study
	11	Choate and Genoways (1966)
	3, 4, 4, 4, 4, 5, 5, 5, 6, 6, 6, 6, 6, 6, 6, 7, 7, 7, 8, 8, 8, 10, 12, 13	Museum notations
North of 70°F. isotherm	2, 3, 6, 7, 7, 10, 13	This study
	2, 3, 3, 3, 3, 4, 4, 4, 4, 4, 6, 6, 6, 7, 7, 8, 8, 8, 9, 11	Museum notations
South of 70°F. isotherm	4, 5, 6, 9	This study
	3, 5, 5, 5, 5, 6, 6, 6, 7	Museum notations
	7, 8	Dice (1937)

TABLE II --Continued

Location	Litter size records	Source
South of 70°F. isotherm	2, 3, 4, 4, 4, 5, 8	Alvarez (1963)
	2, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 4, 4, 7	Hall and Dalquest (1963)

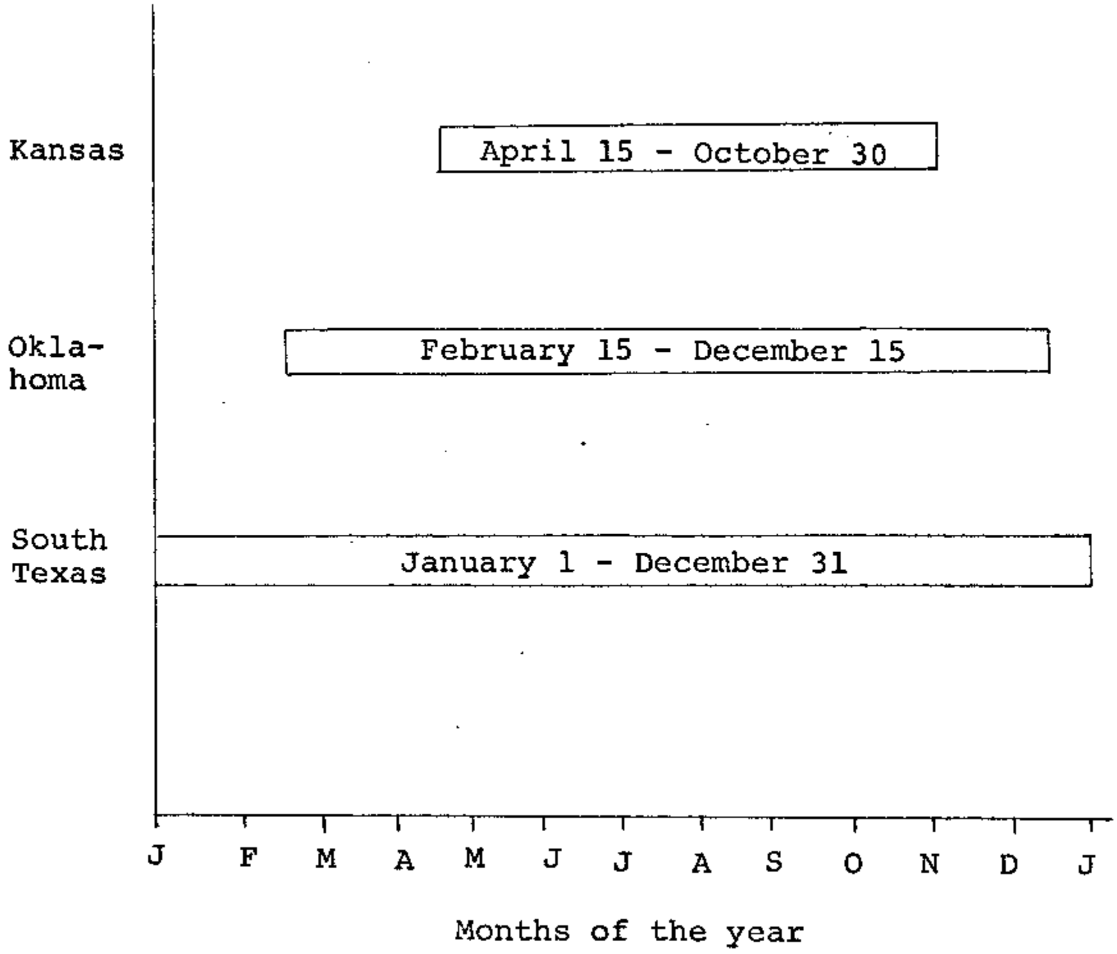

Fig. 12--Periods of sexual activity during the year for *Sigmodon hispidus* as demonstrated in the three areas under study.

are reproductively active year round.

A compilation of male-female ratios in the three study areas is shown in Table III. Chi-square tests of these data reveal that the results are not significantly different from the expected 1:1 ratio of males to females. Included in Table III is the sex ratio of cotton rats from Payne County, Oklahoma (Unpublished data furnished by J. L. Hepworth). No significant variation in sex ratio can be seen in the 1240 animals sampled.

Maximum recorded longevity for each study is presented in Table IV. This represents the longest actual time period a cotton rat continued to be captured during the field studies. The fact that none of the cotton rats on the south Texas study plot were ever recorded for a period over four months is unusual. Likewise, the sixteen month longevity for an Oklahoma cotton rat is a new maximum record. The greatest distance traveled by a single cotton rat was 1315 feet (Figure 13). The only consistent trend shown was for males to have slightly longer travels than females.

Seasonal field rectal temperatures are pooled for the individual study localities in Figure 14. The mean for each season is shown with the exception of spring and winter temperatures for Kansas. At these times population levels were so low that trapping Sigmodon beneath the snow

TABLE III

MALE-FEMALE SEX RATIO

	Males	Females	Chi-Square
Kansas Plot			
Observed	28	28	0.000
Expected	28	28	
Oklahoma Plot			
Observed	383	366	1.107
Expected	374	374	
Payne County Oklahoma*			
Observed	166	162	0.048
Expected	164	164	
South Texas Plot			
Observed	48	59	1.355
Expected	53	53	

*Payne County data from J. L. Hepworth

TABLE IV

MAXIMUM RECORDED LONGEVITY OF SIGMODON HISPIDUS

Location	Sigmodon Identification Number	Greatest length of time between captures	Sex	Capture records
Kansas	111	+ 11 months	Male	July 22, 1969* June 1, 1970 June 4, 1970 June 6, 1970
Oklahoma	215	+ 16 months	Male	March 23, 1968 March 24, 1968 May 4, 1968 August 3, 1969
South Texas	204	+ 4 months	Female	January 17, 1970 January 18, 1970 February 7, 1970 March 14, 1970 May 2, 1970 May 3, 1970

* Born this date to captured female; released August 1, 1969 on study plot.

