8224191

Cothran, Ernest Gus

KARYOTYPIC, MORPHOLOGIC, AND GENIC DIFFERENTIATION OF HYBRIDIZING GROUND SQUIRRELS (SPERMOPHILUS MEXICANUS AND SPERMOPHILUS TRIDECEMLINEATUS)

The University of Oklahoma PH.D. 1982

University Microfilms International 300 N. Zeeb Road, Ann Arbor, MI 48106

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark __✓__.

1. Glossy photographs or pages ______
2. Colored illustrations, paper or print ______
3. Photographs with dark background ______
4. Illustrations are poor copy ______
5. Pages with black marks, not original copy ______
6. Print shows through as there is text on both sides of page ______
7. Indistinct, broken or small print on several pages ______
8. Print exceeds margin requirements ______
9. Tightly bound copy with print lost in spine ______
10. Computer printout pages with indistinct print __✓__
11. Page(s) __________ lacking when material received, and not available from school or author.
12. Page(s) __________ seem to be missing in numbering only as text follows.
13. Two pages numbered __________. Text follows.
14. Curling and wrinkled pages ______
15. Other ____

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

KARYOTYPIC, MORPHOLOGIC, AND GENIC DIFFERENTIATION OF HYBRIDIZING GROUND SQUIRRELS (*SPERMOPHILUS MEXICANUS* AND *SPERMOPHILUS TRIDECEMLINEATUS*)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

E. GUS COTHRAN

Norman, Oklahoma

1982

KARYOTYPIC, MORPHOLOGIC, AND GENIC DIFFERENTIATION

OF HYBRIDIZING GROUND SQUIRRELS

(SPERMOPHILUS MEXICANUS AND SPERMOPHILUS TRIDECEMLINEATUS)

APPROVED BY

Gary D. Schnell

Charles Carpenter

Cluff E. Hopla

James N. Thompson, Jr.

DISSERTATION COMMITTEE

ACKNOWLEDGMENTS

Many people must be thanked for their contribution to this study. I gratefully acknowledge my dissertation committee: G. D. Schnell, C. C. Carpenter, C. E. Hopla, and J. N. Thompson for their time, expertise, and all the other assistance and support they provided. J. B. Coleman prepared the figures and S. B. Brodie typed the manuscript. Their efforts and talents are sincerely appreciated. S. D. Wood, R. D. Owen, and J. D. Felley supervised the preparation of the skeletal material and their assistance was invaluable. Thanks as well to R. J. Baker, R. L. Honeycutt, and M. Haiduk for their assistance in the chromosome banding work. Special thanks to R. K. Chesser, M. H. Smith, and E. G. Zimmerman not only for their professional assistance and advice but for their friendship as well. Finally, I wish to thank my wife Marian who not only assisted me in every aspect of this study but also provided support and encouragement that made my work easier. Portions of this work were financially supported by the Theodore Roosevelt Memorial Fund and the U. S. Department of Energy.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

KARYOTYPIC, MORPHOLOGIC, AND GENIC DIFFERENTIATION

OF HYBRIDIZING GROUND SQUIRRELS

(SPERMOPHILUS MEXICANUS AND SPERMOPHILUS TRIDECEMLINEATUS)

PREFACE

The North American ground squirrel species *Spermophilus tridecemlineatus* and *S. mexicanus* are inhabitants of the Great Plains and the desert grasslands of Texas, New Mexico, and Mexico. These species are members of the ground squirrel subgenus *Ictidomys*. A number of workers have studied *S. tridecemlineatus*, but the studies have primarily concerned the natural history of the species and the physiology of hibernation. Few studies have involved *S. mexicanus* and little was known about the systematic relationships of these ground squirrel taxa. In an earlier study (Cothran et al., 1977. J. Mammal. 58:610-622), I surveyed the levels of electrophoretically determined genetic variability within *S. mexicanus* and *S. tridecemlineatus* and the genic relationships of the subgenus *Ictidomys*. I found that *S. mexicanus* and *S. tridecemlineatus* were hybridizing in southeastern New Mexico. Also, the observed genic similarity of the species was unusually high. The purpose of the work reported here is to examine the relationships of these two ground squirrels species more thoroughly and to determine the geographic extent of the hybridization and whether or not introgression was taking place.

This study is written in three sections. The first concerns the G- and C-banded chromosomal relationships between *S. mexicanus* and *S. tridecemlineatus*. Section II examines the morphometric relationships of the species based upon 40 cranial, skeletal, and external morphometric characters. The third section involves the genic relationships of the species and compares the level of differentiation observed for karyotypic, morphologic, and genic characteristics. Each section is written in the form of a paper for a specific scientific journal. The first will be sent to the Journal of Mammalogy as a note. The morphology paper will be submitted to the same journal as a full length paper. Section III will be sent to Evolution. Additional data and analyses not to be included in the publications are provided for reference in Appendices I-III.

CHROMOSOMAL DIFFERENTIATION OF HYBRIDIZING GROUND SQUIRRELS (SPERMOPHILUS MEXICANUS AND S. TRIDECEMLINEATUS)

Speciation is the process by which one portion of an interbreeding group of organisms becomes reproductively isolated from the rest of the group. Speciation may or may not be an instantaneous process (Stebbins and Ayala, 1981) with geographic isolation being the most commonly advanced explanation for speciation events (Mayr, 1971). That is, genetic differences accumulate through time between geographically separate portions of a species which are presumably under different selection regimes. Hybridization occurs when contact between the incipient species is resumed before premating isolating barriers are perfected. If sufficient genic differentiation to make the hybrids reproductively inferior to the parental types took place during isolation, selection against the hybrids should result in completion of the speciation process. The amount of genetic differentiation required for reproductive isolation is not known and is probably not a constant. It is necessary to examine a variety of species and populations at various stages in the speciation process to determine what level or kind of genetic change is likely to result in reproductive isolation.

The ground squirrels *Spermophilus mexicanus* and *S. tridecemlineatus* represent taxonomic species that have not yet completed the speciation process. Hybrids between the two taxa were first reported by Zimmerman and Cothran (1976). The presence of backcross individuals, in addition to F_1 hybrids, indicated that hybrids were not completely sterile.

Chromosomal changes are often important in speciation (White, 1978). A single chromosomal rearrangement can result in selection against a hybrid individual by meiotic mechanisms. The development of chromosomal banding techniques has allowed a finer scale comparison of the differences of chromosomes of different taxa. My study was undertaken to examine in detail the chromosomal differentiation of *S. mexicanus* and *S. tridecemlineatus*.

Standard karyotypes were prepared following the method of Lee (1969) with preparations having been examined for over 200 squirrels (approximately equal numbers of each species). G- and C-banded chromosomal preparations were from fibroblast tissue-cultured cells. Methods of tissue culture maintenance and chromosomal banding were as described by Greenbaum et al. (1978). The arrangement of the chromosomes in Figs. 1, 2, and 3 follow Nadler and Hughes (1966). G- and C-banded karyotypes were prepared from 19 individuals (16 *S. tridecemlineatus* from Lubbock, Lubbock Co., Texas; 2 *S. mexicanus* from Austin, Travis Co., Texas; and 1 hybrid from Hobbs, Lea Co., New Mexico). Several G- and C-banded spreads were examined and compared for each specimen.

The standard karyotypes examined did not differ from previously published results (Nadler and Hughes, 1966; Zimmerman and Cothran, 1976). No intrapopulational chromosomal variability other than that associated with hybridization was observed. The diploid number of both species is 34. The fundamental number is 64 for S. mexicanus and S. t. texensis and 62 for S. t. arenicola.

A composite C-banded karyotype is shown in Fig. 1. Chromosomes from S. tridecemlineatus are the left side member of each pair; S. mexicanus chromosomes are on the right. There are no obvious differences between the two species in the distribution of heterochromatin. The heterochromatic material of all chromosones is concentrated around the centromere. The least amount of heterochromatin is in the Y chromosome.

A composite G-banded karyotype is shown in Fig. 2 and an idiogram of the composite in Fig. 3. Zimmerman and Cothran (1976) found three pairs of chromosomes to be morphologically different between the two species. These differences are also evident in the G-banded karyotypes (chromosomes 10, 15 and 16). The difference in chromosome 10 between S. tridecemlineatus and S. mexicanus is probably a loss of part of the long arm of the chromosome in S. mexicanus. Whether the length difference represents a deletion or a translocation cannot be determined since there are no obvious bands present on the segment of chromosome 10 that is lost in S. mexicanus.

Both chromosomes 15 and 16 are larger in S. mexicanus than in S. tridecemlineatus. The difference appears to be the addition of unbanded material on the ends of the short arms of both chromosomes 15 and 16. These additions may represent translocations from chromosome 10. The position of the centromere of chromosome 16 also differs between S. mexicanus and S. tridecemlineatus (Fig. 2 and Fig. 3). Chromosome 16 is also subspecifically variable within S.

tridecemlineatus (Fig. 4). The acrocentric form is found in S. t. arenicola while the submetacentric form occurs in S. t. texensis (Zimmerman and Cothran, 1976). The difference appears to represent a pericentric inversion. The submetacentric chromosome 16 of S. t. texensis is similar to, although smaller than, chromosome 16 of S. mexicanus. One individual from Lubbock was heterozygous for the two forms of chromosome 16, and both homozygotes have been observed at other localities but not in the same population. All other individuals from Lubbock were homozygous for the acrocentric form of chromosome 16.

No differences were found between the species in the position of the bands or in the size of any of the other pairs of chromosomes. There do appear to be differences between the species in the position of the darkest trypsin negative band on chromosome 9 (Fig. 2 and Fig. 3). However, although this difference was consistent in the spreads observed, the small sample size of S. mexicanus makes it difficult to determine whether or not the position of this band in S. mexicanus is an artifact or an actual species characteristic.

Little chromosomal divergence between S. mexicanus and S. tridecemlineatus has occurred. Based on G- and C-banded karyotypes, probably no more than two chromosomal rearrangements have occurred since or during the separation of S. mexicanus from S. tridecemlineatus. Both rearrangements are translocations from chromosome 10, one to chromosome 15 and one to chromosome 16. The occurrance of two separate translocations seems more probable than a double translocation. A third possible chromosomal difference, involving the centromere position of chromosome 16 (Fig. 2 and Fig. 3), probably occurred before the divergence of the species as this rearrangement is present in both S. mexicanus and S. t. texensis. Of four subspecies of S. tridecemlineatus that have been karyotyped, three (S. t. tridecemlineatus, S. t. pallidus, and S. t. arenicola) have the acrocentric form of chromosome 16 while S. t. texensis has the biarmed form (Fig. 4; Nadler and Hughes, 1966; Zimmerman and Cothran, 1976). Thus the probable sequence of events that led to the present differences in the chromosomal compliments of S. tridecemlineatus and S. mexicanus involves a pericentric inversion in the S. t. texensis - S. mexicanus line followed by the two translocations from chromosome 10 to chromosomes 15 and 16 in the S. mexicanus line. Spermophilus tridecemlineatus is considered the ancestral species based upon geographic considerations and because the other two members of the subgenus Ictidomys (S. mexicanus and S. spilosoma) are more closely related to S. tridecemlineatus than to each other both chromosomally and electrophoretically (Nadler and Hughes, 1966; Cothran et al., 1977). The small amount of karyotypic differentiation between S. tridecemlineatus and S. mexicanus supports the results of electrophoretic studies (Zimmerman and Cothran, 1976; Cothran et al., 1977). Mean genetic identity (I, Nei, 1971) between these two species based on a survey of 28 loci was 0.965 (Cothran et al., 1977), one of the highest similarity values reported for taxonomically distinct species (Ayala et al., 1975; Zimmerman et al., 1978).

The accumulation of small chromosomal changes may constitute the most effective chromosomal barrier to reproduction (Stebbins, 1950). Complete reproductive isolation between *S. tridecemlineatus* and *S. mexicanus* has not been achieved. Of 630 ground squirrels of these two species that have been examined, about 7% are hybrids (Cothran, 1981). The hybrids are fertile as the majority of the hybrid individuals are the progeny of backcrosses. The possible translocations from chromosome 10 to chromosomes 15 and 16 are small and not likely to cause meiotic problems. The pericentric inversion is a potential meiotic problem. Crossing over within the inverted segment of a chromosome usually results in the production of genetically imbalanced gametes that do not produce viable zygotes. Hybrids between *S. mexicanus* and both *S. t. texensis* and *S. t. arenicola* have been observed. Any F_1 hybrids between *S. mexicanus* and *S. t. arenicola* would be heteromorphic for the acrocentric and the inverted chromosome 16. The greatest number of hybrids were found in the area where the range of *S. mexicanus* contacts or overlaps that of *S. t. arenicola*. Backcross individuals that were heterozygous for chromosome 16 were also found. Thus the pericentric inversion in chromosome 16 has not produced sterility in the hybrids of *S. mexicanus* and *S. tridecemlineatus*. Whether or not the hybrids have reduced fertility relative to the parental types due to the inversion is not known.

Greenbaum et al. (1978) proposed three factors that might reduce the amount of crossing over in the inverted segments of *Peromyscus* chromosomes. Two of these could be relevant in explaining the apparent lack of meiotic difficulties associated with the inversion in the ground squirrel hybrids. The first proposal is that crossing over is repressed in proximity to the centromere. The ground squirrel chromosome 16 is small and much of the inversion would be near the centromere. The second suggestion is that regions adjacent to heterochromatin experience reduced crossing over; most of chromosome 16 is heterochromatic (Fig. 1 and Fig. 4). Whatever the mechanism, the chromosomal differences between S. mexicanus and S. tridecemlineatus have not prevented gene flow, and chromosomal differentiation does not appear to have been important in the evolutionary divergence of S. mexicanus and S. tridecemlineatus.

ACKNOWLEDGMENTS

I thank R. J. Baker for allowing this work to be conducted in his laboratory and R. L. Honeycutt and M. Haiduk for all their assistance in collecting the data. I am also grateful to G. D. Schnell, C. C. Carpenter, C. E. Hopla, and J. N. Thompson for their advice and for their critical readings of an earlier version of this manuscript. J. B. Coleman helped prepare the figures. I am grateful to M. H. Smith and R. K. Chesser for their assistance and support. A special thanks goes to my wife Marian who assisted in every aspect of my research. This study was completed while the author was employed by the Savannah River Ecology Laboratory and was supported by Contract DE-AC09-76SR00819 between the U. S. Department of Energy and the University of Georgia.

Literature Cited

Ayala, F. J., M. L. Tracey, D. Hedgecock, and R. C. Richmond. 1975. Genetic differentiation during the speciation process in *Drosophila*. Evolution 28: 576-592.

Cothran, E. G. 1982. Karyotypic, morphologic, and genic differentiation of the hybridizing ground squirrels (*Spermophilus mexicanus* and *Spermophilus tridecemlineatus*). Unpublished Ph. D. dissertation, Univ. Oklahoma, Norman.

Cothran, E. G., E. G. Zimmerman, and C. F. Nadler. 1977. Genic differentiation and evolution in the ground squirrel subgenus *Ictidomys* (Genus *Spermophilus*). J. Mammal. 58: 610-622.

Greenbaum, I. F., R. J. Baker, and J. H. Bowers. 1978. Chromosomal homology and divergence between sibling species of deer mice: *Peromyscus maniculatus* and *P. melanotis* (Rodentia: Cricetidae). Evolution 32: 334-341.

Lee, M. R. 1969. A widely applicable technique for direct processing of bone marrow for chromosomes of vertebrates. Stain Technol. 44: 155-157.

Mayr, E. 1970. Populations, species and evolution. Belknap Press of Harvard Univ. Press., Cambridge, 453 pp.

Nadler, C. F., and C. E. Hughes. 1966. Chromosomes and taxonomy of the ground squirrel subgenus *Ictidomys*. J. Mammal. 47: 46-53.

Nei, M. 1971. Interspecific gene differences and evolutionary time estimated from electrophoretic data on protein identity. Amer. Nat. 105: 385-398.

Stebbins, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York, 643 pp.

Stebbins, G. L. and F. J. Ayala. 1981. Is a new evolutionary synthesis necessary? Science 213: 967-971.

White, M. J. D. 1978. Modes of speciation. Freeman Press, San Francisco, 455 pp.

Zimmerman, E. G., and E. G. Cothran. 1976. Hybridization in the Mexican and thirteen-lined ground squirrels, *Spermophilus mexicanus* and *Spermophilus tridecemlineatus*. Experientia 32: 704-706.

Zimmerman, E. G., C. W. Kilpatrick, and B. J. Hart. 1978. The genetics of speciation in the rodent genus *Peromyscus*. Evolution 32:565-579.

E. Gus Cothran, Department of Zoology, University of Oklahoma, Norman, OK 73019. (present address: Savannah River Ecology Lab., Drawer E, Aiken, SC 29801).

Figure 1. Composite C-banded karyotype comparing homologous chromosomes of *S. tridecemlineatus* (left) and *S. mexicanus*.

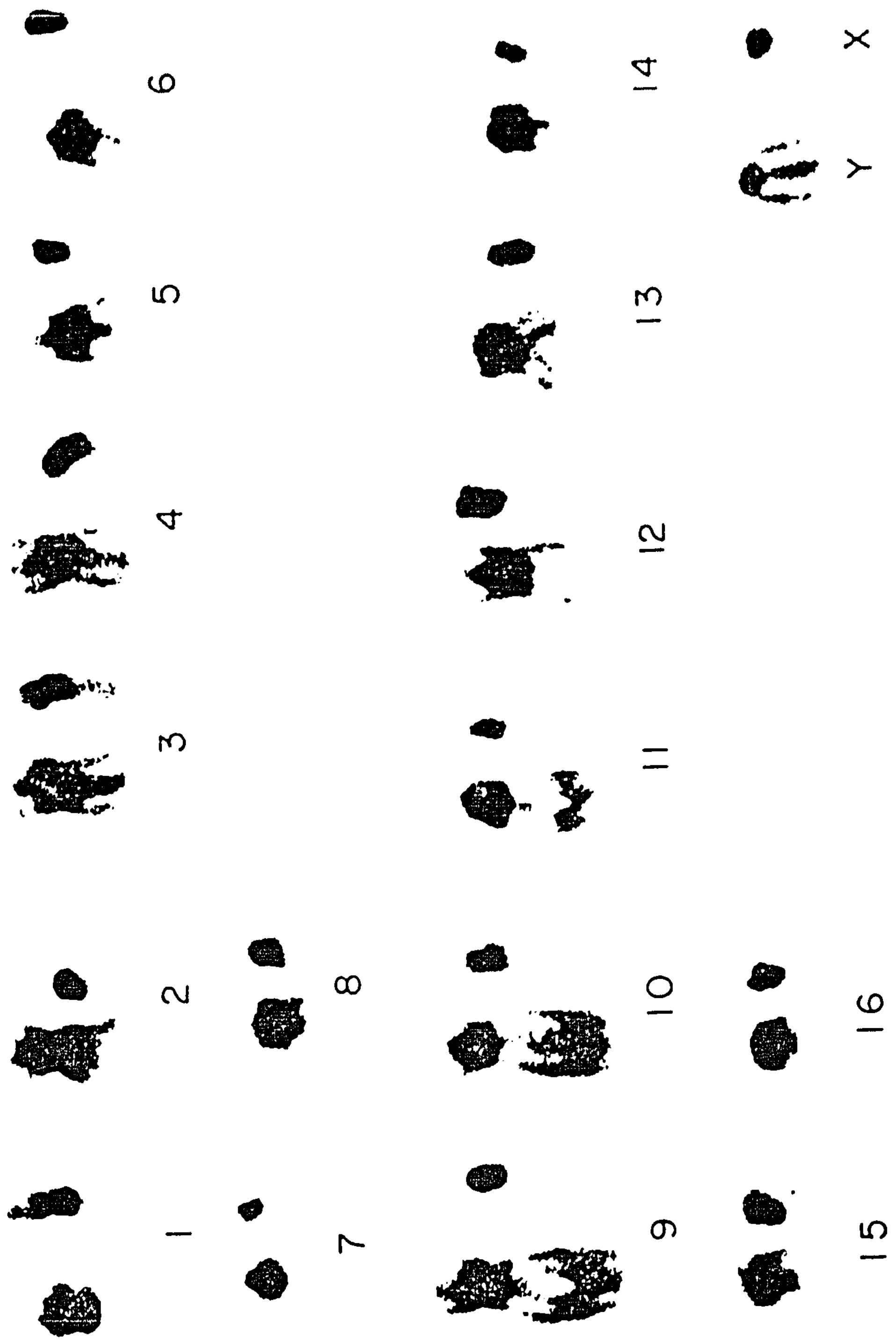

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Y
X

Figure 2. Composite G-banded karyotype comparing homologous chromosomes of *S. tridecemlineatus* (left) and *S. mexicanus*.