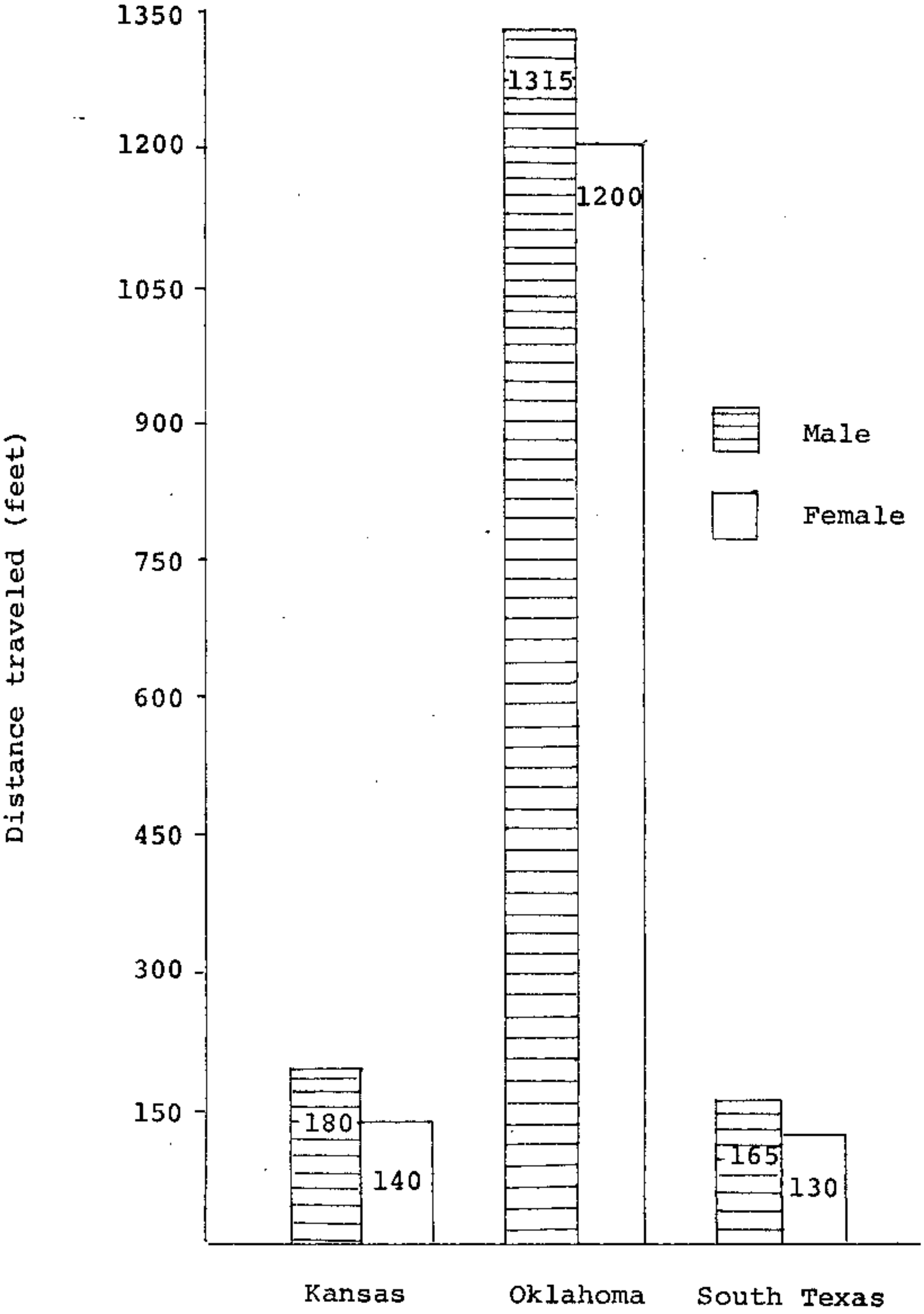

Fig. 13--Greatest distance traveled by individual cotton rats on study plots.

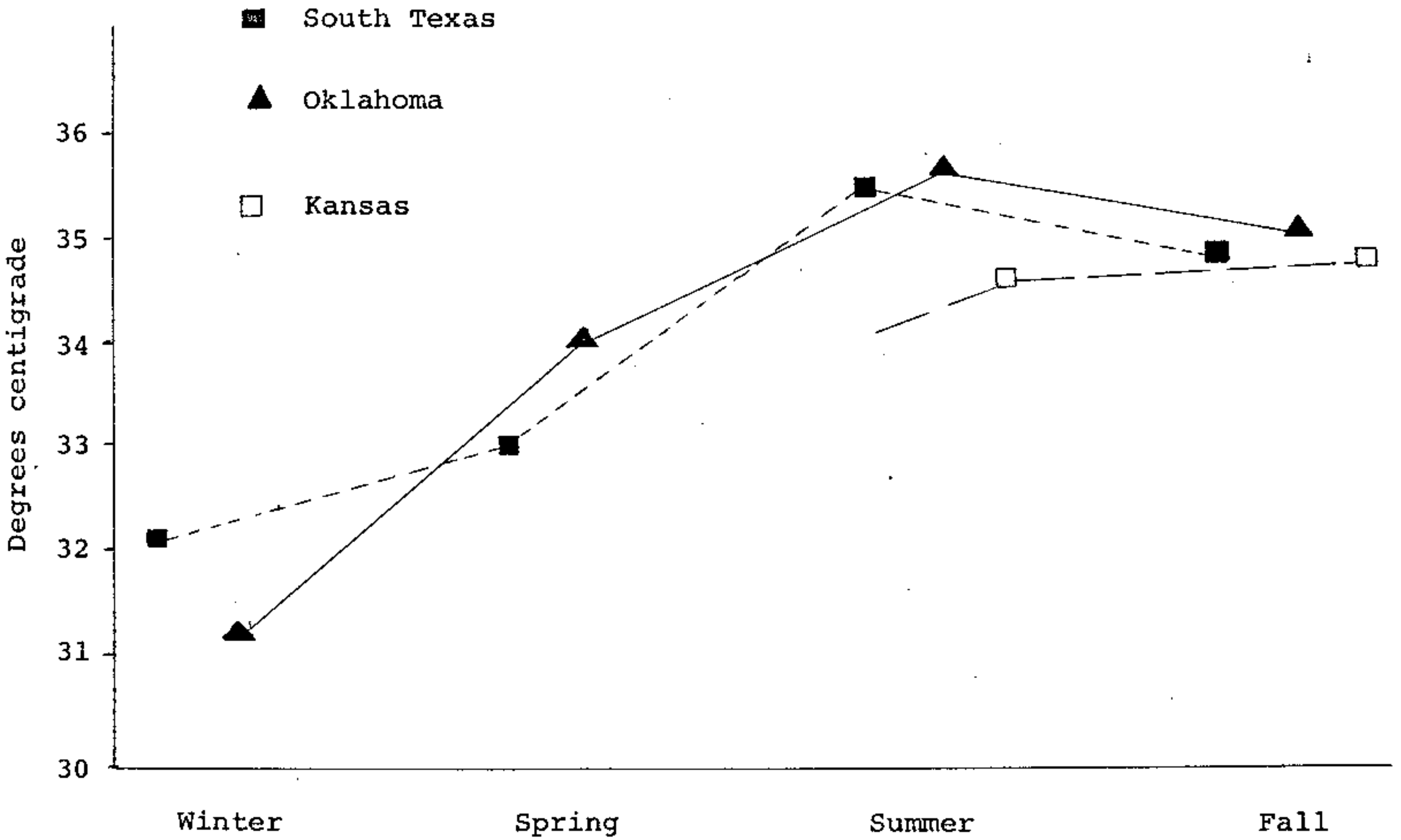

Fig. 14--Seasonal rectal temperature variation in Sigmodon taken on study plots. No cotton rats were taken during the spring and winter months in Kansas.

cover proved fruitless. Temperatures recorded (especially fall) show a remarkable uniformity considering the variation in ambient temperatures from south Texas to Kansas. All means recorded are a single degree centigrade or less within each season.

Laboratory attempts to produce torpor in cotton rats through food and water deprivation and lowered ambient temperature were not successful. The results of a food deprivation trial at room temperature (25°C. ± 1°C.) are shown in Figure 15. No appreciable decrease in rectal temperature was recorded until the fourth day. Even then, the decrease was less than two degrees centigrade. Animals were still active at the end of the test. Removal of food and water in a second trial (Figure 16) under lowered ambient temperature (18°C. ± 1°C.) produced less than a single degree centigrade drop in the first three days. The test was terminated on the sixth day with the death of a test animal. No evidence of torpor was observed.

The results of the starvation of seven cotton rats are shown in Table V. The first three deaths occurred in cotton rats with endoparasitic infection. The last four were determined to be free of endoparasites. Under food and water deprivation, cotton rats with parasitic infection would be under additional stress.