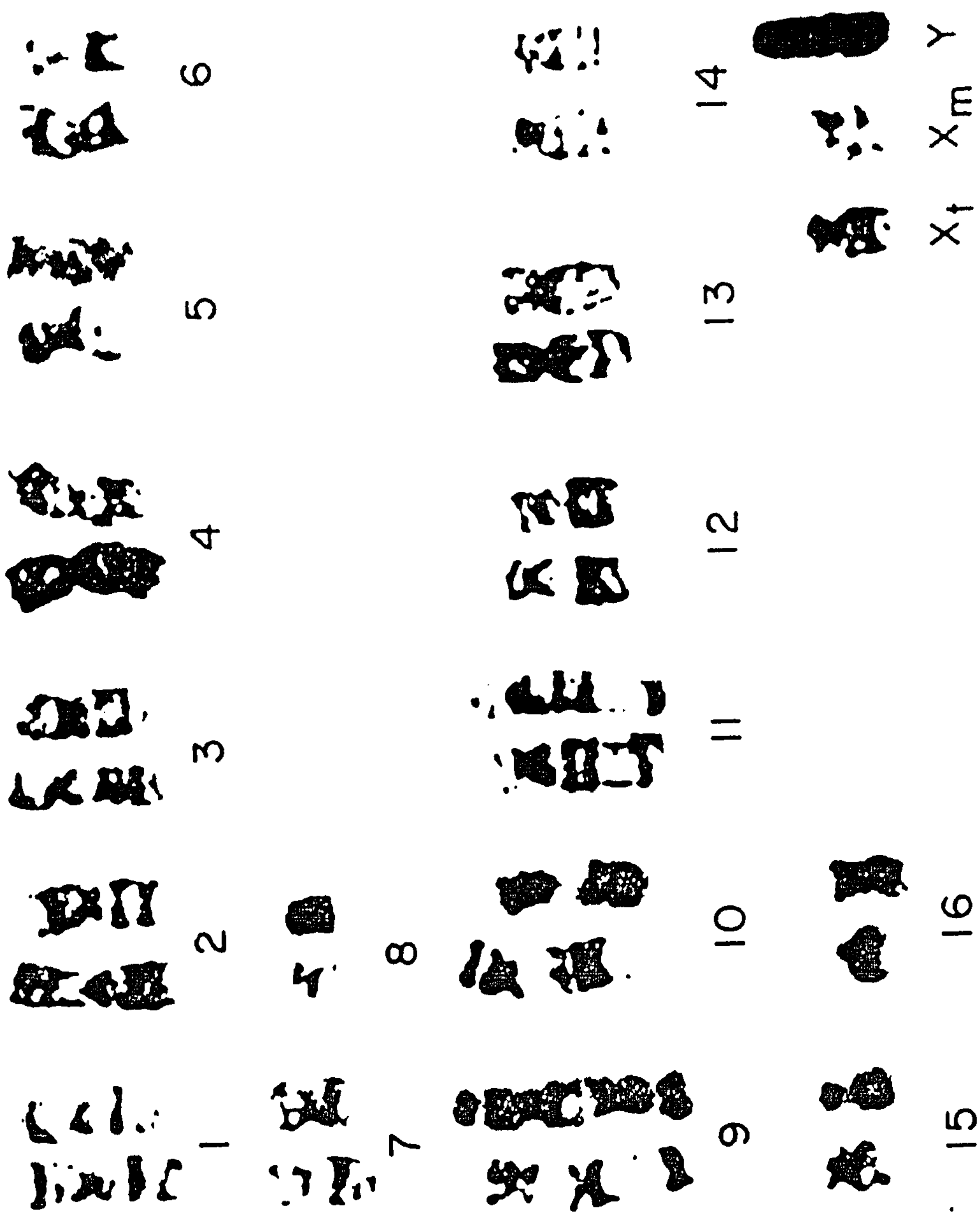

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Xf
Xm
Y

Figure 3. Idiogram showing G-banding pattern of *S. tridecemlineatus* and *S. mexicanus*. Unpaired elements have identical banding patterns in both species. t = *tridecemlineatus*, m = *mexicanus*.

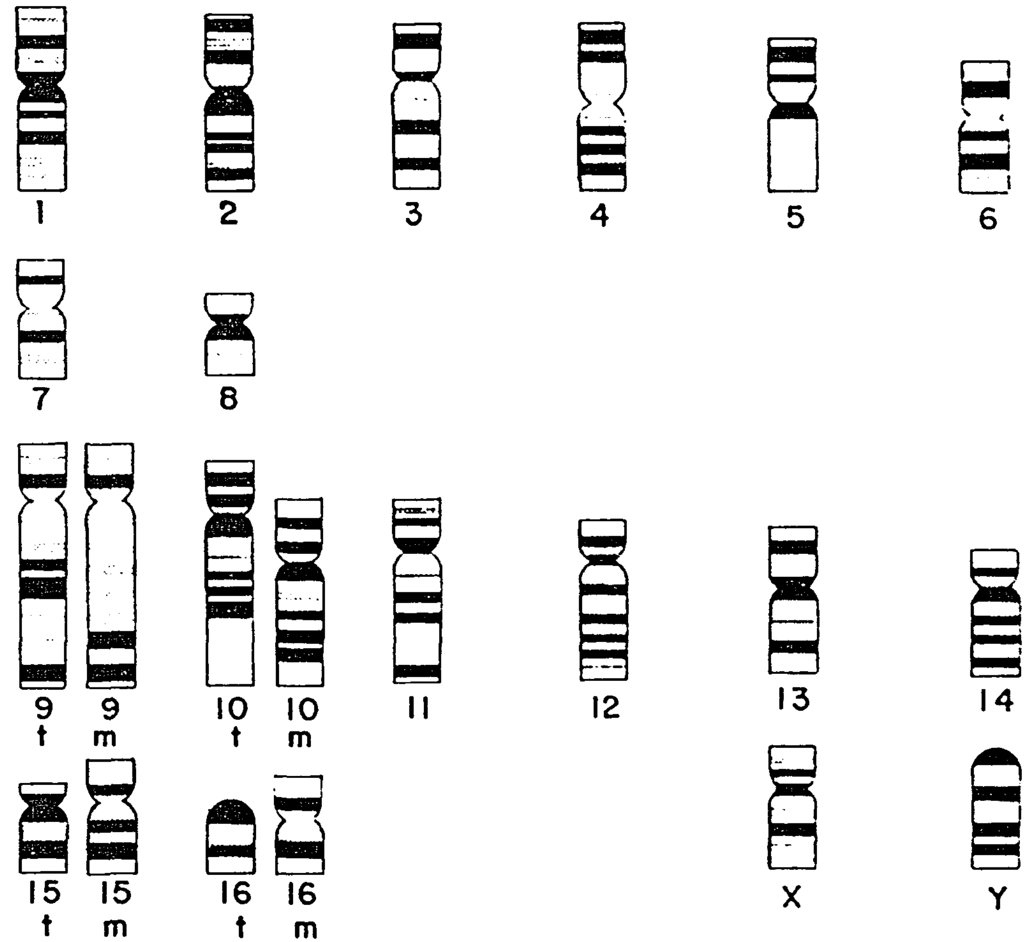

1
2
3
4
5
6
7
8
9 t
9 m
10 t
10 m
11
12
13
14
15 t
15 m
16 t
16 m
X
Y

Figure 4. C- and G-banded chromosome 16 of *S. tridecemlineatus* and *S. mexicanus*. From left to right *S. t. texensis*, *S. t. arenicola*, *S. mexicanus*.

C–Bands G–Bands

MORPHOLOGIC RELATIONSHIPS OF THE HYBRIDIZING GROUND SQUIRRELS

SPERMOPHILUS MEXICANUS AND *S. TRIDECEMLINEATUS*

E. GUS COTHRAN

ABSTRACT.--Interspecific and intraspecific morphologic relationships were analyzed for 267 individuals of *Spermophilus tridecemlineatus* and 265 *S. mexicanus*. Thirty-three localities were sampled and a total of 40 cranial, skeletal, and external measurements were taken. All characters showed significant interspecific variation, which is in contrast to high electrophoretically determined genic similarity found in other studies. Sexual dimorphism of some characters was observed for both species, but *S. mexicanus* had over twice as many sexually dimorphic characters as *S. tridecemlineatus*. Little intraspecific variability was evident. Species relationships were also examined by discriminant function and principal components analyses. Both techniques indicated that size is the major difference between the species. A total of 44 individuals were of probable hybrid origin based on electrophoretic and karyotypic evidence obtained from another study. All hybrids were found in association with *S. mexicanus* and hybridization and introgression appears to be unidirectional into *S. mexicanus*. The majority of the hybrids were not F_1 hybrids. Neither discriminant function nor principal components techniques were effective in providing hybrid identification, primarily due to the high percentage of backcross hybrids.

Species are defined by reproductive isolation. The processes by which reproductive isolating mechanisms are developed are not fully understood although a number of hypothesis have been proposed to explain speciation (Bush, 1975; White, 1978). The basic tenet of such hypotheses is that interbreeding populations become separated by some barrier to gene flow. Genetic differences between the newly isolated populations develop through time and different selection regimes. Reproductive isolation results if the genetic changes accumulated during the period when the populations were separated are great enough to prevent successful reproduction of the populations or if the offspring produced are selectively inferior to the parents. Reproduction between genetically differentiated populations may be the most crucial step in the speciation process as it is at this point that reproductive isolation is perfected or the populations fuse back into a single interbreeding population.

It has long been hypothesized that major genomic modifications accompany speciation (Dobzhansky, 1959; Mayr, 1963). However, the results of a number of recent studies of electrophoretic divergence between species suggest that the amount of genetic change involved in speciation may not be great (Avise et al., 1975; Nevo et al., 1974; Zimmerman and Nejtek, 1977). Questions do remain about the proportion of the genome that encodes structural gene loci and the relevance of structural gene divergence to speciation (Avise, 1976). Additionally, there is good evidence that the processes involved in the divergence of structural genes, chromosomal characters, and morphology are essentially independent (Schnell and Selander, 1981). It is necessary to examine a variety of characteristics of closely related species to gain an understanding of the amount of genetic change underlying speciation and the contributions of the different characteristics to speciation.

The ground squirrels Spermophilus mexicanus and S. tridecemlineatus are taxa that have completed the second stage of speciation. The species are known to hybridize in an area of contact in western Texas and southeastern New Mexico (Zimmerman and Cothran, 1976). The electrophoretically determined genic similarity between S. mexicanus and S. tridecemlineatus is very high (Nei's [1972] I = 0.965; Cothran et al., 1977), and there is little chromosomal differentiation of the species (Nadler and Hughes, 1966; Cothran, 1982). The current study was undertaken to examine the morphometric relationships between these hybridizing ground squirrel taxa and to compare the relative contribution of the morphologic and genic characteristics to the differentiation that accompanies the speciation process.

MATERIALS AND METHODS

Interspecific and intraspecific morphologic relationships were analyzed for 267 S. tridecemlineatus and 265 S. mexicanus. A total of 44 of the 532 ground squirrels were identified as hybrid individuals by electrophoretic and/or karyotypic methods (Cothran, 1982). Thirty-three localities were sampled (Table 1, Fig. 1). A total of 40 measurements (21 cranial and 19 non-cranial) was taken with dial calipers to the nearest 0.1 mm from each specimen. The measurements were as follows: (GLS) greatest length of skull, (BAS) basal length of skull, (ZYB) zygomatic breadth, (ROS) rostral length, (NAS) nasal length, (PMB) premaxillary breadth, (IOB) interorbital breadth, (POB) postorbital breadth, (PPL) post-palatal length, (BAT) breadth across tooth rows, (TRL) tooth row length, (BCB) brain case breadth, (BUL) bullar length, (BUB) bullar breadth, (MOL) 2nd premolar breadth, (UDL) upper diastema length, (PAW) palatal width, (OCD) occipital depth, (SKD) skull depth, (MAL) mandible length, (MAD) mandible depth, (FEL) femur length, (FMW) femur minimal width, (FDW) femur distal width, (FPW) femur proximal width, (HUL) humerus length, (HMW) humerus minimal width, (HDW) humerus distal width, (HPW) humerus proximal width, (RPW) radius proximal width, (UPW) ulna proximal width, (TPW) tibia proximal width, (FIW) fibula proximal width, (SCL) scapula length, (SCW) scapula width, (PEV) pelvis length, (SAW) sacrum width, (TTL) tail length, (HFL) hindfoot length, and (BDL) body length. Descriptions of measurements are given in Cothran (1982). Tail length was used only when individuals had undamaged tails. Cranial characters and HFL, BDL, and TTL were available for all 532 individuals. The remaining characters were only measured on individuals from populations 1 to 23. For most analyses only cranial characters, HFL, BDL, and TTL were used. Measurements were taken from the right side of the skull whenever possible. Only individuals with fully ossified skulls and completely closed cranial sutures were used in order to reduce the variation due to age.

Univariate and multivariate statistics were used to analyze interspecific and intraspecific differentiation as well as sexual dimorphism of skeletal characteristics. Differences between species and among localities were analyzed by single classification analysis of variance and sums of squares simultaneous test procedures (SS-STP; Gabriel, 1964; Power, 1970). Matrices of Pearson's product-moment correlation coefficients between localities and characters were calculated from standardized character values. The proportion of character variability attributable to species, locality, and sexual variation was analyzed by variance components analysis.

Differentiation of the species and the relationship of hybrid individuals to the parental species were examined by discriminant function and principal components analysis (Morrison, 1967; Rohwer, 1972). Populations which were outside the zone of sympatry of S. mexicanus and S. tridecemlineatus, and in which no hybrids were observed, were used as reference samples for the calculation of the discriminant function. The number of characters used to calculate the discriminant function was reduced to the 11 characters with the greatest discriminating power and that had the fewest number of individuals with missing values for the characters. Principal components analysis was performed on the correlation matrix calculated from standardized character means of each locality. Principal components were also extracted from the data for all individuals and for the populations of both species separately.

Associations between matrices of phenetic distance (average taxonomic distance; Sokal, 1961) calculated for the different sets of characters, sexes, or populations were tested by the general regression analysis of Mantel (1967; Sokal, 1979). Computer analyses were performed using the Statistical Analysis System (SAS; Barr et al., 1979), Numerical Taxonomic System (NT-SYS; Rohlf et al., 1974), and programs from Chesser (1980). Matrix correlation (r) were calculated using the MXCOMP procedure of NT-SYS.

The majority of specimens have also been analyzed genetically and karyotypically (Zimmerman and Cothran, 1976; Cothran et al., 1977; Cothran, 1982). Electrophoretic and chromosomal characteristics of individuals were used to determine if the individuals were of probable hybrid origin.

RESULTS

Variance components analysis revealed the amount of variation contributed by species, sex, and locality differences (Table 2). Species differences accounted for two-thirds of the total variation. Both locality and sex differences were relatively unimportant. The error term was the second highest source of variation. One component of the error term was probably age. No attempt was made to age individuals other than to use only adults in the analysis. The proportion of variability attributable to species, locality, and sex was similar for cranial and non-cranial characters. Species differences were of overwhelming importance with both sets of characters.

Relative to species differences, morphometric variation due to sex was unimportant. However, sexual dimorphism was observed within species and the amount of sexual dimorphism was different between species. Of the 39 characters tested (tail length was not used due to the number of individuals with broken tails), 14 characters (35.9%) were significantly sexually dimorphic in *S. tridecemlineatus* and 32 (82.1%) were in *S. mexicanus*. Within both species, males tended to be larger than females. The cranial characters that were sexually variable in *S. tridecemlineatus* were GLS, NAS, BCB, SKD, MAD, and MAL, and the non-cranial characters with statistically significant sex differences were FDW, HMW, HDW, TPW, SCW, SAW, and HFL. Only the cranial characters, POB, BAT, TRL, BUB, MOL, and PAL and the non-cranial character SAW were not significantly sexually dimorphic in *S. mexicanus*. SAW was the only character that was sexually variable in *S. tridecemlineatus* and not in *S. mexicanus*. Non-cranial characters tended to be more sexually dimorphic than cranial characters in both species. When variance components analysis was performed on the data for males and females separately, the results were similar to the results of the analysis with the sexes combined (Table 2). Species accounted for 69.01% and 69.89%, locality 7.09% and 5.69%, and error 23.9% and 24.42% of the variation for males and females, respectively.

The small importance of sexual differences relative to species difference was also indicated by comparing distance matrices. Average taxonomic distance (Sokal, 1961) was calculated from standardized data matrices of population means of the 23 characters available from all populations for males, females, and the sexes combined. Mantel matrix regression analysis was used to compare the three distance matrices.

The distance matrices for males and females were significantly associated to the distance matrix of the combined sexes (t_∞ = 21.11, $P \leq 0.001$, r = 0.946 and t_∞ = 21.57, $P \leq 0.001$, r = 0.955 for males and females respectively). The phenetic distance matrices of males and females were also significantly associated (t_∞ =18.62, $P \leq 0.001$, r = 0.839).

The amount of character variation due to locality was also relatively small compared to species differences. Significant character heterogeneity among localities was found for 13 of 39 characters in S. tridecemlineatus and for 6 of 39 characters in S. mexicanus. Only PMB, BUB, and HMW were significantly variable between localities in both species. The other characters with significant interlocality differences were ZYB, IOB, BCB, BUL, SKD, FDW, HDW, HPW, TPW, and SAW for S. tridecemlineatus and NAS, PAW, and OCD in S. mexicanus. When both species are considered together, all characters showed significant interlocality variation. The results of SS-STP tests for the four characters with the highest F-ratios are shown in Table 3. The results of all SS-STP tests are given in Appendix 3 of Cothran (1982). Most of the variation appeared to be within the S. mexicanus populations as there were more non-significant subsets within S. mexicanus than within S. tridecemlineatus (Table 3). Much of the variation within S. mexicanus appeared to be associated with the populations with the largest number of hybrid individuals.

Discriminant function analysis was also used to examine species differences. The discriminant function was generated from a one-way multivariate analysis of variance applied to the 23 characters measured on undamaged specimens. The 11 characters chosen for the discriminant function were those with the highest *F*-ratios in the analyses of variance. The *F*-ratios and r^2 for each test of the 11 characters in the MANOVA, the character weightings, and the character correlations with the discriminant function are given in Table 4. The discriminant function is a linear combination of the values for an individual of the characters used in the MANOVA. The individual discriminant score, or *z*-value, is the number resulting from the linear combination. Thus,

$$z = 0.0339(\mathrm{GLS}) - 0.0486(\mathrm{BAS}) + 0.0265(\mathrm{ZYB}) \ldots + 0.0166(\mathrm{HFL})$$

for each individual. The correlation between a character and the *z*-value is an indication of the contribution of that character to the discriminant function (Morrison, 1967). The greater the correlation the greater the importance of that character in discriminating between the species.

The discriminant function was calculated using individuals from populations of the two species outside the contact zone (the reference samples). This discriminant function was then used to characterize all the individuals sampled. Individual discriminant scores ranged from 2.73 to 3.72. The lowest *z*-values were found for individuals of *S. tridecemlineatus*. The individual *z*-values of *S. tridecemlineatus* ranged from 2.73 to 3.25. For *S. mexicanus* *z*-values ranged from 3.03 to 3.72. The *z*-values of hybrid individuals ranged from 2.75 to 3.65, nearly spanning the total range of the two species. Population means of discriminant scores of *S. tridecemlineatus* ranged from 2.90 for population 25 to 3.07 for population 7. For *S. mexicanus* populations means of *z*-value ranged from 3.29 for population 30 to 3.53 for population 13. Except for populations 30 and 32, the lowest discriminant scores for populations of *S. mexicanus* were primarily those where hybrids were found.

Histograms of the discriminant scores of the reference samples and of all individuals are shown in Fig. 2. A clear separation of the species in the reference sample is present. However, when the *z*-values of all individuals were plotted, the separation was not as clearcut. The distribution of *z*-values of *S mexicanus* was skewed toward *S. tridecemlineatus* while the *S. tridecemlineatus* distribution was somewhat skewed away from *S. mexicanus*. All the *S. mexicanus* individuals that are on the *S. tridecemlineatus* side of the overall distribution of *z*-values were from populations 2, 5, 14, and 22 and were the populations with the greatest number of hybrids.

Principal components analysis was also used to summarize character variation between the two species. Character means and standard deviations of all 40 characters examined for each species and the character loadings (correlations) on the first two principal components are given in Table 5. The major portion of the variation (90.44%) was explained by principal component I (PCI). Almost all characters had high positive loadings on PCI which indicates that size is the major difference between the species. Characters with the lowest loadings on PCI and the highest loadings on PCII are internal characters such as POB, PMB, TRL, BUL, and BUB. Principal component

II only accounted for 2.03% of the variation. Principal component III is not discussed as it only accounted for 1.64% of the variation and no character had a correlation as great as 0.5.

A bivariate plot of the projections of the populations onto the first two principal components (Fig. 3) was based on 23 characters available for all populations plus tail length. Only individuals with unbroken tails were used to calculate mean TTL for each population. Component I explained 85.00% of the variation and PCII accounted for 3.92% of the variation. Character loadings on the principal components are similar in both the 40-character and the 24-character analyses. Additionally, average taxonomic distances matrices calculated from the various sets of characters (all characters, cranial characters only, or non-cranial characters only) were significantly associated with each other (Mantel tests: all characters vs. cranial characters, $\underline{t}_{\infty}$ = 15.76, $\underline{P} \leq 0.001$, $\underline{r} = 0.993$; all characters vs. non-cranial characters, $\underline{t}_{\infty}$ = 15.75, $\underline{P} \leq 0.001$, $\underline{r} = 0.992$; cranial vs. non-cranial characters, $\underline{t}_{\infty}$ = 15.45, $\underline{P} \leq 0.001$, $\underline{r} = 0.992$). Populations of S. mexicanus had primarily positive scores for PCI while populations of S. tridecemlineatus had primarily negative scores. Populations 2, 5, and 22 of S. mexicanus were somewhat intermediate in PCI scores. The S. mexicanus populations 14, 30, and 32 had negative PCI scores but also had high positive PCII scores which indicated that individuals in these populations are small, but not truly S. tridecemlineatus-like.

Principal components analysis was also used to examine patterns of intraspecific character variation. The same 24 characters as above were employed in the analysis. Projections of the populations onto the first two principal components are shown in Figs. 4a and 4b. Component I accounted for 60.63% of the variation in S. mexicanus. Components II and III explained 9.32% and 8.32%, respectively. Character loadings on the first principal component indicated overall size to be of major importance in explaining the differences between S. mexicanus populations. Characters associated with skull width had the highest loadings on PCII. Three clusters of S. mexicanus populations are evident in Fig. 4a. The cluster with positive PCI scores were the populations with few or no hybrids and the largest individuals. The cluster with populations 2, 5, 8, 14, and 22 was the cluster with the majority of the hybrid squirrels. The third group contained populations 30 and 32 which had small but relatively broad skulls.

Principal component I explained only 46.85% of the variation in S. tridecemlineatus. There was less overall size variation in S. tridecemlineatus than in S. mexicanus. However, the character loadings on PCI of S. tridecemlineatus were similar (although lower) to those of S. mexicanus and to those of the analysis with the data from the species combined. This similarity indicated that size was a major source of variation in S. tridecemlineatus. Components II and III explained 12.18% and 8.89% of the variation, respectively. No pattern was observed in the projection of the populations of S. tridecemlineatus on PCI (Fig. 4b). The two subspecies of S tridecemlineatus that occur within my study area were separated on PCII. Populations of S. t. texensis had negative PCII scores while all populations of S. t. arenicola except population 7 had positive

PCII scores. Individuals of S. t. texensis had narrower skulls than did the individuals of S. t. arenicola.

A bivariate plot of the principal components I and II scores of all individuals examined is shown in Fig. 5. Although the individuals of the two species tend to cluster by species, the species clusters of Fig. 5 are not as distinct as were the species clusters in Fig. 3. The major area of separation in Fig. 5 is indicated by the dashed line which is approximately parallel to the major axis of the species clusters. The S. mexicanus individuals that were in the S. tridecemlineatus cluster were primarily from populations 2 and 22. It is possible that these individuals were hybrids that were not detected by the use of electrophoresis or karyotypes. A few known hybrids were found in the S. tridecemlineatus cluster, although, most were placed with the S. mexicanus specimens. The major concentrations of hybrid individuals in Fig. 5 corresponded to the location of populations 2 and 22 in Fig. 3.

DISCUSSION

In contrast to high genetic and karyotypic similarity between S. mexicanus and S. tridecemlineatus (Cothran et al., 1977; Zimmerman and Cothran, 1976), these ground squirrel taxa are morphologically distinct (Figs. 2 and 3; Tables 2 and 5). Of 42 loci examined electrophoretically, only one locus (the albumin locus) had fixed allelic differences between the species (Cothran et al., 1977; Cothran, 1982). On the other hand, significant differences between the species were found for all morphometric characters. Only characters ROS, PMB, POB, PAW, and BMW had PCI loadings that were less than 0.90 (Table 5). The primary morphometric differences between S. mexicanus and S. tridecemlineatus are related to overall size differences. Additionally, the taxa are clearly different in external morphology. Spermophilus mexicanus is larger than S. tridecemlineatus and has a relatively longer and bushier tail while the latter species has a more complex pelage pattern (Howell, 1938; Hall and Kelson, 1959). The bacular morphology of the species is similar, but the tip of the baculum of S. mexicanus is less widely expanded and more sharply upturned on the sides than that of S. tridecemlineatus (Howell, 1938).

Neither principal components nor discriminant function analyses were particularly effective in distinguishing hybrid individuals (Figs. 2 and 5). There is no tendency for the hybrid ground squirrels to be intermediate to the parental species in either principal component or discriminant function scores. The hybrids primarily clustered with individuals of S. mexicanus.

Interspecific hybrids will not necessarily be morphologically intermediate to the parent species. Laboratory produced hybrids between species of the woodrat genus Neotoma had discriminant function scores that were somewhat intermediate to the parentals but were closer to one parent species or the other (Birney, 1976). Hybrids between species of birch also had discriminant scores that were closer to one parent than to the other (Dancik and Barnes, 1975).

In the case of the S. mexicanus - S. tridecemlineatus hybrids, electrophoretic and karyotypic evidence indicated that the majority of the individual squirrels of probable hybrid origin were either backcrosses or $\underline{F}_2$s (Cothran, 1982). Backcrossing will produce some hybrid individuals that are genetically and karyotypically indistinguishable from the parent species involved in the backcross due to Mendelian inheritance. Also, an $\underline{F}_2$ generation will have individuals identical to the parent species in Mendelian characters. Thus, some of the hybrid individuals were probably misidentified as one of the parental species because identification was based solely on electrophoretic and chromosomal characters. Morphological characteristics are polygenic in nature and may provide evidence of hybridization in backcross and $\underline{F}_2$ individuals. Morphologically, a number of ground squirrels identified as S. mexicanus had principal component and/or discriminant function scores indicative of S. tridecemlineatus (Figs. 2 and 5). Based upon where these individuals were collected, some were probably hybrids. The rest of the S. mexicanus that had low discriminant function scores were primarily from localities 30 and 32 where no hybrids were found.

Morphologically, most of the genetically identified hybrids were most similar to S. mexicanus (Figs. 2 and 5). The morphometric data supports the conclusion that the majority of the hybrid ground squirrels were backcrosses, primarily, if not exclusively, to S. mexicanus. Some hybrid individuals may have been backcrosses to S. tridecemlineatus but these individuals could also represent an $\underline{F}_2$ generation (Cothran, 1982). All hybrids were found in populations that were otherwise S. mexicanus. No hybrids were found associated with S. tridecemlineatus. The majority of the hybrids were concentrated in two populations. At least 50% and 68% of the individuals collected from localities 2 and 22, respectively, were hybrids. Probable hybrids were found at eight other localities, but few if any of these hybrids could have been F_1's. In no case were both parent species collected from the same population, although, localities 2 and 18 were only about 3 km apart.

The evidence suggests that the hybridization between S. mexicanus and S. tridecemlineatus is unidirectional, suggesting that all interspecific matings were between S. mexicanus females and S. tridecemlineatus males. All introgression may also be into S. mexicanus. Asymmetric introgression is not unusual (Short, 1965; Yang and Selander, 1968; Hunt and Selander, 1973); however, unidirectional hybridization and introgression does not appear to be common in nature. The mechanisms for the possible unidirectional hybridization between S. mexicanus and S. tridecemlineatus are not clear. Premating isolation of S. tridecemlineatus females from S. mexicanus males due to behavioral differences between the species or postmating isolation as a result of the size differences between the species are possible explanations (Watson, 1942; Cothran, 1982).

The high genetic similarity between S. mexicanus and S. tridecemlineatus (Cothran et al., 1977; Zimmerman and Cothran, 1976) could be the result of gene flow between the species. However, the apparent unidirectional nature of the hybridization and the morphometric differences between the taxa do not support significant gene exchange. Morphologically, even the populations with 50% or more hybrid individuals were most similar to S. mexicanus (Fig. 3).

Schnell and Selander (1981) pointed out that morphologic, structural gene, and chromosomal divergence processes are essentially independent. The morphologic divergence between S. mexicanus and S. tridecemlineatus is greater than the chromosomal and genic divergence. The question then is which set of characters reflect the amount of differentiation that is relevant to speciation. Unidirectional hybridization indicates that some level of reproductive isolation has developed. Reproductive isolation with little electrophoretic differentiation has been observed in natural populations and in the laboratory (Avise et al., 1975; Kilias et al., 1981). My data suggest that the morphometric relationships are a better estimate of the degree of differentiation relative to speciation than are electrophoretic or chromosomal data for S. mexicanus and S. tridecemlineatus. Whether the morphologic divergence is due to the morphologic characters being more sensitive to selection or is due to a small number of regulatory gene changes cannot be determined from the information available.

The present overlap of the ranges of S. mexicanus and S. tridecemlineatus is likely due to recent range expansion (Howell, 1932; Hall and Kelson, 1959; Hall, 1981), possibly due to habitat alteration as a result of human activities. Habitat disturbance is often cited as a prime cause of hybridization (Mayr, 1963; Moore, 1977). The situation observed for S. mexicanus and S. tridecemlineatus of a wide area of sympatry (Fig. 1) but only scattered hybridization primarily associated with disturbed habitats, has been called localized sympatric hybridization (Woodruff, 1973).

The mode of speciation that may best represent the situation between S. mexicanus and S. tridecemlineatus is the allo-parapatric model of Endler (1977). Under this model populations diverge under conditions of allopatry but speciation is completed after secondary contact. The path of speciation depends upon the amount of differentiation achieved during isolation. With a small amount of divergence (such as the genic differentiation between S. mexicanus and S. tridecemlineatus), there should be the formation of shallow clines followed by steep clines and hybrid zones (Endler, 1977). With high differentiation developed during allopatry (such as the morphologic divergence of the ground squirrel taxa), the clines are not formed and only hybridization precedes speciation. If Endler's model is applicable, then the allo-parapatric model also supports the contention that the morphologic relationships between the species are more indicative of the amount of differentiation between S. mexicanus and S. tridecemlineatus.

Morphological variability was greater in S. mexicanus than in S. tridecemlineatus (Table 5, Figs. 2, 3, and 5). The greater morphometric variability of S. mexicanus is consistent with the higher genic variability of S. mexicanus (Cothran et al., 1977). Spermophilus mexicanus was more variable both morphometrically and genetically than S. tridecemlineatus even when the hybrids were not included in the calculation of variability (present study; Cothran, 1982). There is no reason to expect that morphologic variability will be correlated with the variability at structural gene loci (Schnell and Selander, 1981). Unlike the gene products examined by electrophoretic techniques, morphological characters are determined by a number of loci as well as by interactions between the genome and the environment. However, it is not unreasonable to expect that patterns of morphometric and genic variability will be the same in species comparisons. Members of a species are exposed to similar selection pressures and have similar population structure. Even though morphologic and structural gene loci may evolve at different rates, relative levels of morphologic and genic variability within a species may be similar compared to other closely related taxa. Levels of variability may represent a consistent species-specific characteristic in comparisons between closely related species.

In general, morphologic characters were not good indicators of hybridization (Figs. 2 and 5). Both discriminant function and principal components analyses tended to underestimate the number of hybrid individuals. Of the two techniques, discriminant function analysis was more successful in detecting individuals of hybrid origin than were principal components. These results are consistent with those of Rohwer (1972). Neff and Smith (1978) concluded that discriminant function analysis was less effective in hybrid identification than was principal components analysis for both practical and theoretical considerations and that two assumptions must be met even if the analysis is performed for descriptive purposes only. The assumptions are that the initial groups are correctly defined and that the unknowns belong to one of the populations included in the analysis.

In my study, the first assumption is met as S. mexicanus and S. tridecemlineatus are clearly the parental species. The second assumption depends upon whether or not hybrids are members of the parent species or a separate group. Situations where only sterile F_1 hybrids are produced between two species might represent an example where the hybrids are a distinct group as such hybrids are a combination of two separate gene pools with no genetic interaction with the parent species. Hybrid zones as defined by Short (1969), where only hybrids occur within the hybrid zone, might also represent cases where the hybrids are a separate group. In such an instance the hybrids only interact directly with the parent species on the edges of the hybrid zone. Examples of this type of hybrid zone are provided by Montanucci (1970), as well as Hunt and Selander (1973). A third situation where hybrids could represent a group distinct from the parent species is when the hybrids become a separate species reproductively isolated from the parentals. Examples of this include some species of the lizard genus Cnemidophorus (Lowe and Wright, 1966).

Only occasional hybridization between S. mexicanus and S. tridecemlineatus was observed, and all the hybrids were found in association with S. mexicanus. There appears to be free gene exchange between S. mexicanus and the hybrids although whether there is backcrossing to S. tridecemlineatus is not certain. The high degree of genetic interaction between S. mexicanus and the hybrids indicates that the hybrids are at least a subgroup of S. mexicanus and, therefore, do not violate the assumptions of discriminant function analysis given by Neff and Smith (1978).

Although the discriminant function proved to be a better method for identifying hybrid ground squirrels than was principal components analysis, principal components probably gave a more accurate picture of the relationships between the populations of S. mexicanus and S. tridecemlineatus. The discriminant axis and PCI primarily reflected overall size differences between the species (Table 5). Populations of S. mexicanus composed of the smallest individuals will be closest to S. tridecemlineatus on both PCI and the discriminant axis. Hybrids tended to be smaller than non-hybrid S. mexicanus and the presence of hybrids in a population of S. mexicanus tended to lower the means of the character values of the population. Four of the six S. mexicanus populations (localities 2, 5, 14, and 22; Fig. 3) with low PCI scores, which are most like those of S. tridecemlineatus, had hybrids in the population. Localities 30 and 32 had the lowest PCI and discriminant function scores, but there was no evidence of hybridization within either population. Both localities 30 and 32 are probably outside the influence of introgression of S. tridecemlineatus genes. Populations 30 and 32 are distinct from S. tridecemlineatus on PCII, however, and have the highest positive PCII scores. PCII was primarily related to skull width and individuals from localities 30 and 32 had the greatest relative skull width. Principal components indicate that localities 30 and 32 are distinct from S. tridecemlineatus while discriminant function analysis showed that these two populations were more similar to S. tridecemlineatus than any of the other S. mexicanus populations.

Despite the lack of complete reproductive isolation between S. mexicanus and S. tridecemlineatus, the two taxa appear to be behaving as separate species. The apparent unidirectional hybridization and introgression suggests that S. tridecemlineatus is at least partially reproductively isolated from S. mexicanus. Production of backcross hybrids to S. tridecemlineatus or matings between hybrids could produce individuals that may be able to initiate introgression into S. tridecemlineatus, however, this possibility has not yet been observed. The electrophoretically determined similarity between S. mexicanus and S. tridecemlineatus is unusually high (Cothran et al., 1977; Cothran, 1982) but no unique S. mexicanus alleles have been detected in S. tridecemlineatus in the area of potential contact. The species are morphologically distinct to a point that warrants taxonomic differentiation. Both levels of variability of the taxa and high sexual dimorphism in S. mexicanus, but not in S. tridecemlineatus, represent additional differences between the taxa.