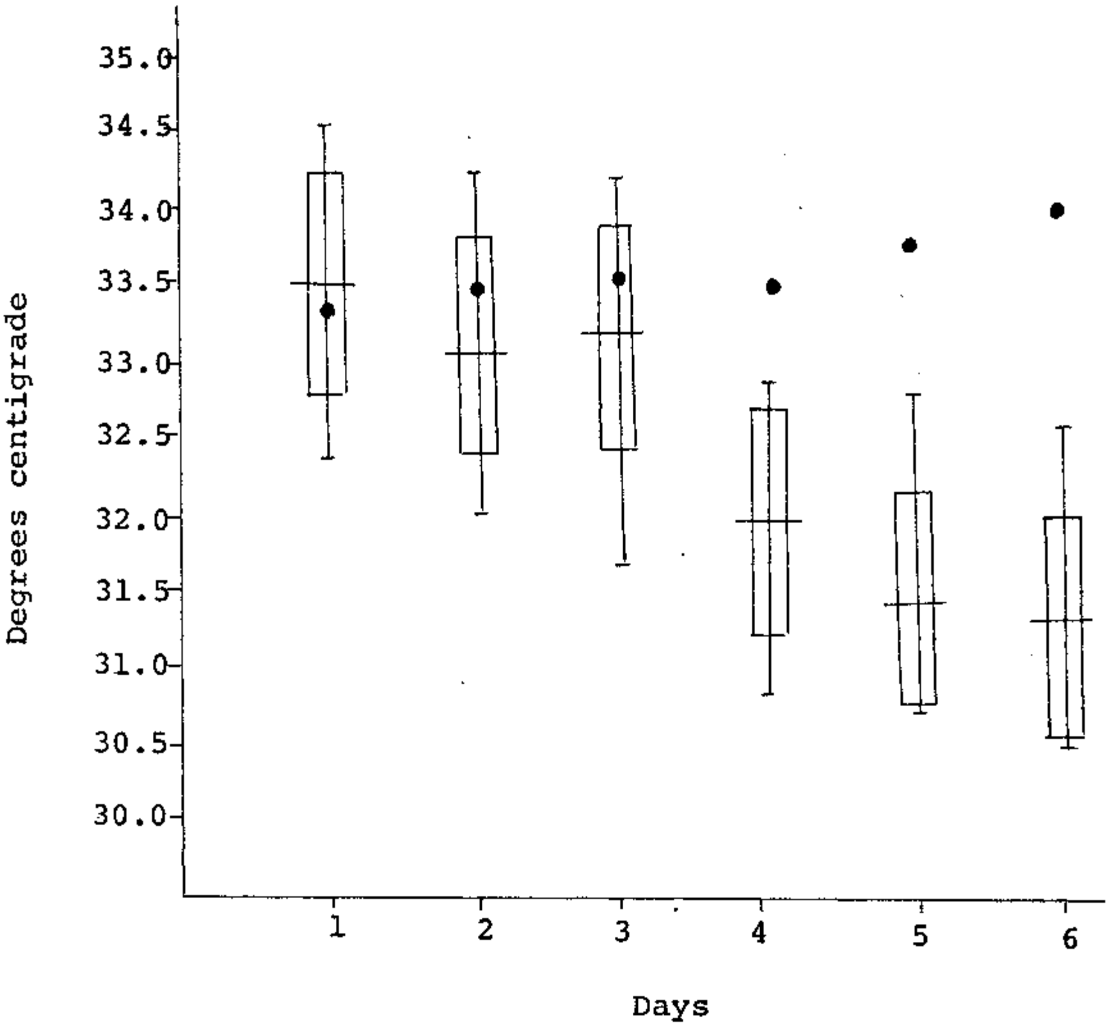

Fig. 15--Ranges and means of rectal temperatures for _Sigmodon_ without food for six days. Mean rectal temperatures for the controls are shown by circles. Ambient temperature is 25°C. ± 1°C.. See Fig. 4 for other explanations.

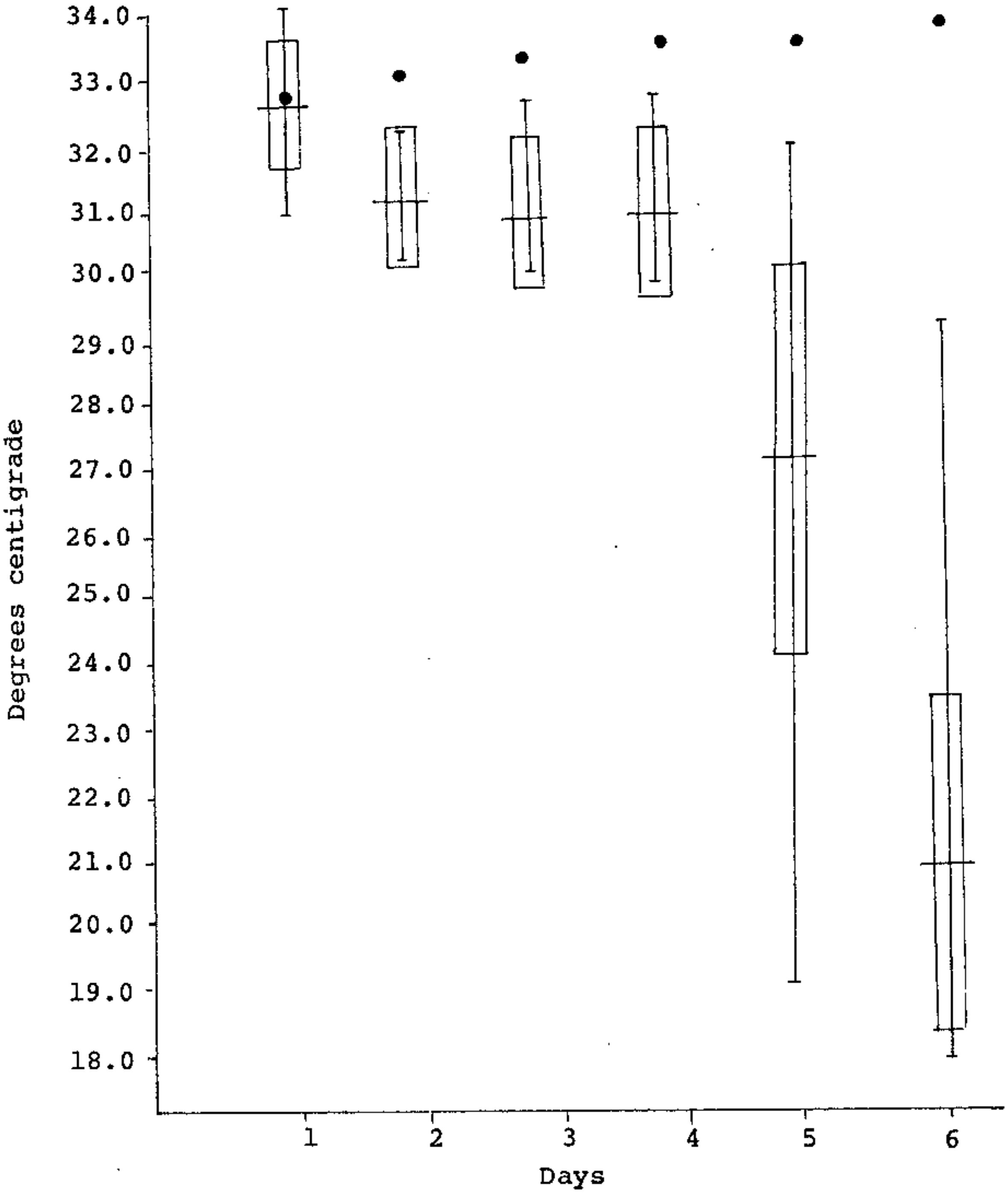

Fig. 16--Rectal temperatures of Sigmodon without food and water under lowered ambient temperature (17°C. ± 1°C.). Mean temperatures for controls are shown by circles. Food and water were removed on day one, after measurement of rectal temperatures. See Fig. 4 for other explanations.

TABLE V

RELATIONSHIPS BETWEEN STARVATION FATALITIES AND PARASITES IN *SIGMODON*

Specimen Number	Parasite Species	Number of Parasites	Location in Rat	Order in Which Death Occurred
27	*Monoecocestus sigmodontis*	2	Intestine	1
	Physaloptera hispida	6	Stomach	
10	*Monoecocestus sigmodontis*	2	Intestine	2
	Physaloptera hispida	1	Stomach	
6	*Physaloptera hispida*	1	Stomach	3
	Unidentified parasite	2	Intestine	
11	None	-	-	4
0	None	-	-	5
16	None	-	-	6
7	None	-	-	7

A total of 477 endoparasites was taken from the sixty-one cotton rats examined for this purpose. Table VI shows the relationships between the three study regions in terms of numbers of hosts and parasites. Only sixteen cotton rats were recorded without observable endoparasites. Between 67.8 and 80.0 percent of the cotton rats were infected with endoparasites in each study area. The nematode, Physaloptera hispida, was found in the three study regions (Table VII). The highest numbers of parasites and the largest percentages of infected rats were reported from the northern areas. It was found in the stomach, often causing this organ to bulge conspicuously. The cestode, Monoecocestus sigmodontis, was reported from an average of 55.7 percent of the populations sampled (Table VIII). This cestode was the predominant intestinal parasite. It appeared uniformly across the area under study. Filarid worm adults were recovered from cotton rats only in the southern populations where 32.1 percent were infected (Table IX). Filarids were recovered from the pleural cavity. No filarids were reported from north-central Texas, Oklahoma, or Kansas. Taenioid cysticerci were found from six cotton rats as shown in Table X. These were all taken from infected livers in a small, but uniform, percent of the populations studied. An unidentified