The majority of the observed hybrids were found at localities 2 and 22; hybridization between S. mexicanus and S. tridecemlineatus is essentially a localized phenomena. The hybridization between S. mexicanus and S. tridecemlineatus does not appear to have compromised the species integrity of either taxa. Similar examples of occasional hybridization between species with little effect to the parent species have been reported for a number of mammals (Patton et al., 1972; Rohwer and Kilgor, 1973; Birney, 1976; Greenbaum, 1981). Due to the high percentage of backcrosses among the hybrids between S. mexicanus and S. tridecemlineatus, morphometric characters were of little use in detecting hybrids and greatly underestimated the percentage of hybrids in the sample. However, the morphologic relationships between the species probably give a more accurate estimate of the degree of divergence between S. *mexicanus* and S. *tridecemlineatus* than do electrophoretic measures. Also, the morphologic data may have detected hybrids that were not identified by electrophoretic characteristics (Fig. 2). The morphologic data indicate that the introgressive hybridization has had less of an impact upon the S. *mexicanus* gene pool than would be predicted by the genic data alone.

ACKNOWLEDGMENTS

I am grateful to G. D. Schnell, C. C. Carpenter, C. E. Hopla, and J. N. Thompson for advice and critical readings of previous versions of the manuscript. I also thank R. K. Chesser, J. D. Felley, R. L. Honeycutt, and R. D. Owen for their help in collecting or preparing specimens. Special thanks to M. H. Smith who provided support during the completion of this study. I also gratefully acknowledge my wife, Marian, who provided assistance and support during all aspects of my research. This work was submitted to the Department of Zoology, University of Oklahoma as partial fulfillment of the doctoral degree. The author was supported by Contract DE-AC09-76SR00819 between the U.S. Department of Energy and the University of Georgia during the completion of the work.

Literature Cited

Avise, J. C. 1976. Genetic differentiation during speciation, p. 106-122. in Molecular evolution. F. J. Ayala (ed.), Sinauer Assoc. Inc., Sunderland, 277 pp.

Avise, J. C., J. J. Smith, and F. J. Ayala. 1975. Adaptive differentiation with little genic change between two native California minnow. Evolution 29:411-426.

Barr, A. J., J. H. Goodnight, J. P. Sall, W. H. Blair, and D. M. Chilko. 1979. SAS user's guide 1979 edition. SAS Institute Inc., Raleigh, 494 pp.

Birney, E. C. 1976. An assessment of relationships and effects of interbreeding among woodrats of the *Neotoma floridana* species-group. J. Mammal., 57:103-132.

Bush, G. L. 1975. Modes of animal speciation. Ann. Rev. Ecol. Syst., 6:339-364.

Chesser, R. K. 1980. Computer systems and programming for the analysis of populations genetics data. Univ. Stockholm Spec. publ., Report no. III.

Cothran, E. G. 1982. Karyotypic, morphologic, and genic differentiation of hybridizing ground squirrels (*Spermophilus mexicanus* and *Spermophilus tridecemlineatus*). Unpublished Ph.D. dissertation, Univ. Oklahoma, Norman.

Cothran, E. G., E. G. Zimmerman, and C. F. Nadler. 1977. Genic differentiation and evolution in the ground squirrel subgenus *Ictidomys* (genus *Spermophilus*). J. Mammal., 58:610-622.

Dancik, B. P., and B. V. Barnes. 1975. Multivariate analyses of hybrid populations. Naturaliste Can., 102:835-843.

Dobzhansky, Th. 1959. Evolution of genes and genes in evolution. Cold Spring Harb. Symp. Quant. Biol., 24:15-30.

Endler, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, 246 pp.

Gabriel, K. R. 1964. A procedure for testing homogeneity of all sets of means of analysis of variance. Biometrics 20:459-477.

Greenbaum, I. F. 1981. Genetic interactions between hybridizing cytotypes of the tent-making bat (Uroderma bilobatum). Evolution 35:306-321.

Hall, E. R. 1981. The Mammals of North America. Second Edition. Wiley-Interscience, New York, 1,181 pp.

Hall, E. R., and K. R. Kelson. 1959. Mammals of North America. Ronald Press, New York, 1,083 pp.

Howell, A. H. 1938. Revision of the North American ground squirrels. North Amer. Fauna 56:1-265.

Hunt, W. G., and R. K. Selander. 1973. Biochemical genetics of hybridization in European house mice. Heredity 31:11-33.

Kilias, G., S. N. Alahiotis, and M. Pelecanos. 1980. A multifactorial genetic investigation of speciation theory using Drosophila melanogaster. Evolution 34:730-737.

Lowe, C. H., and J. W. Wright. 1966. Evolution of parthenogenetic species of Cnemidophorus (whiptail lizards) in western North America. J. Arizona Acad. Sci., 4:81-87.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res., 27:209-220.

Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, 797 pp.

Montanucci, R. R. 1970. Analyses of hybridization between Crotaphytus wislizenii and C. silus (Sauria:Iquanidae) in California. Copeia 1970:104-123.

Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quart. Rev. Biol., 52:263-277.

Morrison, D. F. 1967. Multivariate statistical methods. McGraw-Hill. New York, 415 pp.

Nadler, C. F., and C. E. Hughes. 1966. Chromosomes and taxonomy of the ground squirrel subgenus Ictidomys. J. Mammal., 47:46-53.

Neff, N. A., and G. R. Smith. 1978. Multivariate analysis of hybrid fishes. Syst. Zool., 28:176-196.

Nei, M. 1972. Genetic distance between populations. Amer. Natur., 106:283-292.

Nevo, E., Y. J. Kim, C. R. Shaw, and C. S. Thaeler, Jr. 1974. Genetic variation, selection and speciation in Thomomys talpoides gophers. Evolution 28:1-23.

Patton, J. L., R. K. Selander, and M. H. Smith. 1972. Genic variation in hybridizing populations of gophers (genus Thomomys). Syst. Zool., 21:263-270.

Power, D. M. 1970. Geographic variation of red-winged blackbirds in central North America. Univ. Kansas Publ., Mus. Nat. Hist., 19:1-83.

Rohlf, R. J., J. Kishpaugh, R. Bartcher, and K. Kirk. 1974. NT-SYS. Numerical taxonomy system of multivariate statistical programs. State Univ. New York, Stony Brook, 98 pp.

Rohwer, S. A. 1972. A multivariate assessment of interbreeding between the meadowlarks, Sturnella. Syst. Zool., 21:313-338.

Rohwer, S. A., and D. L. Kilgor, Jr. 1973. Interbreeding in the arid-land foxes, Vulpes velox and V. macrotis. Syst. Zool., 22:157-165.

Schnell, G. D. and R. K. Selander. 1981. Environmental and morphological correlates of genetic variation in mammals. p. 60-99, in Mammalian population genetics. Smith, M. H. and J. J. Joule (eds.), Univ. Georgia Press, Athens, 380 pp.

Short, L. L. 1965. Hybridization in the flickers (Colaptes) of North America. Bull. Am. Mus. Nat. Hist., 129:307-428.

__________. 1969. Taxonomic aspects of avian hybridization. Auk 86:84-105.

Sokal, R. R. 1961. Distance as a measure of taxonomic similarity. Syst. Zool., 10:70-79.

__________. 1979. Testing statistical significance of geographic variation patterns. Syst. Zool., 28:227-232.

Watson, M. L. 1942. Hybridization experiments between *Peromyscus polionotus* and *Peromyscus maniculatus*. J. Mammal., 23:315-316.

White, M. J. D. 1978. Modes of speciation. W. H. Freeman and Co., San Francisco, 455 pp.

Woodruff, D. S. 1973. Natural hybridization and hybrid zones. Syst. Zool., 22:213-218.

Yang, S. Y., and R. K. Selander. 1968. Hybridization in the Grackle *Quiscalus quiscalus* in Louisiana. Syst. Zool., 17:107-143.

Zimmerman, E. G., and E. G. Cothran. 1976. Hybridization in the Mexican and 13-lined ground squirrels, *Spermophilus mexicanus* and *Spermophilus tridecemlineatus*. Experienta 32:704-706.

Zimmerman, E. G., and M. E. Nejtek. 1977. Genetics and speciation in three semispecies of *Neotoma*. J. Mammal., 58:391-402.

Department of Zoology, Univeristy of Oklahoma, Norman, OK 73019 (present address: Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801).

Table 1.--Population identification number, samples size, location, and species occuring at the location of the collecting localities of the specimens used in the this study. t = Spermophilus tridecemlineatus, m = Spermophilus mexicanus.

Population number	N	Location	Species
1	15	Lubbock, Lubbock Co., Texas	t
2	28	Hobbs, Lea Co., New Mexico	m*
3	31	Portales, Roosevelt Co., New Mexico	t
4	18	Big Spring, Howard Co., Texas	m*
5	16	Roswell, Chaves Co., New Mexico	m*
6	17	Artesia, Eddy Co., New Mexico	m*
7	16	Plainview, Hale Co., Texas	t
8	17	Kennedy, Karnes Co., Texas	m*
9	15	Lovington, Lea Co., New Mexico	t
10	15	Levelland, Hockley Co., Texas	t
11	17	Ranger, Eastland Co., Texas	m*
12	17	Snyder, Scurry Co., Texas	m
13	17	Abilene, Taylor Co., Texas	m*
14	25	Austin, Travis Co., Texas	m*
15	15	Waco, McLennan Co., Texas	t
16	20	Andrews, Andrews Co., Texas	m*
17	18	Tahoka, Lynn Co., Texas	t
18	18	Hobbs, Lea Co., New Mexico	t

Table 1.--Continued.

Population number	N	Location	Species
19	19	Matador, Motley Co., Texas	t
20	17	Vernon, Wilbarger Co., Texas	t
21	16	Hillsboro, Hill Co., Texas	t
22	19	Seymour, Baylor Co., Texas	m*
23	14	Munday, Knox Co., Texas	m
24	16	Denton, Denton Co., Texas	t
25	14	Wichata Falls, Wichita Co., Texas	t
26	10	Paris, Lamar Co., Texas	t
27	7	Lewisville, Denton Co., Texas	t
28	8	Gruver, Hansford Co., Texas	t
30	16	Sheffield, Pecos Co., Texas	m
32	5	New Braunfels, Comal Co., Texas	m
34	8	Pecos, Reeves Co., Texas	m
38	17	Norman, Cleveland Co., Oklahoma	t
39	11	Kermit, Winkler Co., Texas	m

*Possible hybrid individuals were collected at these localities.

Table 2.--Mean percentage of morphological variability accounted for by differences among samples within species, among populations, within sexes and due to error for 21 cranial, 19 non-cranial, and 40 total skeletal characters.

	Species	Locality	Sex	Error
Cranial characters	67.15	8.72	0.82	23.21
Non-cranial characters	66.95	5.99	4.05	23.01
All characters	67.05	7.35	2.44	23.16

Table 3.--Results of sums of squares simultaneous test procedures (SS-STP) for the 4 cranial characters with the highest F-ratios. Location abbreviations are the first three letters of the locality given in Table 1. Non-significant subsets of localities are indicated by vertical columns of Is.

GLS	IOB	BCB	MAL
And I	Aus I	Ker I	Ker I
Art I	And II	Abi I	Abi II
Sny II	Ken III	Mun II	Mun II
Ker II	Sny III	Sny III	And II
Abi II	Abi III	And IIII	Sny III
Big III	Ker III	Pec IIII	Big IIII
Mun IIII	Pec III	Big IIII	Art IIII
Ran IIIII	Art IIII	Ken IIII	Pec IIII
Ken IIIIII	Big IIII	Ran IIII	Ros IIII
Ros IIIIII	Mun IIII	Art IIII	Ken IIIII
Pec IIIIII	Ran IIIII	Ros IIII	Ran IIIII
Sey IIIIIII	Sey IIII	She IIIII	Aus IIIII
Hob[1] IIIIII	Hob[1] IIIII	Sey IIIII	New IIIII
Aus IIIIII	New IIIIII	Aus IIII	Hob[1] IIII
New IIIIII	Ros IIIIII	Hob[1] IIII	Sey IIIII
She IIIIII	She IIIIII	New IIII	She IIIII
Wac IIIIII	Wac IIIIII	Wac IIII	Wac IIIII
Nor IIIIII	Par IIIII	Tah III	Hob[2] IIIII

Table 3.--Continued.

GLS		IOB		BCB		MAL	
Pla	IIIII	Tah	IIII	Lub	II	Pla	IIII
Tah	IIIII	Pla	IIII	Lov	II	Den	IIII
Den	IIII	Den	IIII	Lew	II	Hil	III
Hil	IIII	Nor	IIII	Hob[2]	II	Nor	III
Lov	IIII	Wic	IIII	Por	II	Lov	III
Lev	IIII	Hil	III	Pla	II	Tah	III
Lew	IIII	Lew	III	Mat	II	Lew	III
Lub	IIII	Lov	II	Den	II	Lev	III
Mat	IIII	Hob[2]	II	Lev	II	Mat	III
Hob[2]	III	Ver	II	Nor	II	Por	II
Par	II	Lev	II	Par	II	Par	II
Por	II	Mat	II	Wic	II	Lub	II
Gru	I	Por	II	Gru	II	Ver	II
Wic	I	Lub	I	Hil	II	Gru	II
Ver	I	Gru	I	Ver	I	Wic	I

[1]Locality 2 *S. mexicanus*

[2]Locality 18 *S. tridecemlineatus*

Table 4.--F-ratios and r^2 from analysis of variance of each character in the MANOVA for the calculation of the discriminant function, character weights used to determine individual discriminant scores (z-values), and correlations of the characters with the discriminant function. All F-ratios and correlations were significant at the 0.0001 level. The degrees of freedom for the analyses of variance were 1,145. See text for explanation of character abbreviations.

Character	F-ratio	r^2	Character weight	Correlation
GLS	571.5	0.799	0.0339	0.921
BAS	480.4	0.769	-0.0486	0.898
ZYB	505.7	0.769	0.0265	0.908
IOB	386.5	0.729	-0.0043	0.824
PPL	371.0	0.720	0.0391	0.875
BAT	379.9	0.725	0.0245	0.860
TRL	422.2	0.746	0.1367	0.869
BCB	574.2	0.799	-0.0057	0.900
MAD	599.7	0.806	0.0524	0.914
SKD	406.3	0.738	-0.0108	0.837
HFL	462.1	0.762	0.0166	0.902

Table 5.--Means (± standard deviation) by species of the morphological characters used in principal components analysis and loadings of the characters on the first two principal components. See text for explanation of character abbreviations.

Character	*S. tridecemlineatus*	*S. mexicanus*	Principal component I	Principal component II
GLS	39.6 ± 1.50	43.9 ± 2.02	0.994	0.003
BAS	34.6 ± 1.46	38.7 ± 1.97	0.991	0.008
ZYB	23.5 ± 0.99	26.4 ± 1.34	0.988	-0.079
ROS	15.3 ± 0.83	17.0 ± 1.08	0.898	0.161
NAS	13.3 ± 0.85	15.0 ± 1.02	0.973	0.027
PMB	9.2 ± 0.53	9.7 ± 0.60	0.718	0.573
IOB	8.6 ± 0.56	10.3 ± 0.86	0.928	-0.185
POB	12.2 ± 0.59	13.0 ± 0.71	0.764	-0.491
PPL	13.2 ± 0.72	14.9 ± 0.84	0.986	0.032
BAT	10.8 ± 0.40	11.8 ± 0.47	0.961	0.010
TRL	7.6 ± 0.32	8.5 ± 0.41	0.934	-0.123
BCB	17.4 ± 0.53	19.1 ± 0.69	0.983	-0.017

Table 5.--Continued.

Character	*S. tridecemlineatus*	*S. mexicanus*	Principal component I	II
BUL	8.4 ± 0.43	9.3 ± 0.47	0.918	0.141
BUB	6.9 ± 0.37	7.6 ± 0.41	0.929	0.160
MOL	2.0 ± 0.12	2.2 ± 0.16	0.929	-0.072
UDL	12.8 ± 0.79	14.2 ± 1.01	0.967	0.050
PAW	6.6 ± 0.38	7.2 ± 0.39	0.856	-0.128
OCD	5.9 ± 0.52	6.9 ± 0.59	0.951	0.003
MAL	16.5 ± 0.60	18.3 ± 0.83	0.983	-0.079
MAD	12.3 ± 0.67	14.2 ± 0.90	0.983	-0.040
SKD	17.0 ± 0.51	18.4 ± 0.78	0.974	-0.081
FEL	28.7 ± 1.73	34.0 ± 2.40	0.994	-0.042
FMW	2.1 ± 0.18	2.5 ± 0.22	0.957	0.012
FDW	4.9 ± 0.35	5.7 ± 0.46	0.977	-0.037
FPW	6.3 ± 0.38	7.4 ± 0.57	0.985	-0.042
HUL	23.1 ± 1.31	26.8 ± 1.84	0.988	-0.062

Table 5.--Continued.

Character	*S. tridecemlineatus*	*S. mexicanus*	Principal component I	II
HMW	2.3 ± 0.30	2.7 ± 0.39	0.807	0.084
HPW	6.1 ± 0.34	6.9 ± 0.43	0.979	-0.017
HPW	4.5 ± 0.25	5.2 ± 0.35	0.993	0.012
RPW	1.9 ± 0.13	2.1 ± 0.16	0.951	0.076
UPW	2.7 ± 0.19	3.1 ± 0.23	0.985	0.001
TPW	4.5 ± 0.27	5.3 ± 0.42	0.984	-0.043
FIW	1.5 ± 0.15	1.8 ± 0.22	0.967	0.123
SCL	18.2 ± 1.63	21.7 ± 2.13	0.976	0.045
SCW	3.2 ± 0.26	3.8 ± 0.35	0.960	0.073
PEV	11.2 ± 0.80	13.4 ± 1.22	0.984	0.108
SAW	9.9 ± 1.05	11.6 ± 1.22	0.958	0.063
HFL	34.3 ± 1.68	40.6 ± 2.62	0.978	-0.063
BDL	163.0 ± 12.17	187.4 ± 15.68	0.966	-0.011

Figure 1. Map of collecting localities for ground squirrels in Oklahoma, Texas, and New Mexico. The shading indicates the probable ranges of the two species, and the ranges of the two subspecies of *S. tridecemlineatus* in the collecting area are also indicated. Locality numbers are explained in Table 1.