TABLE VI

NUMBERS OF INFECTED SIGMODON AND TOTAL NUMBERS OF PARASITES FOR EACH AREA

Location	Number Examined	Rats Infected		Total Numbers of Parasites
		Number	Percent	
Kansas	18	14	72.2	75
Oklahoma	15	12	80.0	113
South Texas	28	19	67.8	289
Total	61	45	73.7	477

TABLE VII

PHYSALOPTERA HISPIDA FROM SIGMODON HISPIDUS

Location	Number Examined	Rats Infected		Total Parasites Collected	Average No. Per Infected Host	Largest No. From Single Host
		Number	Percent			
Kansas	18	5	27.7	32	6.4	19
Oklahoma	15	3	20.0	23	7.7	21
South Texas	28	4	14.3	6	1.5	3
Total	61	12	19.6	61	5.8	--

TABLE VIII

MONOECOCESTUS SIGMODONTIS FROM *SIGMODON HISPIDUS*

Location	Number Examined	Rats Infected		Total Parasites Collected	Average No. Per Infected Host	Largest No. From Single Host
		Number	Percent			
Kansas	18	10	55.6	33	3.3	9
Oklahoma	15	10	66.7	76	7.6	17
South Texas	28	14	50.0	89	6.4	15
Total	61	34	55.7	198	5.8	--

TABLE IX

LITOMOSOIDES CARNII FROM *SIGMODON HISPIDUS*

Location	Number Examined	Rats Infected		Total Parasites Collected	Average No. Per Infected Host	Largest No. From Single Host
		Number	Percent			
Kansas	18	0	0	0	-	-
Oklahoma	15	0	0	0	-	-
South Texas	28	9	32.1	130	14.4	37
Total	61	9	14.7	130	8.8	-

TABLE X

TAENIOID CYSTICERCI IN THE LIVER OF *SIGMODON*

Location	Number Examined	Rats Infected		Total Parasites Collected	Average No. Per Infected Host	Largest No. From Single Host
		Number	Percent			
Kansas	18	3	16.7	3	1	1
Oklahoma	15	1	6.7	2	2	2
South Texas	28	2	7.1	4	2	2
Total	61	6	9.8	9	1.5	-

intestinal parasite was collected from cotton rats from all three areas (Table XI). It has been previously unreported from Sigmodon hispidus. An unidentified trematode species was found in two cotton rats (Nueces and Bee counties in south Texas). No parasites were found in the kidneys, urinary bladders, or caecum.

Other mammalian species, either trapped or sighted on the study plot areas, and therefore associated directly or indirectly with Sigmodon, are listed in Table XII.

TABLE XI

UNIDENTIFIED INTESTINAL PARASITE FROM SIGMODON

Location	Number Examined	Rats Infected		Total Parasites Collected	Average No. Per Infected Host	Largest No. From Single Host
		Number	Percent			
Kansas	18	3	16.7	7	2.3	4
Oklahoma	15	2	13.3	6	3.0	3
South Texas	28	2	7.1	6	3.0	4
Total	61	7	11.3	19	2.7	-

TABLE XII

MAMMALIAN ASSOCIATES OF *SIGMODON HISPIDUS*

-Trapped-		
Kansas	Oklahoma	Texas
Peromyscus leucopus *Neotoma floridana* *Synaptomys cooperi* *Microtus ochrogaster* *Blarina brevicauda*	*Peromyscus leucopus* *Neotoma floridana* *Sylvilagus floridanus* *Didelphis marsupialis* *Mus musculus* *Reithrodontomys fulvescens* *Perognathus hispidus*	*Peromyscus leucopus* *Neotoma micropus* *Baiomys taylori* *Didelphis marsupialis* *Mus musculus* *Reithrodontomys fulvescens* *Perognathus hispidus* *Oryzomys palustris* *Geomys bursarius*
-Sighted-		
Canis latrans	*Geomys bursarius* *Dasypus novemcinctus* *Mephitis mephitis*	*Canis latrans* *Dasypus novemcinctus* *Lynx rufus* *Tayassu tajacu* *Odocoileus virginianus*

DISCUSSION

Taxonomy and Bioclimatic Variation

Sigmodon hispidus has a wide geographic range and occupies a rather diverse habitat and might be expected to exhibit considerable geographic variation. That geographic variation has been observed is indicated by the fact that thirty-three described subspecies are listed by Hall and Kelson (1959). However, *Sigmodon hispidus* has been demonstrated to be undergoing rapid range expansion (Cockrum, 1948; Jones, 1960; and Genoways and Schlitter, 1966). Much of this has occurred in post-Wisconsin time (Zimmerman, 1970), and there seems to be a discrepancy between this expansion and the implied subspeciation. *Sigmodon hispidus*, with an expanding, relatively continuous range covering several thousand miles, does not appear to conform to the basic concept of a species which is diverging into "subspecies" (Mayr, 1963) at least in the United States. Geographic or other barriers would be expected to separate, for example, populations of *Sigmodon arizonae* west of the Sierra Madre Occidental of Mexico and *Sigmodon hispidus* to the east (Zimmerman, 1970). No such barriers exist across the present continuous range of *Sigmodon hispidus* (excluding insular populations). Temporary isolation may occur when local populations are separated (periodically) by temporary barriers and elimination of populations from certain localities by predators (Schnell, 1968), drought (Inglis, 1955), severe winters (Dunaway and Kaye, 1964), fires, flooding, or similar catastrophic events.

The subspecific status of *S. h. texianus* and *S. h. berlandieri* has hardly been seriously questioned since the evaluation made by Coues (1877). Rather, efforts have generally attempted to support this concept. However, even Coues was reluctant to support the division into subspecies as the following quotations indicate:

> "...Baird's own measurements of *S. berlandieri* do not bear out his statement that the *tail is 'equal* to or longer than the trunk'..."
> "...the type of '*berlandieri*', certainly does not show us the slightest *shade* of color different from many Carolina skins..."
> "Thus it is impossible for us to regard '*berlandieri*' ...as specifically different from *hispidus*..."

In this synopsis of North American species of *Sigmodon*, Bailey (1902), in describing *berlandieri*, says:

> "Typical specimens of *berlandieri* are no nearer to typical *texianus* than *that species* is to *hispidus* (reference to *eastern* subspecies), so that *if texianus* is to be recognized, *berlandieri* must also be."

The tone of these statements, together with the questionable map (Figure 1) of Bailey (1905) and the findings of this study, point to the undesireability of retaining such a separation of these two subspecies. The map of Bailey is obviously an attempt to show distinct separation of subspecies where no such division ever existed as shown. The original map by Bailey shows *texianus* and *berlandieri* both absent from most of Bexar County, Texas (location of San Antonio). No *texianus* are shown being in this county, despite the fact that the text mentions *texianus* becoming "...slightly paler at San Antonio." An explosive year for cotton rats in Bexar County is described by Attwater several years prior to the paper of Bailey as quoted by Allen (1896). Under such circumstances, little validity can be seen in Figure 1 or the fact that they are considered two taxonomic units. Furthermore, Allen (1905), in his description of *berlandieri* says: "it grades into *texianus*, except in so far as modified by the arid desert country in which it lives." Finally, Allen had earlier (1891) placed the subspecies of *texianus* and *berlandieri* in synonymy.

Among the 2013 cotton rats examined from Veracruz to Nebraska, there was a subtle change in a lighter coloration in the more arid regions to a deeper brown in the more mesic conditions of eastern Texas, eastern Oklahoma, Louisiana, Arkansas, and Missouri. This clinal effect on fur coloration is described as a basic evolutionary variation commonly called Gloger's Rule. Generally, this rule states that endotherms have lighter pigmentation in drier environments and relatively darker pigmentation in more humid situations (Heese, Allee, and Schmidt, 1937). Results of the present study, especially those results depicted in

Figures 4 through 12, indicate a clinal effect which is demonstrated not only morphologically but also physiologically. Further discussion of these results will follow. No further justification for the continuation of S. h. berlandieri as a separate subspecies can be seen to exist.

More recent accounts of massive population increases in cotton rats were reported by Haines (1963) for Texas and generally reviewed by Goertz (1964). In the past five years, cotton rats may have retreated from Nebraska. Rodent populations across the southwestern United States have dropped to very low numbers (numerous personal communications). Isolated populations (along well-drained, heavily-covered habitats) of moderately large numbers have scattered across the range. As is the general rule small numbers of Sigmodon hispidus remain in most areas despite severe drops in population numbers (Gier and Bradshaw, 1957; Gier, 1968). Drastic reductions have also been recorded in more southern locations (Raun and Wilks, 1964) in south Texas. These extremely small population remnants are made up of individuals who have survived the environmental factors that caused the decimation of their relatives. Natural selection of the cotton rats most likely to survive and produce offspring is undoubtedly strong. Genetic composition of resulting litters originates from a small parentage of survivors. The alternating of massive population explosions (range expansion) coupled with "near-extinction" in low years (strong natural selection pressures) produces a species ideally suited for the creation of a cline.

Hoffmeister (1951) has suggested that north-south clines exist in *Peromyscus* species with the size of body and skull decreasing from north to south. This theory has been supported by work on *Peromyscus maniculatus* (Judd, 1970). Actually, this theory suggested by Hoffmeister was a restatement of the bioclimatic rule of Bergmann (Mayr, 1956). The demonstration of Bergmann's Rule in *Neotoma* by Brown and Lee (1969) was considerably more evident. In Figure 4, field weights taken over several years revealed a pronounced north-south variation in cotton rat weights. Figure 5, which eliminated all sub-adults using criterion by Chipman (1965), showed a slight, but consistent increase in body weight from south to north. Even if body weight were considered too variable to be examined in demonstrating Bergmann's Rule, the marked clinal variation in total skull length (Figure 6) and increase in inter-auditory bullae distances (Figure 8) should eliminate any skepticism. Even body length (Figure 7) presented a trend toward increase in size of northern populations. The basic nature of the increase could also be seen in the increase in molar tooth row

(Figure 10). No particular selective advantage is suggested for this slight increase in molar tooth row. Rather this is more likely a reflection of an increase in skull size. Schreider (1964) has summerized the research which supports Bergmann's Rule as an evolutionary adaptation to a changing thermal environment. The results presented here are actually conservative in that generally Chipman's (1965) definitions of adult cotton rats was used. His animals were from scattered locations mainly in southeastern localities in the United States. When his criterion are applied to morphologically smaller cotton rats from Veracruz (for example) the sample becomes biased in favor of presenting an image of a larger animal than actually exists. That is, what might be considered a sub-adult (by nasal length, weight, and other measurements) in Louisiana might actually be an adult in Tamaulipas, Mexico. Care needs to be exercised in applying Chipman's age determination to animals from the entire range of Sigmodon hispidus. The periodic range extensions and gradual northward movement may represent an indication of how rapidly Bergmann's Rule is being applied by cotton rats; i.e., how quickly adaptations for larger size are genetically incorporated into populations.

The extremely flat, small ears of Sigmodon hispidus, together with the inaccuracy of their measurement by many investigators, make them unfavorable as a means of demonstrating Allen's Rule. Tail length variation (longer in southern populations) was demonstrated in a clinal presentation.

Population Dynamics

Examination of data presented by Goertz (1964) showed considerable variation in different geographic locations in regard to reproduction and litter size in Sigmodon. Unfortunately, Goertz included (through no fault of his own) another species of Sigmodon in his analysis. This inclusion confused his treatment of the subject.

A compilation of litter sizes (and embryo numbers *in utero*) from various sources, presented in Table II and Figure 11, demonstrated a clinal effect similar to those found in litter sizes of various North American mammals (Lord, 1960; Smith and McGinnis, 1968). Barkalow (1962) suggested that latitude is apparently related to reproduction (including litter size) in the cottontail rabbit. However, Barkalow failed to indicate any relationship between latitude and change in temperature. He did relate this to the fact that reproductive activity commences in southern populations earlier than northern ones. Therefore, to compensate for the decreased days per year for reproduction, Barkalow suggested a corresponding increase in litter size. This was in agreement with studies of

Lord (1960), Smith and McGinnis (1968), and Keith, Rongstad and Meslow (1966). Reproductive activity in *Sigmodon hispidus* (Figure 12) agreed with the trends suggested by the above authors in relationship to litter size as shown in Figure 11. Clayton (1952) and Inglis (1955) suggested possible differences in sex ratios in *Sigmodon*. However, Table III presents an examination of the sex ratio in 1240 cotton rats. The lack of a significant difference in such a large sample refutes the idea of a sex ratio imbalance in *Sigmodon*.

Maximum recorded time between capture for cotton rats reveals extreme variation. This is in agreement with results in other studies such as those by Odum (1955) where maximum length was less than five months. McCulloch (1959) noted seven months as his largest record; and Goertz (1964) recorded twelve months as the longest individual survival. The study by Goertz (1964) supported the theory that habitat quality was the most important factor in survivorship in a local population of cotton rats. The dense composition of the Oklahoma study plot probably influenced the long life of the sixteen month old cotton rat reported in Table IV. The sixteen month age is a new field record for life span in *Sigmodon hispidus*. Since few cotton rats ever exceed six months in age (Odum, 1955; Goertz, 1964) both Oklahoma and Kansas sites recorded rats that lived for an exceptionally long period. No explanation for the short life for cotton rats on the south Texas plot is offered, although predation on Sigmodon hispidus by barn owls (Tyto alba) in this area has been observed to be heavy (Raun, 1960).

Further evidence for the influence of habitat cover in the Oklahoma study plot is the wide-ranging of cotton rats as shown by a comparison of greatest distance traveled with the other study areas (Figure 13). The consistently larger distances traveled by males agrees with other studies (Abegg, 1939; Inglis, 1955; Arnwine, 1966).

It has been noted that cotton rats, being of sonoran origin, are apparently more susceptible to environmental stress than many other rodents (Chipman, 1966; Sealander and Guess, 1970). Further evidence points to temperature as being the most important of these environmental stresses (Cockrum, 1952; Goertz, 1964; Cleveland, 1968; Sealander and Guess, 1970; Kilgore, 1970; Dunaway and Kaye, 1971). The similarities between summer and fall rectal temperatures of all three study locations indicates cotton rats maintain uniform endothermy across their range in Texas, Oklahoma and Kansas. The body must therefore be compensating for environmental temperature differences through morphological and physiological adaptations. The demonstration of Allen's and Bergmann's Rules is important in explaining two ways these adaptations may be expressed.

The failure of Sigmodon hispidus to enter torpor within twenty-four hours (Figures 15, 16) lends support to the evidence for seasonal variation in rectal temperature reported by Cleveland (1968). The combined deprivation of food and water produced a gradual drop in rectal temperature. Combined with a drop in ambient temperature, these factors produce a dramatic drop in rectal temperature after four days. This substantiates the theory advanced by Dunaway and Kaye (1961) relating effects of prolonged, lowered ambient temperature to cotton rat mortality.

Parasitology

Parasitological examinations revealed variation in the percentage of cotton rats infected (Table VII, Table IX, Table XI) in the three study areas. Of special interest was the failure of adult filarids to be demonstrated from the two northern populations. This parasite (Litomosoides carinii) is a common inhabitant of Sigmodon hispidus from Florida to south Texas. However, Hugghins (1951) mentioned his failure to locate a single filarid in his sample from Brazos County, Texas. Kimbrough (1970) failed to report filarids from Haskell County, Texas. Kimbrough (personal communication) says his investigation of each specimen was complete and included an examination of the pleural cavity. There were positive filarid findings from southwest Texas (Eads and Hightower, 1952). Except for the observations in Oklahoma by Goertz (1964), parasitological examinations of cotton rats have not been previously made in north central Texas, Oklahoma, or Kansas. Examination of a small sample of cotton rats from Denton County, Texas revealed no filarid infection. The intermediate host for _Litomosoides carinii_, the tropical rat mite (_Ornithonyssus bacoti_), is a widespread mite across the United States (Bertram, 1968). Specimens have been taken from areas where no filarids were reported. The suggestion that cotton rats can become immune to _Litomosoides carinii_ after an initial infection was discounted by Scott, et. al. (1946). Williams (1948) mentioned that some localities, without filarid infection, had larger cotton rats. If they do, in fact, grow to larger size without filarids and northern regions are without such infection, cotton rats would become better suited for their environment.