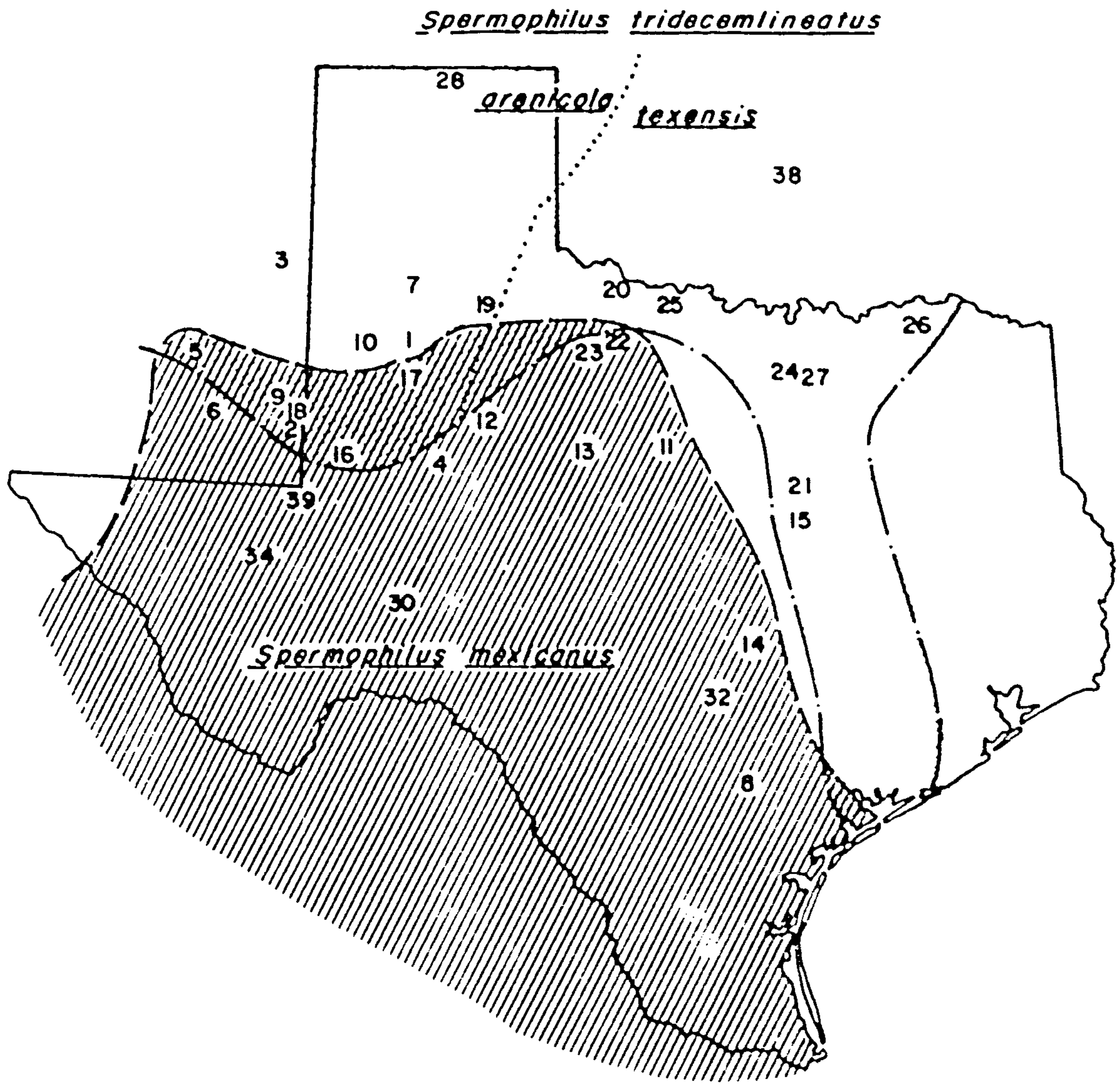
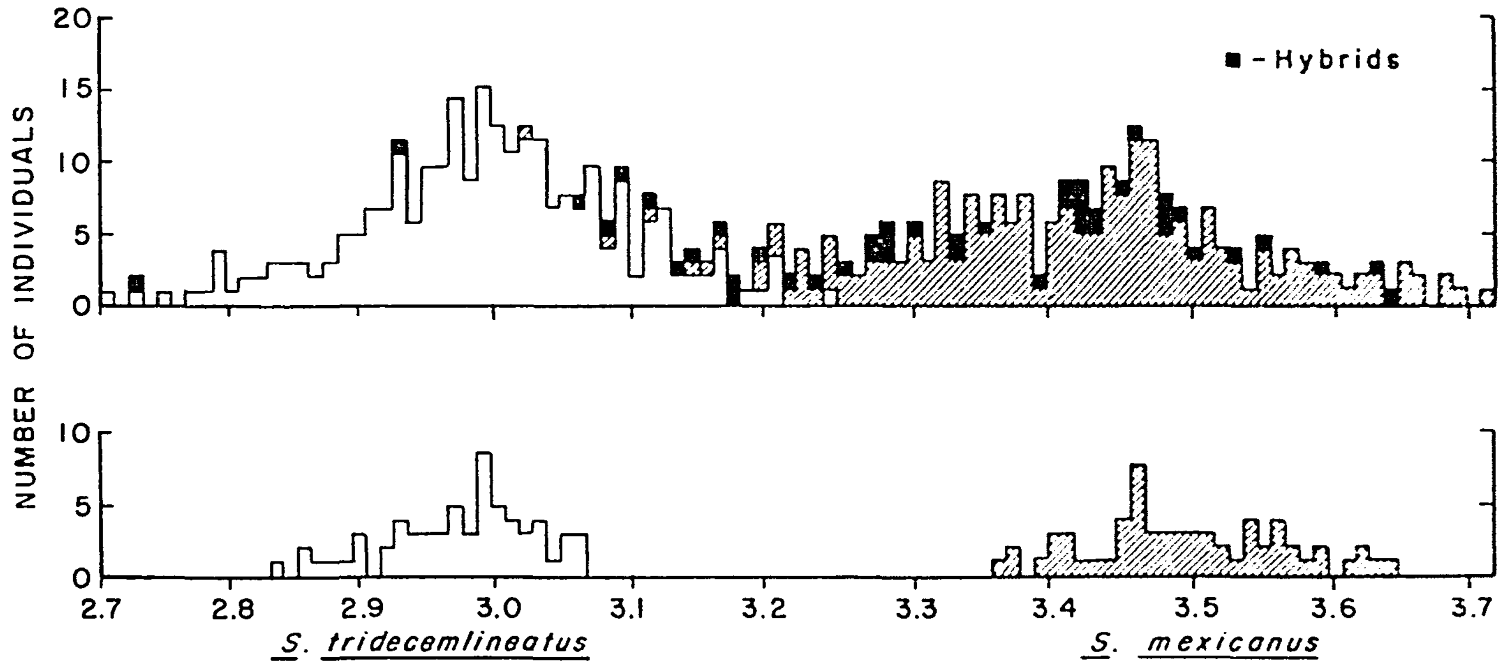

Spermophilus tridecemlineatus
arenicola
texensis
Spermophilus mexicanus
28
38
3
7
19
20
25
26
10
1
22
23
24
27
5
9
17
18
6
2
12
16
4
13
11
39
21
15
34
30
14
32
8

Figure 2. Frequency histogram of discriminant function scores of individuals of the ground squirrel species. The lower graph includes the reference samples while the upper is of the combined sample (including the reference sample).



NUMBER OF INDIVIDUALS
■ - Hybrids
20
15
10
5
0
10
5
0
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
3.5
3.6
3.7
S. tridecemlineatus
S. mexicanus

Figure 3. Scatter diagram of scores for principal components I and II of ground squirrel populations shown in Fig. 1. See Table 1 for locality codes.

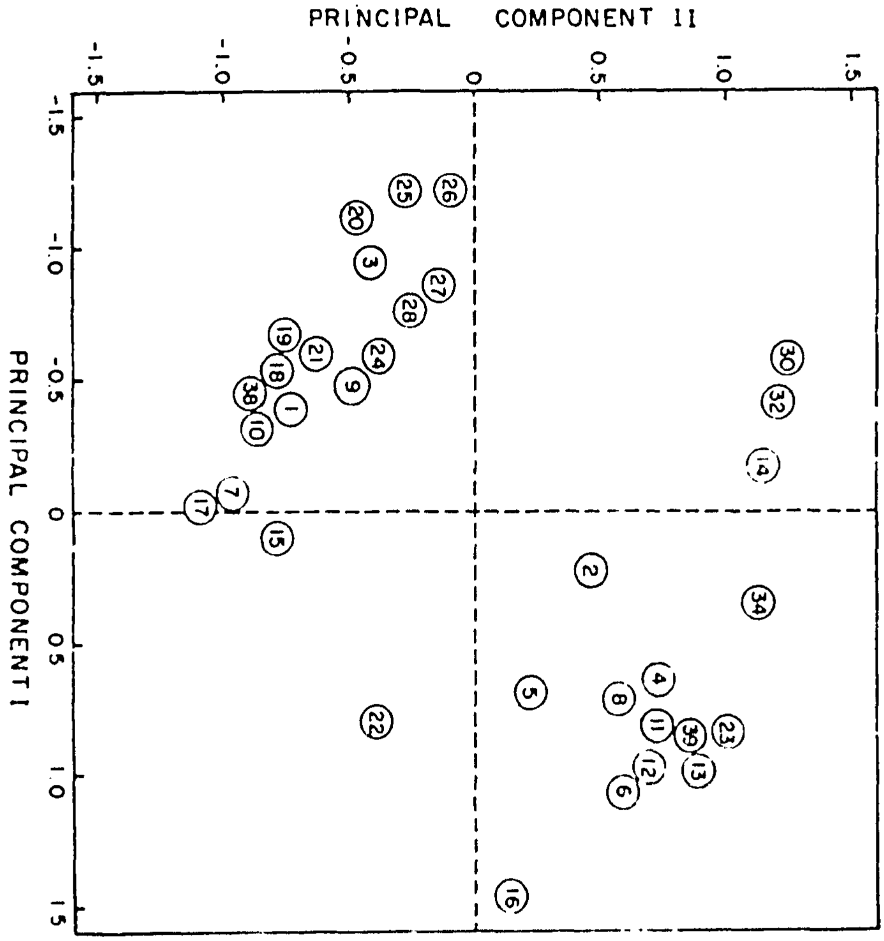

PRINCIPAL COMPONENT II
PRINCIPAL COMPONENT I

Figure 4. Intraspecific scatter diagrams of scores for principal components I and II of ground squirrel populations. A. Populations of S. mexicanus. B. Populations of S. tridecemlineatus. See Table 1 for locality codes.

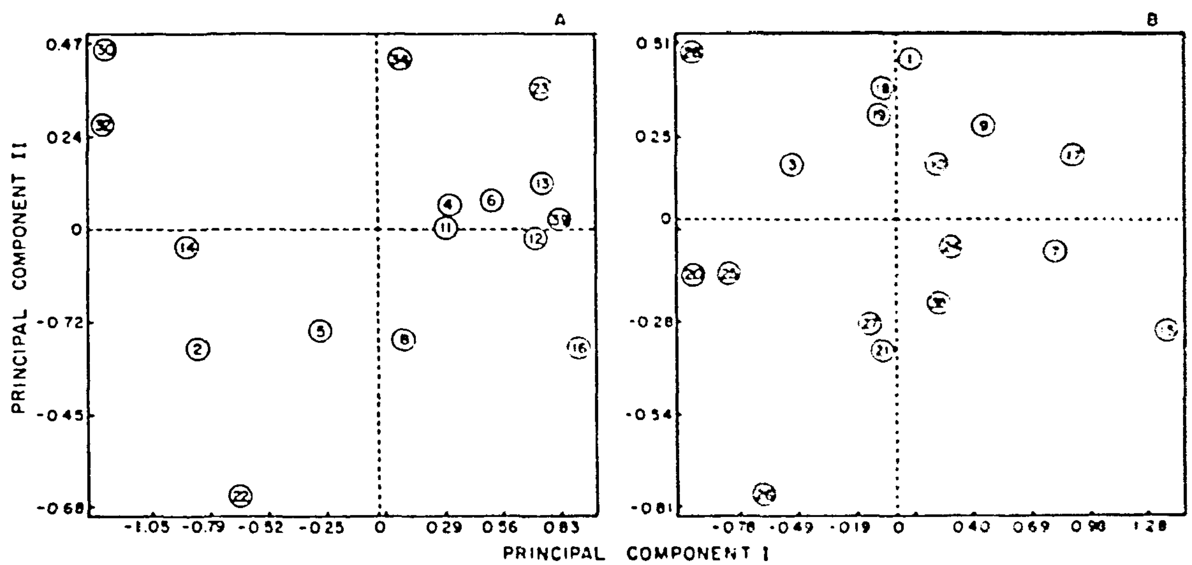
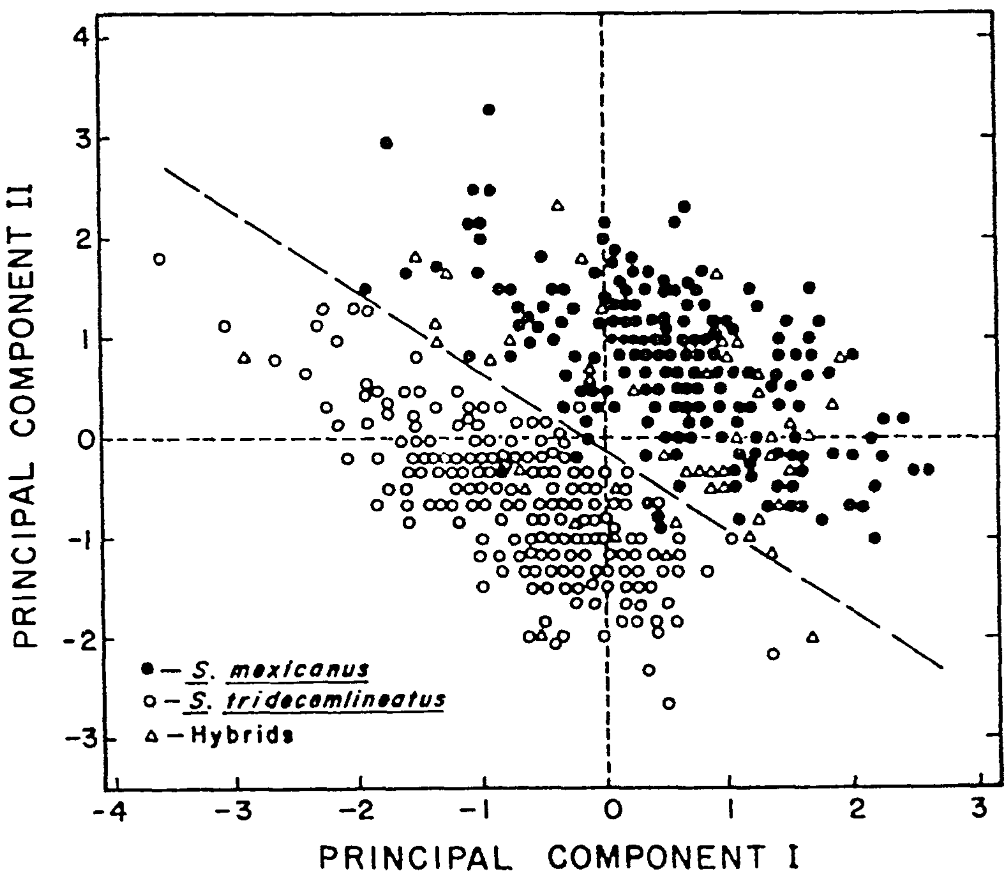

A
B
PRINCIPAL COMPONENT II
PRINCIPAL COMPONENT I
0.47
0.24
0
-0.72
-0.45
-0.68
-1.05 -0.79 -0.52 -0.25 0 0.29 0.56 0.83
0.51
0.25
-0.28
-0.54
-0.81
-0.78 -0.49 -0.19 0 0.40 0.69 0.98 1.28

Figure 5. Scatter diagram of scores for principal components I and II of all individual ground squirrels examined. The dashed line was drawn by eye to indicate the separation of the two clusters.


PRINCIPAL COMPONENT II
4
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
PRINCIPAL COMPONENT I
● — S. mexicanus
○ — S. tridecemlineatus
△ — Hybrids

ELECTROPHORETIC AND MORPHOLOGIC COMPARISONS OF EVOLUTIONARY DIVERGENCE OF THE HYBRIDIZING GROUND SQUIRRELS *SPERMOPHILUS MEXICANUS* AND *S. TRIDECEMLINEATUS*

E. Gus Cothran

Department of Zoology

University of Oklahoma

Norman, Oklahoma 73019

Present address:

Savannah River Ecology Laboratory

Drawer E

Aiken, South Carolina 29801

Speciation is the process that divides a single interbreeding gene pool into two independent evolutionary units. Numerous models have been proposed to explain how speciation occurs (see Mayr, 1963; Endler, 1977; and White, 1978 for reviews). In general, speciation occurs when portions of a population become isolated either geographically, ecologically, or by some other means. During isolation the separate populations are subjected to different selection pressures and accumulate genetic differences. If sufficient genetic differences between the populations are built up, resumed contact will not result in successful interbreeding and the populations will be separate gene pools or species.

Often the genetic differences between the populations accumulated during isolation will not result in reproductive isolation, and hybridization will occur when contact is resumed. Hybridization is often considered an intermediate stage of speciation where reproductive isolating mechanisms are perfected (Mayr, 1963). Hybrids between species or insipient species may be selectively inferior to the parentals as a result of combining two differently coadapted gene complexes (Endler, 1977). On the other hand, when hybridization occurs in ecotones or in distured habitats, the hybrids may have a competitive advantage over the parental forms, as long as there are no major genetic incompatabilities (Wright and Lowe, 1968). Additionally, zones of hybridization may become stable over long periods of time without the development of reproductive isolation (Meise, 1928; Hunt and Selander, 1973; Jackson, 1973; Hubbard, 1969).

Just how much genetic differentiation is sufficient for the establishment of reproductive isolation is not clear. The traditional view is that major genetic reorganization accompanies speciation (Mayr, 1963). Recent electrophoretic studies have provided evidence that speciation can occur with very little genic differentiation (Avise, 1975). Other studies have found little electromorphic differentiation but considerable morphologic divergence between presumed species (Turner, 1974) or large karyotypic differences with high genic or morphologic similarity between hybridizing taxa (Greenbaum, 1981). There is probably no constant amount of genetic differentiation required for speciation, and different sets of characters may give different estimates of the amount of differentiation that has taken place. It is necessary to examine a variety of populations at various stages of the speciation process to understand what level or kind of genetic change is likely to result in complete reproductive isolation.

The ground squirrels Spermophilus mexicanus and S. tridecemlineatus represent taxa that have not completed the speciation process. Hybrids between these species were first reported by Zimmerman and Cothran (1976), although the hybridization between the species was predicted by Remington (1968) based on his suture zone hypothesis. Electrophoretic relationships between S. mexicanus and S. tridecemlineatus were examined by Cothran et al. (1977) and Zimmerman and Cothran (1976), and Cothran (1982) studied the karyotypic relationships of these taxonomic species. The electromorphic and karyotypic differences were small. The purpose of the present study was to examine the electromorphic relationships between S. mexicanus and S. tridecemlineatus more extensively and to compare the genetic relationships with the morphologic and karyotypic relationships of these species. Differences between patterns of morphologic and genic differentiation can be used to infer which set of characters were most important in the divergence of these taxa. The genic and morphometric characters can also be used to examine the extent and direction of hybridization and introgression of S. mexicanus and S. tridecemlineatus. Additionally, measures of fluctuating asymmetry (Van Valen, 1962; Soulé, 1967) were examined in an attempt to access the fitness of the hybrids relative to the parent species.

MATERIALS AND METHODS

A total of 596 ground squirrels representing 39 collecting localities were examined. Morphometric, karyotypic, and electrophoretic data were collected. All three types of data were not available for every specimen and Table 1 gives the sample size for each population for morphometric and electrophoretic data. Figure 1 shows the locality of each population and the ranges of the species. Results of the karyotypic analyses are given in Zimmerman and Cothran (1976) and Cothran (1982).

Details of the morphometric analysis are given in Cothran (1982). Forty cranial, skeletal, and external measurements were taken. In this paper, I will concentrate on the 21 cranial and 2 external measurements that were available for all undamaged specimens. The characters and character abbreviations are as follows: greatest length of skull (GLS), basal length (BAS), zygomatic breadth (ZYB), rostral length (ROS), nasal length (NAS), premaxillary breadth (PMB), inter-orbital breadth (IOB), post-orbital breadth (POP), postpalatal length (PPL), breadth across tooth rows (BAT), tooth tow length (TRL), braincase breadth (BCB), bular length (BUL), bular breadth (BUB), second premolar breadth (PMW), upper diastema length (ULD), palatal width (PAW), occipital depth (OCD), skull depth (SKD), mandible length (MAL), mandible depth (MAD), hind foot length (HFL), and body length (BDL). Morphometric variation within species and morphologic relationships between the species were summarized by discriminant function and principal components analysis.

Thirty proteins encoded by 42 loci have been examined electrophoretically for both species. Of these loci, 28 were previously examined (Cothran et al., 1977). Six esterase loci examined by Cothran et al. (1977) were not used in the present study. The 36 loci that were utilized are as follows: phosphoglucomutase 1, 2, and 3 (PGM-1, PGM-2, PGM-3), lactate dehydrogenase 1, 2, and 3 (LDH-1, LDH-2, LDH-3), malate dehydrogenase 1 and 2 (MDH-1, MDH-2), malic enzyme (ME), isocitrate dehydrogenase 1 and 2 (IDH-1, IDH-2), glutamate-oxaloacetate transaminase 1 and 2 (GOT-1, GOT-2), α and β hemoglobin (αHb-1, αHb-2, βHb), adenosine deaminase (ADA), indolphenol oxidase (IPO), alcohol dehydrogenase (ADH), nucleoside phosphorylase (NSP), phosphoglucose isomerase (PGI), glucose-6-phosphate dehydrogenase (G-6-PDH), 6-phosphogluconate dehydrogenase (6-PGD), acid phosphatase 1 and 2 (AP-1, AP-2), peptidase 1, 2, and 3 (PEP-1, PEP-2, PEP-3), albumin (ALB), transferrin (TRF), protein 1 (PT-1), mannose-6-phosphate isomerase (MPI), glutamate dehydrogenase (GDH), α-glycerophosphate dehydrogenase (α-GPD), leucine aminopeptidase (LAP), and adenylate kinase (ADK). Electrophoretic methods follow Selander et al. (1971) and Harris and Hopkinson (1976). Alleles were designated alphabetically in order of decreasing mobility with the assumption of homology between species. Allelic designations match those of Cothran et al. (1977) for loci in common with the present study.

Nei's (1971) coefficients of genetic identity (I) and genetic distance (D) as well as Rogers' (1972) coefficient of similarity (S) were calculated for paired combinations for all populations. Wrights' (1969) F-statistics were calculated using the methods of Nei (1977) as modified by Chesser (1981). The weighted separation index (Vogt and McPherson, 1972) was used as a hybrid index for the genetic data. The index was designated S by Vogt and McPherson (1972), but to avoid confusion with Rogers' (1972) S I will use the letter X when referring to the values of the weighted separation index.

Bilateral asymmetry of some paired morphological characters was calculated as the difference between the right and left sides (R-L). To correct for differences in size between the two species the asymmetry value used was (R-L)/(R+L). The cranial characters used in the asymmetry analyses were PPL, TRL, BUL, PMW, UDL, and MAL. Additionally, for populations where complete skeletons were available, the noncranial characters femur length (FEL), femur proximal width (FPW), humerus length (HUL), humerus proximal width (HPW), scapula length (SCL), and scapula width (SCW) were used in the asymmetry analysis. Since asymmetry values did not fit a normal distribution, non-parametric ANOVAS were performed on distributions of absolute values of asymmetry, sums of all asymmetry values, and sums of cranial asymmetry values.

Associations between matricies of phenetic distance (average taxonomic distance, Sokal, 1961), genetic distance (D), and geographic distance were tested by the general regression analysis of Mantel (1967; Sokal, 1979). Computer analyses were performed using the Statistical Analysis System (SAS; Barr et al., 1979), Numerical Taxonomic Systems (NT-SYS; Rohlf et al., 1974), and programs from Chesser (1980). Matrix correlations (r) were calculated using the MXCOMP procedure of NT-SYS.

RESULTS

Of the 42 loci examined, 19 were variable in at least two populations. For S. tridecemlineatus 14 loci (33.3%) were polymorphic at the 0.95 level (i.e., the common allele of a locus had a frequency $\leq$ 0.95) and 15 loci (38.1%) were polymorphic at the 0.99 level. Spermophilus mexicanus was more variable than S. tridecemlineatus with 15 loci (35.7%) and 18 loci (42.9%) polymorphic at the 0.95 and 0.99 levels, respectively. The following loci were monomorphic in both species: LDH-1, LDH-2, LDH-3, MDH-1, MDH-2, ME, IDH-2, GOT-2, αHb-1, αHb-2, βHb, IPO, ADH, PGI, G-6-PDH, AP2, PEP-2, PEP-3, TRF, Pt-1, GDH, α-GPD, and EST-4. Additionally, the ALB locus was fixed for the a allele and the EST-6 locus had a common allele frequency of 0.991 in S. tridecemlineatus. The 6-PGD locus was variable in both species, but the common allele had a mean frequency of 0.998 in S. tridecemlineatus and 0.991 in S. mexicanus. The ALB locus was highly polymorphic in S. mexicanus with three alleles present (Table 2). The c allele was the most common allele. The ALB a allele which was fixed in S. tridecemlineatus was also present in some S. mexicanus populations but was always associated with probable hybrids (Fig. 2). The remaining loci were variable in both species (Table 2). For information on the esterase loci see Cothran et al. (1977).

Nucleoside Phosphorylase (NSP).--The NSP locus requires more study. The a allele was the common allele in S. tridecemlineatus while the d allele was the common allele in S. mexicanus. The b allele was a rare allele found only in S. tridecemlineatus and the e allele was a low frequency allele found only in S. mexicanus. The c allele occurred at low frequency in both species. The a allele was also found in S. mexicanus. It appeared to be associated with hybridization (Table 2); but this determination is not certain.

Glutamate-oxaloacetate Transaminase-1 (GOT-1).--In both species b was the most common allele, and the a allele was also found in both species. The c allele was the second most common allele in S. mexicanus but was not present in S. tridecemlineatus.

Isocitrate Dehydrogenase-1 (IDH-1).--The a and b alleles were present in both species and the b allele was the common allele. The c allele was found in S. mexicanus only.

Adenylate Kinase (ADK).--The ADK locus, with two alleles, was highly variable in both species (Table 3). All populations for which this locus was examined were polymorphic at the ADK locus except PLA and VER. The a allele was the common allele in both species.

Peptidase-1 (PEP-1).--The PEP-1 locus was moderately variable in both species. The b allele was the common allele.

Leucine Aminopeptidase (LAP).--The LAP locus was one of the more variable loci. The b allele was the common allele in both species. The a allele was found in S. tridecemlineatus and in three hybrid individuals. The c allele was only found in S. mexicanus.

Acid Phosphatase-1 (AP-1).--Two alleles were observed in both species at the AP-1 locus. The a allele was the common allele.

Adenosine Deaminase (ADA).--Three alleles were present in both species. The c allele was the common allele while the a allele was rare.

Mannose-6-Phosphate Isomerase (MPI).--The a allele was the common allele in both S. tridecemlineatus and S. mexicanus. The b allele was more common in S. tridecemlineatus than in S. mexicanus and within S. mexicanus the b allele was primarily, but not exclusively, found in probable hybrids. However, the b allele was only found in populations of S. mexicanus where hybrids were observed, thus, the b allele may be unique to S. tridecemlineatus.

Phosphoglucomutase-1, -2, and -3 (PGM-1, PGM-2, PGM-3).--The PGM-1 and PGM-3 loci were slightly polymorphic in both species. For both loci and both species, b was the predominate allele. PGM-2 was more variable than PGM-1 and PGM-3. Again b was the common allele.

Zimmerman and Cothran (1976) showed that karyotypically S. mexicanus differed from S. tridecemlineatus by three pairs of chromosomes. The present study (Table 2) and Cothran et al. (1977) found unique electrophoretic alleles for S. mexicanus or S. tridecemlineatus at the ALB, NSP, GOT, IDH, and LAP loci. Heterozygosity for these three pairs of chromosomes or for species specific alleles at the protein loci was considered to be evidence of hybridization. Individuals that were heterozygous for all three chromosome pairs, that had an ALB genotype of ab, ac, or ad, and that were not homozygous for any of the species specific alleles at the remaining loci were possible F_1 hybrids. If all of these conditions were not met, the individual was either a backcross or a F_2. Backcross hybrids could not be distinguished from F_2s.

The proportion of loci polymorphic per population (P) for the 36 loci used in the present study ranged from 0.171 to 0.314 for S. tridecemlineatus and from 0.178 to 0.343 for S. mexicanus. HIL and VER were the least polymorphic populations, and POR was the most polymorphic population of S. tridecemlineatus. MUN was the least variable population of S. mexicanus, while AND, ART, AUS, BIG, and HOM were the most polymorhpic populations. All of the most polymorphic populations had hybrid individuals. Mean individual heterozygosity ($\bar{H}$) per population was higher in S. mexicanus than in S. tridecemlineatus. Of the populations for which all 36 non-esterase loci were examined, PLA had the lowest $\bar{H}$ (0.0286) and MAT the highest $\bar{H}$ (0.0555) in S. tridecemlineatus populations. Of the S. mexicanus populations, HOM had the highest $\bar{H}$ (0.0741) and MUN had the lowest $\bar{H}$ (0.0381). The heterozygosities for the populations marked with an asterix in Table 3 were taken from Cothran (1975) and included the esterase loci. Mean heterozygosity was lower in S. tridecemlineatus (0.0395) than in S. mexicanus (0.0573). If hybrids are not considered in the S. mexicanus sample, $\bar{H}$ for S. mexicanus was 0.053. Mean heterozygosity for the probable hybrid squirrels was 0.073.

With the exception of the ALB locus, the patterns of individual heterozygosity at each locus were similar in the two species (Table 3). ALB was the most variable locus in S. mexicanus with 38.6% of the individuals heterozygous. The ALB locus was invariant in S. tridecemlineatus. The NSP locus was the most variable locus in S. tridecemlineatus with 27% of the individuals heterozygous. The remaining 11 loci were more variable in S. mexicanus than in S. tridecemlineatus. The heterozygosity values for S. mexicanus in Table 3 were calculated including the hybrid squirrels in the sample. When the hybrids were not included in the S. mexicanus sample, only a few of the loci showed major differences in heterozygosity. The percentage of individuals heterozygous at the ADK, ADA, LAP, PGM-2, PEP-1, AP-1, IDH-1, GOT-1, PGM-1, and PGM-3 loci was higher in S. mexicanus with no hybrids than in S. tridecemlineatus. Heterozygosity at the MPI locus was higher in S. tridecemlineatus than in S. mexicanus without hybrids. Only two S. mexicanus individuals that were not identified as probable hybrids were heterozygous at the MPI locus.

The elimination of the hybrids reduced the mean heterozygosity of S. mexicanus at the NSP locus from 0.16 to 0.099 and at the ALB locus from 0.386 to 0.298. The mean heterozygosity of the hybrid sample was greater than that of S. tridecemlineatus at every locus except PGM-1 and PGM-3. The hybrids had higher heterozygosity than S. mexicanus at the ALB, IDH-1, AP-1, PEP1, MPI, NSP, LAP, ADK, and ADA loci. Fifty percent of the hybrids were heterozygous at the ALB locus and 37.5% were heterozygous at the NSP locus. Additionally, over 25% of the hybrids were heterozygous at the LAP, ADK, and ADA loci. Except for ADA and ADK, the loci with the greatest heterozygosities within the hybrid sample were those loci where unique alleles were present in one of the two species (Table 2).

Significant differentiation among populations of ground squirrels of both species was indicated by the results of the analysis of the standardized variance of alleles frequencies (F_{ST}, Table 4). The differentiation of allele frequencies was significant for all variable loci except MPI and PGM-3 for S. tridecemlineatus . The total F_{ST} for S. tridecemlineatus was significant as well. The total F_{ST} and the F_{ST} values for the ALB, IDH-1, PGM-3, NSP, AP-1, and ADA loci were significant for S. mexicanus with the hybrids included. When the hybrids were removed from the S. mexicanus sample, the F_{ST} values for the PGM-2, LAP, NSP, and PEP-1 loci were nonsignificant. Analysis of the variance of allele frequencies was also performed on all populations of both species combined. Heterogeneity of allele frequencies was significant for all variable loci and highly significant for all variable loci except MPI (Table 4). In all cases, high positive values of F_{IT} were found which denoted that in both species the number of homozygous individuals was greater than expected, based on the pooled data of all populations of a species.

High positive F_{IS} values indicated that there were more homozygous individuals than expected within each population.

Genetic similarity between S. mexicanus and S. tridecemlineatus was very high (Table 5). Nei's (1971) and Rogers' (1972) coefficients gave similar results, although values of Rogers' coefficient were lower. Populations of S. tridecemlineatus were virtually indistinguishable from each other. Populations of S. mexicanus were also very similar to each other. The sample of hybrid squirrels were more similar to S. mexicanus than to S. tridecemlineatus.

Population LEW had the lowest mean genic identity ($\bar{I}$) with other S. tridecemlineatus populations (0.992), while WIC (0.962) and LEW (0.961) had the greatest identity with S. mexicanus. Mean intraspecific I of S. tridecemlineatus populations ranged from 0.992 to 0.997. Mean interspecific I of S. tridecemlineatus populations with S. mexicanus populations ranged from 0.993 to 0.962. With hybrids included in the S. mexicanus sample, mean interspecific I of S. mexicanus populations with S. tridecemlineatus ranged from 0.908 (SHE) to 0.982 (SEY). Without hybrids included in the S. mexicanus sample, population RAN ($\bar{I}$ = 0.966) was most similar to S. tridecemlineatus. Mean intraspecific I between S. mexicanus populations ranged from 0.973 to 0.991. Hybrid individuals from HOM and SEY were more similar to S. tridecemlineatus than to S. mexicanus. An UPGMA cluster analysis dendrogram of I is given in Fig. 3b. The two species form distinct clusters and populations of S. tridecemlineatus are more tightly clustered than are those of S. mexicanus. The dissimilarity of populations PEC, CCH, HAR, and MID was due to high frequencies of the ALB b, GOT-1 c, and PGM-2 a alleles in these populations.

The weighted separation index of Vogt and McPherson (1971) was used as a hybrid index for the electrophoretic data. This index provides a method to weight qualitative characters, such as genotypes, for use in differentiating two groups. Only loci with allele frequency differences between the two species were used for the calculation of the weighted separations index (X). The loci used were ALB, LAP, NSP, GOT-1, IDH-1, MPI and ADA. The ALB and NSP loci had the greatest weights. Population means of X ranged from 1.88 for HOT to 1.46 for VER of S. tridecemlineatus and -0.43 for SEY to -1.68 for RAN and SNY of S. mexicanus. When hybrids were not included in the S. mexicanus samples, mean X ranged from -1.62 for ART to -1.77 for SEY. Mean values of X were 1.69 for S. tridecemlineatus, -1.38 for S. mexicanus with hybrids, -1.70 for S. mexicanus without hybrids, and -0.27 for the probable hybrids.

The individual values of X were significantly correlated with the individual discriminant function scores, z ($r = -0.848$, $P \leq 0.0001$), calculated from morphological data. Comparisons of the distributions of X and z within each species are shown in Fig. 4. The correlation between X and z was also significant within the S. mexicanus sample ($r = -0.293$, $P \leq 0.0001$). The z values of S. tridecemlineatus ranged from 2.73 for an individual from LUB to 3.25 for an individual from DEN. For S. mexicanus, z ranged from 3.03 for an individual from AUS to 3.72 for an individual from ABI. The z values of the hybrids were from 2.75 to 3.65, nearly spanning the total range of the two species.

Within S. *mexicanus*, *z* values were also related to the genotypes at the ALB and NSP loci ($P \leq 0.0001$ and 0.05 respectively).

The asymmetry values (R-L) of the characters used in the analysis of asymmetry generally had non-normal distributions. However, there were no trends towards skewness or kurtosis and the mean signed asymmetry values of each character were not significantly different from zero for each species and the hybrids (Table 6). The exception was UDL asymmetry. The mean signed asymmetry values of UDL were significantly greater than zero for S. *tridecemlineatus*, S. *mexicanus* with hybrids included in the sample, and S. *mexicanus* without the hybrids in the sample. Asymmetry of UDL for the hybrids was not significantly different from zero.

The means and standard deviations of the absolute values of asymmetry, (R-L)/(R+L), of each character for each group are also given in Table 6. Cranial asymmetry was calculated as the sum of the absolute values of asymmetry of the six cranial characters (UDL, TRL, BUL, PMW, MAN, and PPL). Skeletal asymmetry was the sum of the absolute values of asymmetry of the six non-cranial characters (FEL, FPW, HUL, HDW, SCL, and SCW). Total asymmetry was the sum of the absolute values of asymmetry of all characters. Skeletal and total asymmetry were not calculated for individuals for which complete skeletons were unavailable. Skeletal and total asymmetries were higher in S. *tridecemlineatus* than in S. *mexicanus* or the hybrids. Population LUB had the highest mean total asymmetry (0.069) of the S. *tridecemlineatus* populations, while the lowest mean total asymmetry of S. *tridecemlineatus* populations for which complete skeletons were available was at POR (0.042). The greatest mean total asymmetry among S. mexicanus populations with the hybrids included in the samples was for populations MUN (0.056) and SEY (0.049). The lowest mean total asymmetry for S. mexicanus was 0.041 at ART. In 7 of the 10 S. mexicanus populations where hybrids were found, the mean total asymmetry of the population decreased when the hybrid data was not included in the calculation of the population mean. For example, total asymmetry for SEY and HOM was 0.049 and 0.044, respectively, with hybrids included. When data from the hybrids from these populations was not used in the calculation of mean total asymmetry the total asymmetry means of SEY and HOM were 0.038 and 0.042 respectively.