The effect of parasites on cotton rats under food and water deprivation, shown in Table V, reveals a situation which is probably detrimental during drought periods. The large percentage (55.7) of cotton rats infected with _Monoecocestus sigmodontis_ is not as large as that reported for Haskell County, Texas by Kimbrough (1970). He reported 306 out of 397, or seventy-seven percent infected with this cestode. However, the Oklahoma population reveals a 66.7

percent infection. Hugghins (1951) reported twenty percent of the cotton rats in Brazos County, Texas infected with Monoecocestus sigmodontis. This cestode is apparently well distributed throughout cotton rat populations.

Physaloptera hispida was found in increasingly larger percentages of cotton rats in a south to north direction. Kimbrough (1970) reported sixteen percent infection in Haskell County, Texas. This study revealed an average of 19.6 percent. None were recorded by Hugghins (1951) in Brazos County, Texas.

Taenioid cysticerci are widespread, but have a general low incidence in cotton rats. The small numbers (usually one or two) per infected host were not universal, however. Hugghins (1951) reported a cotton rat with eight embedded in its liver. His thirty-three percent infection rate for cysticerci is unusually high. The twelve percent reported by Kimbrough (1970) is more in line with the results of this study (nearly ten percent). Local conditions may vary greatly with cysticercus infection, however, since the Kansas site recorded 16.7 percent. The unknown intestinal parasite (Table XI), although in low incidence (only 11.3 percent), was found in all three study areas. This wide distribution, together with the lack of a description of this parasite in cotton rats, points to a further study in this field.

CONCLUSIONS

The subspecific designation of Sigmodon hispidus berlandieri should be placed in synonymy with Sigmodon hispidus texianus. The demonstration of clinal effect across the range of these "subspecies" eliminates the validity of such a designation.

Bergmann's Rule of bioclimatic variation has been demonstrated in Sigmodon hispidus from northeastern Mexico to Kansas. Larger-bodied cotton rats inhabit cooler northern areas. Smaller-bodied cotton rats occupy habitats in warmer southern regions. The tendency for Sigmodon hispidus to exhibit shorter tails in the north and longer tails in the south (Allen's Rule) was shown.

Litter size was shown to increase from southern to northern areas. An inverse relationship to length of breeding season was shown. Differences in sex ratios in Sigmodon hispidus from northeastern Mexico to Kansas are not statistically significant. Maximum life span for an individual cotton rat can be up to sixteen months, although this is noted to be the maximum for any individual recorded to date. Distance traveled by cotton rats, although influenced by many factors, is consistently greater for males. The actual distance traveled is too dependent upon local conditions such as habitat cover.

No isolated field studies of Sigmodon population dynamics should be applied to the species as a whole. Variations in populations through a clinal effect and variations locally in the habitat dictate caution in making generalizations. This was especially shown through differences in maximum life span, length of breeding season, litter size, greatest distances traveled, and morphological characters. With a clinal nature shown, restraint should be exercised even in making age determinations based upon calculations from studies like the one by Chipman (1965).

Temperatures of cotton rats follow a relatively uniform seasonal pattern in the three isotherms under study. Sigmodon hispidus does not enter torpor under the conditions produced in these studies. This inability to decrease metabolic processes and lower body temperature under stress heightens the necessity for morphological adaptations (such as increase in body size) to a changing environment along the northern extent of its range.

A quantitative comparison of cotton rat endoparasites was performed from south Texas, Oklahoma, and Kansas. The absence of filarid infection in the two northern populations was demonstrated. Laboratory findings, which point to parasitic infection as detrimental to cotton rats under food and water deprivation, suggest that the role of cotton rat parasites needs additional study.

APPENDIX I

STUDIES ON SIGMODON HISPIDUS

HABITATS IN VARIOUS REGIONS

Area	Habitat	Source
Southern Nebraska	Mixed grasses along ridge	Jones, 1960
Elk County, Kansas	Open grassland	Arnwine, 1964
Kansas	Grass areas, especially weeded areas	Hall, 1955
Piedmont section, Georgia	Greatest numbers along terraces in fields in thickets	Odum, 1955
Tennessee	"...dried lake bed amid sedges, rushes, willows..."	Dunaway and Kaye, 1961
Northeastern Oklahoma	Oak-elm association	Blair, 1938
	Plum thickets	
	Bluejoint-switchgrass association	
	Grama-beardgrass association	
	Clumps of prickly pear cactus	
Southern Louisiana	"...cane fields and truck farms...on ridges surrounding marshes...under thick matted grasses..."	Svihla, 1929

APPENDIX I --Continued

Area	Habitat	Source
Brazos Valley, Texas	"...under logs and fallen branches... ...in hollow trees... ...along cotton fields living inside abandoned railroad cars..."	Strecker, 1929
Central Texas	"...lodged stems of a stand of cattail left by a receding lake..."	Inglis, 1955
Southern New Mexico	Tamarix stand	Troy Best (personal communication)
South Texas (near Sequin)	"...thickets of horny chapparrel and bunches of cactus ...edges of cotton fields..."	Allen, 1905
South Texas	Prickly pear-short grass association	Hall, 1955
Lower Sonoran of New Mexico	Chihuahuan desert	Bailey, 1913
Northern New Mexico	"...dense stand of grass clumps amid scattered brush..."	Anderson and Berg, 1959
Globe Arizona	Beargrass, Johnson grass, _Agave_ _sp_., _Yucca_ _sp_.	Zimmerman, 1970
Eastern Durango	Overgrazed Chihuahuan desert	Zimmerman, 1970

APPENDIX I --Continued

Area	Habitat	Source
Tamaulipas	"...grassy areas, on a beach having sparse grass..."	Alvarez, 1963
Veracruz	"...grasslands, overgrown clearings, weed-grown borders of fields, dense growths of saw-grass or bunchgrass, borders of jungles or forest..."	Hall and Dalquest, 1963
Central Texas	"...dense stand of lodged grasses on the edge of an ungrazed field..."	Halloran, 1942

APPENDIX II

LIFE HISTORY AND OTHER OBSERVATIONS ON INDIVIDUAL COTTON RATS AND AREAS UNDER STUDY

Nebraska

Although trapping failed to produce cotton rats from this state, residents of Auburn (in southern Nebraska) spoke of "strange brown rats" having been present several years prior to my investigations. Sites trapped in Nebraska were those determined to be highest in potential for *Sigmodon*.

Iowa - Missouri

Trapping in these states resulted in a recording of *Microtus*, *Mus*, *Peromyscus*, *Rattus*, *Blarina*, and *Reithrodontomys* species. Railroad right-of-ways, river banks and other sites holding most potential for *Sigmodon* were investigated. Areas surrounding Shenandoah, Iowa, were heavily trapped producing mainly the "northern counterpart" of the cotton rat, *Microtus*.

Kansas

Extreme northern Kansas trap sites likewise produced no *Sigmodon*.

Populations of *Sigmodon* in central Kansas were found especially in conjunction with *Blarina*, *Microtus*, and

Peromyscus populations. A single southern bog lemming (*Synaptomys cooperi*) was taken at the central Kansas study area.

Of special interest is the trap site in Chase County where nineteen *Sigmodon* were taken in two days. These rats were trapped on steep slopes between two sets of railroad tracks (separated by about 25 feet). The previous day the local game warden stated that cotton rats were no longer found in his county. These animals were divided between juveniles, large males, and pregnant and non-pregnant females. The *Andropogon*-*Rubus*-*Helianthus* vegetation provided heavy cover between the tract areas, especially on the slopes. At least fifteen other trap sites in the Chase and Lyon County area failed to produce a single *Sigmodon*.

The study plot near Americus was an old field situation with a dark clay soil. Heavy precipitation (rain or snow) produced long water retention and a very mesic environment. Summer days in excess of 100° F. together with winter snow cover lasting into April, produces environmental conditions which are not favorable for maximum population numbers, especially in marginal local situations.

APPENDIX II --Continued

Fall populations of Sigmodon concentrated along the forested edges of grass fields (especially along clumps of sumac and bois d' arc).