Non-parametric ANOVA was performed with the asymmetry data for each character, as well as for cranial, skeletal, and total asymmetry values. Spermophilus tridecemlineatus, S. mexicanus, and the hybrid sample were treated as separate groups. There were no significant differences in asymmetry associated with group for the asymmetry values for UDL, TRL, BUL, MAN, HUL, and SCW. There were significant differences ($P < 0.05$) between groups for the asymmetry values for FEL, FPW, HDW, and SCL, as well as for cranial, skeletal, and total asymmetry. In every case where there were significant differences in asymmetry between groups, except cranial asymmetry, the highest asymmetry values were those of S. tridecemlineatus and the lowest were those of S. mexicanus (Table 6). The cranial asymmetry of the hybrids was greater than that of S. tridecemlineatus or S. mexicanus. Cranial, PMW, and FEL asymmetries were significantly greater in the hybrids than in S. mexicanus. Skeletal, PPL, FEL, FPW, and SCL asymmetries were significantly greater in S. tridecemlineatus than in the hybrid sample. Skeletal, total, FPW, HDW, and SCL asymmetries were significantly higher in S. tridecemlineatus than in S. mexicanus. The variance in total asymmetry tended to be highest in the hybrid sample.

DISCUSSION

Probable hybrids were found in 10 of the 39 populations sampled. A total of 44 individuals (about 7% of the total sample) were considered to be of hybrid origin based on electrophoretic and/or karyotypic characteristics. Positive classification of individuals as either hybrid or parental was not possible. One difficulty in the classification of individuals was that the majority of hybrids were backcross hybrids. Only 10 of the 44 hybrid ground squirrels could have been F_1s. The high electrophoretic similarity (Table 5) and karyotypic similarity (Zimmerman and Cothran, 1976) means that a number of backcross hybrids would be indistinguishable from the parental type involved in the backcross. Secondly, several of the hybrid determinations were based on the presence of the NSP-a allele in S. mexicanus individuals. The NSP-a allele was the common allele in S. tridecemlineatus but was primarily associated with hybrids (as determined by ALB genotype or karyotype) in S. mexicanus (Table 2). However, three S. mexicanus populations, ART, ABI, and AUS had a total of nine individuals that possessed the NSP-a allele but, with the exception of one individual from ART that was karyotypically a hybrid, showed no other indication of hybrid origin. Three of these nine individuals had discriminant function scores less than 3.22, which is near the middle of the distribution of z values. There remains some uncertainty as to whether the NSP-a allele is only present in S. mexicanus due to hybridization with S. tridecemlineatus.

All probable hybrids were found in populations of S. mexicanus. Additionally, all sampled populations consisted of either one of the parental species or one of the parental species and hybrids. There was no indication of hybridization within S. tridecemlineatus populations. The unidirectional nature of the hybridization between S. mexicanus and S. tridecemlineatus is best exemplified by populations HOM and HOT. These two populations (both in the vicinity of Hobbs, New Mexico) were separated by approximately 3 km. All individuals at locality HOT were unquestionably S. tridecemlineatus. Indeed, electrophoretically HOT was the population least like S. mexicanus with a mean X of 1.88 compared to a species mean of 1.69 (Fig. 4). Also, the mean value of z for HOT was 3.01, which is less than the species mean. On the other hand, at least 50% of the individuals collected at HOM were of hybrid origin. The remainder of the HOM population consisted of "pure" S. mexicanus individuals or undetected backcross hybrids. The indication from the available data is that the hybridization between S. mexicanus and S. tridecemlineatus only results in the incorporation of genes from the later species into the S. mexicanus gene pool and not the reverse situation.

Asymmetric introgression is not unknown. In the house mouse, introgression of Mus domesticus alleles into M. musculus was greater than the reverse situation (Hunt and Selander, 1973). Populations of the tree frog *Hyla gratiosa* appeared to be more substantially modified by the effects of introgression of *H. cinerea* genes than the *H. cinerea* populations were affected by *H. gratiosa* genes (Mecham, 1960). Similar examples of asymmetric introgression have been reported for salamanders, fish, frogs, and grasshoppers (Wake et al., 1980; Radocinski, 1980; McDonnell et al., 1978; Shaw et al., 1979). In the above cases, introgression involved both species. A possible case of unidirectional hybridization was reported for hybrids between the mule deer *Odocoileus hemionus* and white-tailed deer *O. virginianus* (Wishart, 1980). Although only four hybrids were observed, all hybrids were associated with mule deer. Wishart (1980) indicated that hybridization between mule deer females and white-tailed deer males was more likely than the reciprocal cross due to behavioral differences between the species during the breeding season.

The mechanism for unidirectional hybridization between *S. mexicanus* and *S. tridecemlineatus* is not clear. Some form of premating isolating mechanism such as breeding behavior is a likely explanation. The behavior of *S. tridecemlineatus* has been studied (Wistrand, 1974), but there is no comparable study of *S mexicanus*. Ground squirrels are diurnal mammals and visually oriented (Wistrand, 1974); visually the two species are distinctive (see Howell, 1938 for a description of external morphology). According to McCarley (1966), a large majority of transient ground squirrels in a population of *S. tridecemilneatus* were males. If the majority of migratory individuals of *S. mexicanus* are also males, the unidirectional hybridization between the two species may be the result of greater species discrimination by S. tridecemlineatus females than S. mexicanus females, possibly due to visual cues.

A second possible explanation for the unidirectional hybridization between the ground squirrel species is that physical differences between S. mexicanus and S. tridecemlineatus allow hybridization between S. mexicanus females and S. tridecemlineatus males but not the reciprocal cross. Spermophilus mexicanus averages about 15% larger than S. tridecemlineatus. Matings between S. mexicanus males and S. tridecemlineatus females might produce larger fetuses that the female could not bring to term. The average litter size (7; McCarley, 1966) of S. tridecemlineatus in northern Texas could increase the potential difficulty large fetuses would cause. Watson (1942) attributed lower success in producing offspring from laboratory crosses of Peromyscus polionotus females with P. maniculatus males than from the reciprocal cross to the greater size of P. maniculatus. Similarly Dawson (1965; 1966) observed lower success in producing hybrid litters when P. polionotus females were crossed with P. maniculatus males than when the opposite cross was made. The greater size of P. maniculatus was also implicated by Dawson; however, size difference between these two species is probably not the only difficulty in parturition of hybrid young (Watson, 1942).

There are also size differences between the mule deer and white-tailed deer. The mule deer tends to be larger than the white-tail (Wishart, 1980; Hall and Kelson, 1959) and hybrids were only observed associated with the larger species. Laboratory crosses between S. mexicanus and S. tridecemlineatus must be made before a judgement can be made as to whether or not size differences between the ground squirrel species are a postmating isolating mechanism.

Actual contact between S. mexicanus and S. tridecemlineatus does not appear to occur over a broad area, although the range overlap of the species may be as wide as 130 km (Fig. 1). Most of the area of sympatry in Western Texas is agricultural land with one of the primary crops being cotton. Ground squirrels were difficult to find in the potential contact zone. Almost 50% of the time spent collecting was concentrated in the contact zone, but only about 23% of the ground squirrels sampled were taken there. The area of sympatry between S. mexicanus and S. tridecemlineatus is not a hybrid zone in the sense of Short (1969). Hybridization appears to be only an occasional and isolated event. Of the six S. mexicanus populations that were potentially in contact with S. tridecemlineatus, probable hybrids were found in five of them. The five populations, with the percent of population that was hybrid in parentheses, were AND (5%), BIG (12%), HOM (50%), ROS(6%), and SEY (68%). Only populations AND, BIG, HOM, and SEY had possible F_1 hybrids. Morphologically the single possible F_1s from AND and BIG were more like S. mexicanus than S. tridecemlineatus with z values of 3.34 and 3.44, respectively (see Fig. 4). Two of the four possible F_1s from HOM and one of three possible F_1s from SEY had high, S. mexicanus-like z values. It is probable that of the 10 S. mexicanus populations where probable hybrids were found, only populations HOM and SEY had F_1 hybrids while the remainder of the hybrids were the result of backcrosses and introgression.

Most of the observed hybrids, based on genotype and/or karyotype, were backcrosses to S. mexicanus. However, some of the observed genotypes were indicative of either F_2s or backcrosses to S. tridecemlineatus. Eight hybrid individuals were homozygous for the ABL-a allele and nine were homozygous for the NSP-a allele. It was not possible to distinguish between F_2 hybrids and backcrosses to S. tridecemlineatus. However, the low percentage of possible F_1 hybrids in the samples points to only occasional hybridization and the morphological evidence supports this contention. The z value midway between the mean z values of S. tridecemlineatus and S. mexicanus was 3.22. The mean z value of all hybrids was 3.33 compared to a mean of 3.43 for S. mexicanus and 3.00 for S. tridecemlineatus. Only one of the possible F_1 hybrids had a z value as low as 3.22. There were 13 individuals that had the characteristics of a F_2 or backcross to S. tridecemlineatus. Six of these individuals had z values below 3.22 including three individuals that were homozygous for the S. tridecemlineatus allele at both the ALB and NSP loci. Actual hybridization between the parent species is probably a rare event, but the ability of the hybrids to backcross produced populations such as HOM and SEY that were predominately composed of hybrids and allowed introgression of S. tridecemlineatus genes into S. mexicanus populations not directly in contact with S. tridecemlineatus.

The apparent fertility of the hybrids raises questions concerning the fitness of the hybrid individuals relative to the parental species. No direct attempt was made to compare the reproductive potential of hybrids and parentals. A possible indirect measure of fitness is fluctuating asymmetry as defined by Van Valen (1962). Asymmetry of bilateral characters is the result of imperfections in development. Levels of fluctuating asymmetry are predicted to be greater in populations subjected to evolutionary stress (Soulé, 1967). Zones of contact and hybridization are such stress areas. The breakdown in developmental canalization due to hybridization is presumed to be the result of the combination of the two different coadapted linkage groups (Soulé, 1967). Thus, hybrids theoretically will have higher levels of fluctuating asymmetry than the parent species.

The hybrids between S. mexicanus and S. tridecemlineatus tended to have higher levels of asymmetry than S. mexicanus (Table 6) and had significantly higher asymmetry values for three characters. Conversely, the hybrid ground squirrels had higher cranial asymmetry than S. tridecemlineatus but tended to be equally or less asymmetric than S. tridecemlineatus for all other characters (Table 6). Spermophilus tridecemlineatus was significantly more asymmetric than the hybrids for five characters. Jackson (1973) found no increase in asymmetry in populations of lizards in a zone of hybridization. Felley (1980) also found that intergrade populations of bluegill sunfish were no more asymmetric than populations outside the area of intergradation. Only one of the nine bilateral characters measured by Felley (1980) was significantly different over the groups, and that character was less asymmetric in the intergrades than in the parentals. Hybrids between S. mexicanus and S. tridecemlineatus were more asymmetric than S. mexicanus, but not S. tridecemlineatus. The contact area may be marginal habitat for S. tridecemlineatus and, thus, populations of S. tridecemlineatus are also in a zone of evolutionary stress in this area (see Soulé, 1967). That the hybrids are more asymmetric than S. mexicanus (the species that is experiencing introgression) is suggestive that the hybrids are less fit than parental S. mexicanus.

Morphologically S. mexicanus is fairly distinct from S. tridecemlineatus (Figs. 3a and 4). However, genetically the two species are very similar (Table 5). Values of genetic similarity between congeneric species typically range from 0.30 to 0.80 with the mean between 0.50 and 0.60 (Avise, 1975). The mean genetic similarity (I) between S. mexicanus and S. tridecemlineatus of 0.959 is comparable to that between geographic populations within a species (Ayala et al., 1974; Zimmerman et al., 1978). A number of explanations can be offered for high genic similarity between morphologically distinct species. Avise (1975), discussed several possible alternatives to explain the high genetic similarity (I = 0.948) between two species of minnows. The explanation he preferred was that the species had only recently diverged. Recent divergence is also the most likely explanation for the high genic identity between S. mexicanus and S. tridecemlineatus. It is difficult to estimate how long ago the species diverged. A fossil record for the two species is practically non-existant, although, fossil records of S. tridecemlineatus from the Pleistocene are known (Bryant, 1945).

Evolutionary divergence time for a pair of species can be estimated from electrophoretic data (Nei, 1971). A number of assumptions are involved in Nei's estimate of divergence time, and the estimates should be considered with reservation. The best estimate of time since divergence between S. mexicanus and S. tridecemlineatus based on Nei's formula is approximately 30,000 years. Fossil pollen analyses (Martin, 1964) indicated that much if not all of the present contact zone between the ground squirrel species was pine forest during the peak glacier advance from 23,000 to 17,000 years BP. Such habitat would be unsuitable for these species of ground squirrels.

Most zones of hybridization are considered to represent areas of secondary contact between previously disjunct species (Mayr, 1963; Moore, 1977). The hybridization between S. mexicanus and S. tridecemlineatus is also probably an example of secondary contact. The high genetic similarity of the two species might argue for continuous gene flow between the species during divergence. Greenbaum (1981) invoked sympatric divergence to account for the high genetic identity (I = 0.99) of hybridizing cytotypes of bats. He postulated that gene flow between karyotypically differentiated races maintained the high genic and morphologic similarity of the races. In the case of S. mexicanus and S. tridecemlineatus, differentiation of quantitative morphologic characters has not been accompanied by differentiation of Mendelian traits such as chromosomes and genes coding for the proteins detected by electrophoresis. A similar situation was observed by Turner (1974) for pupfish in Death Valley, California. These pupfish species were clearly distinct morphologically and ecologically but not electrophoretically. Turner (1974) suggested that the lack of genic differentiation was the result of these proteins being part of a strongly coadapted set of metabolic enzymes while that portion of the genome responsible for morphologic and ecologic traits was more responsive to environmental selection pressures. Regardless of whether or not all the populations of pupfish represent different species, the rate of differentiation of morphologic and genic characteristics was not the same. Kilias et al. (1980) demonstrated that high genetic identity, as determined electrophoretically, between populations under conditions of isolation and different selection regimes can be maintained even though reproductive isolation is achieved. The data for S. mexicanus and S. tridecemlineatus is most consistent with the hypothesis that the observed differences were achieved during isolation under different selection pressures.

Speciation of S. mexicanus and S. tridecemlineatus appears to fit the allo-parapatric model of Endler (1977). Under this model populations of the ancestral species become spread over a heterogeneous area and eventually some population or populations become isolated from the others and diverge to a varying extent. The degree of differentiation achieved before contact is resumed determines the outcome of renewed contact. Low differentiation would lead to the formation of shallow clines followed by steep clines, hybrid zones and eventual reproductive isolation. High differentiation would lead directly to the formation of hybrid zones. The steps outlined above are based on the assumption that secondary contact will lead to speciation, which will not always be the case (Templeton, 1981). The degree of differentiation between S. mexicanus and S. tridecemlineatus depends upon which set of characters are considered, either morphologic or karyotypic and electrophoretic. There is no clear cut evidence of a cline for any of the characteristics. The lack of a cline combined with the presence of a contact zone with hybridization indicates that, in regards to Endler's (1977) model, the greatest differentiation (i.e., morphologic differentiation) between the ground squirrel species has been most important in determining the path of speciation.

Speciation of populations that have achieved some level of differentiation, but not complete reproductive isolation (adaptive divergence; Templeton, 1980), is usually assumed to be completed by the process of reinforcement. Under this mechanism, speciation is completed by selection for post-mating isolation due to hybrid inferiority. Templeton (1981) has pointed out that pre-mating isolating mechanisms are most likely to evolve under the adaptive divergence model for a variety of reasons. The optimal conditions for the adaptive divergence model are an ancestral species subdivided into small demes with low rates of migration and high F_{ST}s (Templeton, 1980).

Both S. mexicanus and S. tridecemlineatus have a subdivided population structure as revealed by high and significant F_{ST}s for most polymorphic loci (Table 4). Under Wright's (1932; 1980) shifting balance theory, rapid adaptive divergence should occur when populations are subdivided and gene flow between the subdivisions is limited. Although under these conditions high genic differentiation would be expected, little electrophoreticaly detectable differentiation between the ground squirrel species has occurred. However, the adaptive divergence may be more closely related to the morphologic differentiation than to the genic divergence. The limited gene flow and population subdivision indicated by the F statistics (Table 4) could still be influencing the complete speciation of S. mexicanus and S. tridecemlineatus even though the species are now in contact and hybridizing. Populations of S. mexicanus that are not close to the contact zone are essentially not in contact with S. tridecemlineatus, thus divergence between the species could continue. At least partial reproductive isolation between the species is indicated by the lack of introgression into S. tridecemlineatus and the asymmetry data is suggestive of some incompatibility between the genomes of S. mexicanus and S. tridecemlineatus. Whether the reproductive isolation that has been observed is premating or post-mating isolation is not yet known. Continued divergence of the populations of S. mexicanus that are isolated from S. tridecemlineatus could increase the level of reproductive isolation between the species and halt a southward influx of S. tridecemlineatus genes into S. mexicanus.

Secondary contact between S. mexicanus and S. tridecemlineatus is probably a result of human alteration of the environment. Spermophilus tridecemlineatus is a natural inhabitant of the shortgrass prairies of the Great Plains and S. mexicanus is commonly found in the mesquite, cactus, short-grass associations of southwest

Texas and northern Mexico (Hall and Kelson, 1959). The development of highway, railroad, and power-line right-of-ways has provided ideal dispersal pathways for both species. Additionally, grazing and agricultural land uses have provided suitable habitat for both species where the native environment may have been suitable to only one of the species. Distribution records give some indication that both species have expanded their ranges towards each other (Hall and Kelson, 1959; Davis, 1966; Howell, 1938; Hall, 1980). Habitat alteration is often cited as the most frequent cause of hybridization (Mayr, 1963; Stebbins, 1950). Disturbance of the habitat not only breaks down ecological barriers to species contact but also can provide conditions under which the hybrid may be more successful than the parental forms (Wright and Lowe, 1968; Moore, 1977). There is no indication that the ground squirrel hybrids are better suited to the conditions in the contact zone than are the parent species. However, the disturbed habitat may have produced a situation where the ground squirrel hybrids are able to compete successfully with the parental species and not face intense negative selection.