Oklahoma

Vegetative cover at the Oklahoma study site was very dense year round. Tall thickets of Smilax-Rubus with Andropogon undergrowth between thickets were highly favored, especially during the winter months.

A grass fire in April, 1970, swept across the study plot burning junipers severely. Grasses were burned uniformly to the ground across the plot. Smilax thickets were destroyed. Thirty days later (May 16) an encouraging regrowth was evident. Four Peromyscus leucopus, three Sigmodon hispidus, and a single Didelphis marsupialis were trapped. Syvilagus floridanus and Dasypus novemcinctus were observed to be active on the plot. On November 7, 1970, five Sigmodon hispidus, three Peromyscus leucopus, one Perognathus hispidus and one Mus musculus were taken amid excellent regrowth in this sandy old field.

At maximum density (for this study), few other rodents were taken along with Sigmodon hispidus during a night of trapping.

APPENDIX II --Continued

Nineteen Sigmodon were taken in a single night (June 29, 1970) in the Fobb Bottom Public Hunting Area in southern Oklahoma (three miles west of Willis). These were among those used in parasitological examinations.

Texas

Sigmodon were numerous among cactus-mesquite associations in the arid western third of Wise County during 1968-1969. Cotton rats and Neotoma micropus were occupying the same habitat - even using the same runways. Numbers of cotton rats taken at similar (often identical) sites in 1970 produced few Sigmodon or Neotoma.

The south Texas study plot was on a sandy field (Andropogon species) overlooking a large shallow lake. A dramatic increase and decrease in the Baiomys taylori population was correlated with corresponding skeletal information from barn owl (Tyto alba) pellets taken from the area. This information will be presented separately by Cleveland and Otteni (in preparation for publication).

The Bee County site (ironweed clumps) is described in detail by Kennerly (1958) who trapped this site along the Medio Creek for Geomys bursarius. Several Sigmodon from this large population were used in parasitological examinations. Other animals taken in the immediate area included:

Peromyscus leucopus, *Neotoma micropus*, and *Oryzomys palustris*.

Cotton rats in Nueces, Kleburg, Kenedy, Refugio, and San Patricio counties (other than the study plot) in south Texas were taken primarily along railroad right-of-ways and fence rows in well-drained sandy areas. A large population of cotton rats was sampled in the tall grass around the Norias gate to the King Ranch.

Mexico - Chihuahua

A population of *Sigmodon*, sampled along a very sandy area covered by a dense stand of Tamarix with thick Bermuda grass, was trapped along with *Neotoma albigula* and a *Peromyscus* species.

LITERATURE CITED

Abegg, R. 1939. A preliminary study of the home range and territory of the cotton rat, *Sigmodon h. hispidus*. Master's Thesis. Louisiana State Univ.

Allen, J. A. 1891. On a collection of mammals from southern Texas and northeastern Mexico. Amer. Mus. Nat. Hist. Bull. 3: 219-289.

_____. 1896. On mammals collected in Bexar County, Texas. Amer. Mus. Nat. Hist. Bull. 8: 47-80.

Alvarez, T. 1963. The recent mammals of Tamaulipas, Mexico. Univ. Kan. Mus. Nat. Hist. Publ. 14(15): pp. 363-473.

Anderson, S. and W. N. Berg. 1959. Extension of the known range of the cotton rat, *Sigmodon hispidus*, in New Mexico. Southwestern Nat. 4: 40-42.

Anthony, H. E. 1928. Field book of North American mammals. G. P. Putnam's Sons, New York. 674 pp.

Arnwine, J. E. 1964. Factors influencing the activity and local distribution of certain small mammals in Elk County, Kansas. Unpublished research report. Kansas State Teachers College.

_______. 1966. A population of cotton rats (*Sigmodon hispidus*) at the University of Oklahoma Biological Station, Marshall County, Oklahoma. Unpublished research report. Independence Community College, Kansas.

Baccus, J., Greer, R. and G. Raun. 1971. Additional records of *Baiomys taylori* in north central Texas. In Press.

Bailey, V. 1902. Synopsis of the North American species of *Sigmodon*. Proc. Biol. Soc. Washington 15: 101-116.

______. 1905. Biological survey of Texas. North Amer. Fauna 25: 145.

______. 1913. Life zones and crop zones of New Mexico. North Amer. Fauna 35: 1-100.

Baker, R. H. 1969. Cotton rats of the *Sigmodon fulviventer* group. Univ. Kan. Mus. Nat. Hist. Publ. 51: 177-23.

Barkalow, F. S. 1962. Latitude related to reproduction in the cottontail rabbit. J. Widl. Mgmt. 26: 32-37.

Bartholomew, G. A. 1968. Body temperature and energy metabolism, pp. 290-354. *In* M. S. Gordon, Animal function: principles and adaptations. Macmillan, New York.

Bartholomew, G. A. and T. J. Cade. 1957. Temperature regulation, hibernation, and aestivation in the little pocket mouse, *Perognathus longimembris*. J. Mamm. 38: 60-72.

Bartholomew, G. A. and R. E. MacMillen. 1961. Oxygen consumption, estivation, and hibernation in the kangaroo mouse, *Microdipodops pallaidus*. Physiol. Zool. 34: 177-183.

Bertram, D. S. 1966. Dynamics of parasitic equilibrium in cotton rat filariasis, pp. 255-319. *In* B. Dawes. Advances in Parasitology, Vol. 4, Academic Press, New York.

Blair, W. F. 1938. Ecological relationships of mammals of the Bird Creek region, northeast Oklahoma. Amer. Midl. Nat. 20: 473-526.

_____. 1941. Techniques for the study of mammal populations. J. Mamm. 22: 148-157.

Boatwright, V. E. 1955. Seasonal variations of small mammal populations in Lyon County State Park. Master's Thesis. Kansas State Teachers College.

Bowers, J. R. 1971. Resting metabolic rate in the cotton rat, *Sigmodon*. Physiol. Zool. 44(3): 137-148.

Brown, J. H. and A. K. Lee. 1969. Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). Evolution 23: 329-338.

Chipman, R. K. 1965. Age determination of the cotton rat (*Sigmodon hispidus*).

_______. 1966. Cotton rat age classes during a population decline. J. Mamm. 47: 138-141.

Choate, J. R. and H. H. Genoways. 1967. Notes on some mammals from Nebraska. Trans. Kan. Acad. Sci. 69: 238-241.

Clayton, K. 1952. Some phases of the winter ecology of some small mammals in a blue-stem, blue-grass meadow of Lyon County, Kansas. Master's Thesis. Kansas State Teachers College.

Cleveland, A. G. 1968. Rectal temperatures of the cotton rat, *Sigmodon hispidus*. Master's Thesis. North Texas State Univ.

_________. 1970. The current geographic distribution of the armadillo in the United States. Tex. J. Sci. 22: 90-92.

Cockrum, E. L. 1948. The distribution of the hispid cotton rat in Kansas. Trans. Kan. Acad. Sci. 51: 306-312.

Coues, E. 1877. Monographs of North American Rodentia. No. I. Muridae. U. S. Geological Survey, Washington, pp. 31-42.

Dice, L. R. 1937. Variation in the wood-mouse, *Peromyscus leucopus noveboracensis*, in the northeastern United States. Occas. Papers Mus. Zool., Univ. Michigan 352: 1-32.

Dunaway, P. B. and S. V. Kaye. 1961. Cotton rat mortality during severe winter. J. Mamm. 42: 265-268.

________. 1964. Weights of cotton rats in relation to season, breeding, and environmental radioactive contamination. Amer. Midl. Nat. 71: 141-155.

Eads, R. B. and B. G. Hightower. 1952. Blood parasites of southwest Texas rodents. J. Parasit. 38:89-90.

Genoways, H. H. and D. A. Schlitter. 1966. Northward dispersal of the hispid cotton rat in Nebraska and Missouri. Trans. Kan. Acad. Sci. 69: 356-357.

Getz, L. L. 1968. Relationship between ambient temperature and respiratory water loss of small mammals. Comp. Biochem. Physiol. 24: 335-342.

Gier, H. T. 1968. The Kansas small mammal census: terminal report. Trans. Kan. Acad. Sci. 70: 505-518.

Gier, H. T. and G. V. R. Bradshaw. 1957. Five-year report on the Kansas small mammal census. Trans. Kan. Acad. Sci. 60: 259-272.

Goertz, J. W. 1964. The influence of habitat quality upon density of cotton rat populations. Ecol. Monog. 34: 359-381.

______. 1965. Reproductive variation in cotton rats. Amer. Midl. Nat. 74: 329-340.

Haines, H. 1963. Geographical extent and duration of the cotton rat, Sigmodon hispidus, 1958-1960 fluctuation in Texas. Ecol. 44: 771-772.

Hainsworth, F. R. 1967. Saliva spreading, activity, and body temperature regulation in the rat. Amer. J. Physiol. 212: 1288-1292.

Hall, E. R. 1955. Handbook of Mammals of Kansas. Univ. Kan. Mus. Nat. Hist. Publ. 7: 1-303.

Hall, E. R. and W. W. Dalquest. 1963. Mammals of Veracruz. Univ. Kan. Mus. Nat. Hist. Publ. 14: 165-362.

Hall, E. R. and K. R. Kelson. 1959. The mammals of North America. Roland Press, New York. Vol. II: 547-1083.

Halloran, A. F. 1942. A surface nest and the young of Sigmodon in Texas. J. Mamm. 23: 91.

Hart, J. S. and O. Heroux. 1953. A comparison of some seasonal and temperature-induced changes in Peromyscus: cold resistance, metabolism, and pelage insulation. Can. J. Zool. 31: 80-98.

Hart, J. S., H. Pohl, and J. Tenner. 1965. Seasonal acclimatization in varying hare (Lepus americanus). Can. J. Zool. 43: 731-744.

Heese, R., W. C. Allee, and K. P. Schmidt. 1937. Ecological Animal Geography. John Wiley and Sons, New York.

Hoffmann, R. S. 1958. The role of reproduction and mortality in population fluctuations of Voles (Microtus). Ecol. Monog. 28(1): 79-109.

Hoffmeister, D. F. 1951. A taxonomic and evolutionary study of the pinion mouse, Peromyscus truei. Ill. Biol. Mono., Univ. Ill. 21: 4-104.

Hudson, J. W., and G. A. Bartholomew. 1964. Terrestrial animals in dry heat, pp. 541-550. In Handbook of Physiology, Vol. 4. Amer. Physiol. Soc., Washington, D. C..

Hugghins, E. J. 1951. A survey of the helminths and ectoparasites of roof and cotton rats in Brazos County, Texas. Amer. Midl. Nat. 46: 230-244.

Inglis, J. M. 1955. Population dynamics of the cotton rat (genus Sigmodon). Master's Thesis. Texas A. and M. College.

Jackson, W. B. 1965. Litter size in relation to latitude in two murid rodents. Amer. Midl. Nat. 73: 245-247.

Johansen, K. and J. Krog. 1960. Diurnal body temperature variations and hibernation in the birchmouse, Sicista betulina. Physiol. Zool. 34: 126-144.

Jones, J. K. 1960. The hispid cotton rat in Nebraska. J. Mamm. 41: 132.

Judd, F. W. 1970. Geographic variation in the deer mouse, Peromyscus maniculatus, on the Llano Estacado. Southwest. Nat. 14: 261-282.

Keith, L. B., O. J. Rongstad, and E. C. Meslow. 1966. Regional differences in reproductive traits of the snowshoe hare. Can. J. Zool. 44: 953-961.

Kennerly, T. E. 1958. Comparisons of morphology and life history of two species of pocket gophers. Tex. J. Sci. 10: 133-146.

Kilgore, D. L. 1970. The effects of northward dispersal on growth rate of young, size of young at birth, and litter size in Sigmodon hispidus. Amer. Midl. Nat. 84: 510-520.

Kimbrough, J. D. 1970. A survey of endohelminths of the cotton rat, Sigmodon hispidus in Haskell County, Texas. Master's Thesis. Southern Methodist Univ.

Lord, D., Jr. 1960. Litter size and latitude in North American mammals. Amer. Midl. Nat. 64(2): 488-499.

Mayr, E. 1956. Geographic character gradients and climatic adaptation. Evolution 10: 105-108.

____. 1963. Animal Species and Evolution. Belknap Press, Harvard University Press, Cambridge, Mass.

McCulloch, C. Y. 1959. Populations and range effects of rodents on the sand sagebrush grasslands of western Oklahoma. Ph.D. Thesis. Oklahoma State Univ. 159 p.

Mearns, E. A. 1897. Preliminary diagnoses of new mammals of the genera _Sciurus_, _Castor_, _Neotoma_, and _Sigmodon_, from the Mexican border to the United States. (pre-print of Proc. U. S. Nat. Mus. 20: 504, Jan. 19, 1898).

Melvin, D. M. and A. C. Chandler. 1950. New helminth records from the cotton rat, _Sigmodon hispidus_, including a new species, _Strongyloides sigmodontis_. J. Parasit. 36 (6): 505-510.

Moore, J. C. 1971. Geographic variation in some reproductive characteristics of diurnal squirrels. Bull. Amer. Mus. Nat. Hist. 122: 1-32.

Odum, E. P. 1955. An eleven year history of a _Sigmodon_ population. J. Mamm. 36: 368-378.

Packard, R. L. 1970. Speciation and evolution of the pygmy mice, genus _Baiomys_. Univ. Kan. Publ., Mus. Nat. Hist. 9: 579-670.

Provo, M. M. 1962. The role of energy utilization, habitat selection, temperature and light in the regulation of a _Sigmodon_ population. Doctoral dissertation. Univ. of Georgia.

Raun, G. G. 1960. Barn owl pellets and small mammal populations near Mathis, Texas, in 1956 and 1959. Southwest. Nat. 5: 194-200.

Raun, G. G. and B. J. Wilks. 1964. Natural history of _Baiomys taylori_ in southern Texas and competition with _Sigmodon hispidus_ in a mixed population. Tex. J. Sci. 16: 28-49.

Say, T. and G. Ord. 1825. Description of a new species of Mammalia, whereon a genus is proposed to be founded. J. Acad. Nat. Sci. Philadelphia 4: 353.

Schendel, R. H. 1940. Life history notes on Sigmodon hispidus texianus with special emphasis on populations and nesting habits. Master's Thesis. Oklahoma A. and M. College.

Schnell, Jay H. 1968. The limiting effects of natural predation on experimental cotton rat populations. J. Wild. Mgmt. 32: 698-711.

Schreider, E. 1964. Ecological rules, body-heat regulation, and human evolution. Evolution 18: 1-9.

Scott, J. A., N. M. Sisley, and V. A. Stembridge. 1946. The susceptibility of cotton rats and white rats to Litomosoides carinii in relation to the presence of previous infections. J. Parasitol. 32 (Sup): 17.

Sealander, J. A. and C. E. Guess. 1970. Effect of forced swimming on body temperatures and eosinophil levels in cotton rats (Sigmodon hispidus). J. Mamm. 51: 348-357.

Smith, M. H. and J. T. McGinnis. 1968. Relationships of latitude, altitude, and body size to litter size and mean annual production of offspring in Peromyscus. Res. Popul. Ecol. 10: 115-126.

Strecker, J. K. 1929. Notes on the Texas cotton and Attwater wood rats in Texas. J. Mamm. 10: 216-220.

Svihla, A. 1929. Life history notes on Sigmodon hispidus hispidus. J. Mamm. 10: 352-353.

Thornthwaite, C. W. 1931. The climates of North America according to a new classification. Geog. Rev. 21(4): 633-656.

Tucker, V. A. 1962. Diurnal torpidity in the California pocket mouse. Sci. 136: 380-381.

Walker, E. P. 1964. Mammals of the world. John Hopkins Press, Baltimore. Vol. II: 647-1500.

Westbrook, M. G. and J. A. Scott. 1955. A statistical analysis of the growth in length of the filarial worms in the cotton rat. Tex. Rep. Biol. Med. 13: 537-558.

Williams, R. W. 1948. Studies on the life cycle of *Litomosoides carinii*, filarid parasite of the cotton rat, *Sigmodon hispidus* latoralis. J. Parasit. 34: 24-42.

Zimmerman, E. G. 1970. Karyology, systematics and chromosomal evolution in the rodent genus, *Sigmodon*. Michigan State Univ., Publ. Mus., Biol. Ser. 4(9): 389-454.