The three events that are the most likely outcomes of hybridization following secondary contact are speciation, fusion of the species, or the establishment of a stable hybrid zone. The high percentage of backcross hybrids between S. mexicanus and S. tridecemlineatus and the presence of hybrids in populations outside the probable contact zone are evidence that species fusion is possible. On the other hand, the observed introgression was only into S. mexicanus and it appears that S. tridecemlineatus has not significantly, if at all, contributed to the backcrosses. Populations HOM and SEY (which were composed of 50% and 68% hybrid individuals, respectively), as well as the other populations where hybrids were observed, were more similar to S. mexicanus than to S. tridecemlineatus both genetically and morphologically. Unless the incidence of hybridization and introgression increases, complete reproductive isolation between S. mexicanus and S. tridecemlineatus would appear more likely than fusion of the species.

The establishment of a stable hybrid zone is another possible outcome of the contact between S. mexicanus and S. tridecemlineatus. Moore (1977) hypothesized that only narrow hybrid zones or those formed along an ecotone are likely to become stable. The contact zone of the ground squirrel species is in an area disturbed by human activities rather than an ecotone, although the contact is within one of the "suture zones" of Remington (1968). The greatest width of the potential overlap of the ranges of the species is approximately 130 km, and the width of the contact zone is over 50 km for at least 250 km of its length (Fig. 1). Hybrids are not the most common individuals within the contact area and are only common in two populations. The contact zone can best be described as an area of overlap with hybridization (Short, 1969). The width of the overlap zone combined with a scattered incidence of hybridization makes the establishment of a stable hybrid zone unlikely.

Although S. mexicanus and S. tridecemlineatus are capable of hybridization and the hybrids are able to backcross with at least one of the parental species (S. mexicanus), the data presented do not justify a change in the taxonomy of the two species. Spermophilus tridecemlineatus appears to be maintaining a separate gene pool from S. mexicanus and, except for a small percentage of individuals, outside the contact zone the same can be said for S. mexicanus. The species are distinct morphologically, there are slight karyotypic differences, and two electrophoretically determined loci have major allelic differences while several other loci have species specific minor alleles (Table 2). Although the degree of differentiation of morphologic and electrophoretic chareteristics between the two species are different, the relationships of the species based upon the two sets of characters are very similar. Phenetic distance was significantly associated with genetic distance (Mantel, 1967 test, $t_\infty = 17.38$, $P \leq 0.001$, $r = 0.827$). Speciation is a dynamic process and organisms representing all stages of the continuum from local populations to completely reproductively isolated species are likely to be found. The ground squirrel species S. mexicanus and S. tridecemlineatus appear to be closer to the separate species end of the spectrum.

SUMMARY

Forty-four of 596 ground squirrels of the species S. mexicanus and S. tridecemlineatus were hybrids between the two species. The majority of the hybrid individuals (~ 77%) were either F_2 or backcross individuals. All observed hybrids were associated with populations of S. mexicanus, and it appeared that both hybridization and introgression were unidirectional and into S. mexicanus.

Electrophoretically S. mexicanus was more variable than S. tridecemlineatus with mean observed heterozygosity of 5.7% and 4.0%, respectively. Both species exhibited population subdivision with the higher F_{ST} values found for S. tridecemlineatus. Genetic similarity between the species was high with a mean I of 0.956 (mean D = 0.045). The high genic similarity was in contrast with morphologic distinctiveness of the species. Levels of fluctuating asymmetry were measured to try to assess the fitness of the hybrids relative to the parentals. Hybrid asymmetry was greater than that of S. mexicanus but tended to be less than the levels of asymmetry of S. tridecemlineatus. The asymmetry data suggested lower fitness of the hybrids relative to that of S. mexicanus, the species that is experiencing introgression.

The genetic and morphologic differences between S. mexicanus and S. tridecemlineatus probably arose during a period of geographic isolation of the species. Divergence of the species probably occurred approximately 30,000 years BP. Secondary contact and hybridization between the species may be a result of range expansion due to habitat alteration by human activities. Speciation of S. mexicanus and S. tridecemlineatus seems to fit best the allo-parapatric model of Endler (1977). The morphologic differentiation may be more indicative of the relationships between the species than are electrophoretic differences. Although reproductive isolation has not been completed, the ground squirrel taxa have maintained their genetic integrity except for a few scattered incidences of hybridization and should be considered separate species.

ACKNOWLEDGMENTS

I am sincerely grateful to G. D. Schnell, J. N. Thompson, C. C. Carpenter, and C. E. Hopla for assistance in data collection and critical reading of previous versions of this manuscript. I also thank V. H. Hutchinson and M. H. Smith for support during the collection of the data for this manuscript. R. K. Chesser and R. L. Honeycutt helped in the collection of specimens for analysis; R. K. Chesser developed and provided computer programs for the analysis of my data. A very special thanks goes to my wife M. L. Cothran for her assistance in every aspect of my research. This study was supported by a grant from the Theodore Roosevelt Memorial Fund and Contract DE-AC09-76SR00819 between the U.S. Department of Energy and the University of Georgia while the author was an employee at the Savannah River Ecology Laboratory.

Literature Cited

Avise, J. C., J. J. Smith, and F. J. Ayala. 1975. Adaptive differentiation with little genic change between two native California minnows. Evolution 29:411-426.

Ayala, F. J., M. L. Tracey, D. Hedgecock, and R. C. Richmond. 1975. Genetic differentiation during the speciation process in Drosophila. Evolution 28:576-592.

Barr, A. J., J. H. Goodnight, J. P. Sall, W. H. Blair, and D. M. Chilko. 1979. SAS User's Guide 1979 Edition. SAS Institute Inc., Raleigh.

Bryant, M. D. 1945. Phylogeny of Neartic Sciuridae. Amer. Midland Nat. 33:257-390.

Chesser, R. K. 1980. Computer systems and programming for the analysis of population genetics data. Univ. Stockholm spec. publ., Report no. III.

__________. 1982. A review of Wright's F-statistics: Uses and misuses. submitted to Genetics.

Cothran, E. G. 1975. Genic differentiation and evolution in the ground squirrel subgenus Ictidomys (Spermophilus). Masters thesis, North Texas State Univ., Denton.

__________. 1982. Genic, karyotypic, and morphologic differentiation of the hybridizing ground squirrels Spermophilus mexicanus and S. tridecemlineatus. Ph.D. dissertation, Univ. Oklahoma, Norman.

Cothran, E. G., E. G. Zimmerman, and C. F. Nadler. 1977. Genic differentiation and evolution in the ground squirrel subgenus Ictidomys (genus Spermophilus). J. Mammal. 58:610-622.

Davis, W. B. 1966. The Mammals of Texas. Texas Parks Widl. Dept. Bull. 44.

Davison, W. D. 1965. Fertility and size inheritance in a Peromyscus species cross. Evolution 19:44-55.

__________. 1966. Postnatal development in Peromyscus maniculatus-polionotus hybrids I. Developmental landmarks and litter mortality. Ohio J. Sci. 66:518-522.

Endler, J. A. 1977. Geographic Variation, Speciation, and Clines. Princeton Univ. Press, Princeton.

Felley, J. 1980. Analysis of morphology and asymmetry in bluegill sunfish (Lepomis macrochirus) in the southeastern United States. Copeia 1980:18-29.

Greenbaum, I. F. 1981. Genetic interactions between hybridizing cytotypes of the tent-making bat (Uroderma bilobatum). Evolution 35:306-321.

Hall, E. R. 1981. The Mammals of North America. Second Edition. Wiley-Interscience, New York.

Hall, E. R., and K. R. Kelson. 1959. Mammals of North America. Ronald Press, New York.

Harris, H., and D. A. Hopkinson. 1977. Handbook of Enzyme Electrophoresis in Human Genetics. North-Holland Publ. Co., Amsterdam.

Howell, A. H. 1938. Revision of the North American ground squirrels. North Amer. Fauna 56:1-256.

Hubbard, J. P. 1969. The relationships and evolution of the *Dendroica coronata* complex. Auk 86:393-442.

Hunt, W. G., and R. K. Selander. 1973. Biochemical genetics of hybridization in European house mice. Heredity 31:11-33.

Jackson, J. F. 1973. A search for the population asymmetry parameter. Syst. Zool. 22:166-170.

Kilias, G., S. N. Alahiotis, and M. Pelecanos. 1980. A multifactorial genetic investigation of speciation theory using *Drosophila melanogaster*. Evolution 34:730-737.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209-220.

Martin, P. S. 1964. Pollen analysis and the full-glacial landscape. Pp. 66-74, In The Reconstruction of Past Environments (J. J. Hester and J. Schoenwether, eds.), Fort Bergwin Research Center, Taos, New Mexico, 3:1-89.

Mayr, E. 1963. Animal Species and Evolution. Harvard Univ. Press, Cambridge, Mass.

Mecham, J. S. 1960. Introgressive hybridization between two southeastern treefrogs. Evolution 14:445-457.

Meise, W. 1928. Die Verbreitung der Aaskrähe (Formenkreis *Corvus corone* L.) J. Ornithol. 76:1-203.

McCarley, H. 1966. Annual cycle, population dynamics and adaptive behavior of *Citellus tridecemlineatus*. J. Mammal. 47:294-316.

McDonnell, L. J., D. F. Gartside, and M. J. Littlejohn. 1978. Analysis of a narrow hybrid zone between two species of Pseudophryne (Anura:Leptodactylidae) in south-eastern Australia. Evolution 32:602-612.

Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quart. Rev. Biol. 52:263-277.

Nei, M. 1971. Interspecific gene differences and evolutionary time estimated from electrophoretic data on protein identity. Amer. Natur. 105:385-398.

Nei, M. 1977. F-statistics and analysis of gene diversity in subdivided populations. Ann. Hum. Genet., Lond. 41:225-233.

Rakocinski, C. F. 1980. Hybridization and introgression between Campostoma oligolepis and C. anomalum pullum (Cypriniformes: Cyprinidae). Copeia 1980:584-594.

Remington, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. Evolutionary Biology (M. K. Hecht and W. C. Steere eds.). 2:321-428.

Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. Stud. in Genet. VII. Univ. Texas Publ. 7213:145-153.

Rohlf, R. J., J. Kishpaugh, R. Bartcher, and K. Kirk. 1974. NT-SYS. Numerical taxonomy system of multivariate statistical programs. State Univ. New York, Stony Brook.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (Peromyscus polionotus). Univ. Texas Publ. 7103:49-90.

Shaw, D. D., P. Wilkinson, and C. Moran. 1979. A comparison of chromosomal and allozymal variation across a narrow hybrid zone in the grasshopper Caledia captiva. Chromosoma 75:333-351.

Short, L. L. 1969. Taxonomic aspects of avian hybridization. Auk 86:84-105.

Sokal, R. R. 1961. Distance as a measure of taxonomic similarity. Syst. Zool. 10:70-79.

__________. 1979. Testing statistical significance of geographic variation patterns. Syst. Zool. 28:227-232.

Soulé, M. 1967. Phenetics of natural populations. II. Asymmetry and evolution in a lizard. Amer. Natur. 101:141-160.

Stebbins, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.

Templeton, A. R. 1980. Modes of speciation and inferences based on genetic distances. Evolution 34:719-729.

__________. 1981. Mechanisms of speciation - A population genetic approach. Ann. Rev. Ecol. Syst. 12:23-48.

Turner, B. J. 1974. Genetic divergence of death valley pupfish species: Biochemical versus morphological evidence. Evolution 28:281-294.

Van Valen, L. 1962. A study of fluctuating asymmetry. Evolution 16:125-142.

Vogt, W. G., and D. G. McPherson. 1972. The weighted separation index: A multivariate technique for separating members of closely-related species using qualitative differences. Syst. Zool. 21:187-198.

Wake, D. B., S. Y. Yang, and T. J. Papenfuss. 1980. Natural hybridization and its evolutionary implications in Guatemalan plethodontid salamanders of the genus Bolitoglossa. Herpetologica 36:335-345.

Watson, M. L. 1942. Hybridization experiments between Peromyscus polionotus and Peromyscus maniculatus. J. Mammal. 23:315-316.

White, M. J. D. 1978. Modes of Speciation. W. H. Freeman and Co., San Francisco.

Wishart, W. D. 1980. Hybrids of white-tailed and mule deer in Alberta. J. Mammal. 61:716-720.

Wistrand, H. 1974. Individual, social, and seasonal behavior of the thirteen-lined ground squirrel (Spermophilus tridecemlineatus). J. Mammal. 55:329-347.

Wright, J. W., and C. H. Lowe. 1968. Weeds, polyploids, and the geographical and ecological distribution of all-female species of Chemidophorus. Copeia 1968:128-138.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. Proc. 6th Internatl. Cong. Genet. 1:356-366.

__________. 1969. Evolution and Genetics of Populations. Volume 2, The Theory of Gene Frequencies. Univ. Chicago Press, Chicago.

__________. 1980. Genic and organismal selection. Evolution 34:825-842.

Zimmerman, E. G., and E. G. Cothran. 1976. Hybridization in the Mexican and 13-lined ground squirrels, Spermophilus mexicanus and Spermophilus tridecemlineatus. Experientia 32:704-706.

Zimmerman, E. G., C. W. Kilpatrick, and B. J. Hart. 1978. The genetics of speciation in the rodent genus *Peromyscus*. Evolution 32:565-579.

Table 1. Population abbreviation, collection locality, total sample size (N), number of individuals analyzed electrophoretically (E), and number of individuals analyzed morphologically (M).

	Spermophilus tridecemlineatus	N	E	M
LUB	Lubbock, Lubbock Co., Texas	17	17	15
POR	Portales, Roosevelt Co., New Mexico	36	18	31
PLA	Plainview, Hale Co., Texas	17	12	16
LOV	Lovington, Lea Co., New Mexico	15	11	15
LEV	Levelland, Hockley Co., Texas	15	12	15
WAC	Waco, McLennan Co., Texas	18	14	15
TAH	Tahoka, Lynn Co., Texas	18	16	18
HOT	Hobbs, Lea Co., New Mexico	19	19	18
MAT	Matador, Motley Co., Texas	19	17	19
VER	Vernon, Wilbarger Co., Texas	17	16	17
HIL	Hillsboro, Hill Co., Texas	16	12	16
DEN	Denton, Denton Co., Texas	18	18	16
WIC	Wichita Falls, Wichita Co., Texas	17	17	14
PAR	Paris, Lamar Co., Texas	10	10	10
LEW	Lewisville, Denton Co., Texas	7	7	7
GRU	Gruver, Hansford Co., Texas	8	6	8
AMA	Amarillo, Potter Co., Texas	5	5	-
COR	Corsicanna, Navarro Co., Texas	5	5	-
NOR	Norman, Cleveland Co., Oklahoma	17	-	17

Table 1. Continued.

	Spermophilus mexicanus	N	E	M
HOM	Hobbs, Lea Co., New Mexico	30	27	28
BIG	Big Spring, Howard Co., Texas	18	15	18
ROS	Roswell, Chaves Co., New Mexico	16	13	16
ART	Artesia, Eddy Co., New Mexico	18	15	17
KEN	Kennedy, Karnes Co., Texas	17	13	17
RAN	Ranger, Eastland Co., Texas	18	15	17
SNY	Snyder, Scurry Co., Texas	17	13	17
ABI	Abilene, Taylor Co., Texas	17	15	17
AUS	Austin, Travis Co., Texas	25	25	25
AND	Andrews, Andrews Co., Texas	20	20	20
SEY	Seymour, Baylor Co., Texas	19	18	19
MUN	Munday, Knox Co., Texas	14	9	14
SHE	Sheffield, Pecos Co., Texas	16	15	16
CAR	Carlsbad, Eddy Co., New Mexico	7	7	-
NEW	New Braunfels, Comal Co., Texas	5	5	5
MID	Midland, Midland Co., Texas	10	10	-
PEC	Pecos, Reeves Co., Texas	8	5	8
HAR	Harlingen, Cameron Co., Texas	7	7	-
CCH	Corpus Christe, Nueces Co., Texas	9	9	-
KER	Kermit, Winkler Co., Texas	11	-	11

Table 2. Mean frequency of electrophoretically determined alleles for *S. tridecemlineatus*, *S. mexicanus* with hybrids, *S. mexicanus* without hybrids, and the hybrid sample.

Locus	Allele	*S. tridecemlineatus*	*S. mexicanus* with hybrids	*S. mexicanus* without hybrids	Hybrids
Alb	A	1.000	0.048	0	0.400
	B	0	0.269	0.195	0.112
	C	0	0.427	0.585	0.375
	D	0	0.256	0.220	0.113
NSP	A	0.613	0.080	0	0.363
	B	0.033	0	0	0
	C	0.005	0.034	0.021	0.050
	D	0.349	0.870	0.950	0.587
	E	0	0.016	0.220	0
GOT-1	A	0.046	0.086	0.092	0.032
	B	0.954	0.845	0.812	0.943
	C	0	0.069	0.096	0.025
IDH-1	A	0.056	0.040	0.039	0.025

Table 2. Continued.

Locus	Allele	*S. tridecemlineatus*	*S. mexicanus* with hybrids	*S. mexicanus* without hybrids	Hybrids
	B	0.944	0.892	0.897	0.888
	C	0	0.068	0.064	0.087
ADK	A	0.680	0.667	0.656	0.675
	B	0.320	0.333	0.344	0.325
PEP-1	A	0.103	0.168	0.103	0.200
	B	0.897	0.832	0.897	0.800
LAP	A	0.173	0.007	0	0.038
	B	0.827	0.795	0.809	0.749
	C	0	0.199	0.191	0.213
AP-1	A	0.825	0.826	0.840	0.750
	B	0.175	0.174	0.160	0.250
ADA	A	0.011	0.020	0.014	0.038
	B	0.210	0.342	0.326	0.337
	C	0.779	0.638	0.660	0.625

Table 2. Continued.

Locus	Allele	*S. tridecemlineatus*	*S. mexicanus* with hybrids	*S. mexicanus* without hybrids	Hybrids
MPI	A	0.944	0.984	0.996	0.937
	B	0.056	0.016	0.004	0.063
6-PGD	A	0	0.009	0.011	0.013
	B	0.998	0.991	0.989	0.987
	C	0.002	0	0	0
PGM-1	A	0.052	0.072	0.082	0.063
	B	0.948	0.928	0.918	0.937
PGM-2	A	0.169	0.162	0.159	0.213
	B	0.831	0.838	0.841	0.787
PGM-3	A	0.024	0.033	0.039	0.013
	B	0.976	0.967	0.961	0.987

Table 3. Proportion of individuals heterozygous at each polymorphic locus for each population of *S. tridecemlineatus* and *S. mexicanus*. The column means are the mean proportion of individuals heterozygous at each locus for the two species. Population (Pop) means are the mean proportion of loci heterozygous per individual ($\bar{H}$) for each population. $\bar{H}$ was calculated from 13 polymorphic loci and 23 invariant loci except for populations marked with an asterix (*). $\bar{H}$ for the marked populations were calculated from the 28 loci reported in Cothran et al. (1977). Dashes indicate that the locus was not examined for that population.

Pop.	ALB	NSP	GOT-1	IDH-1	LAP	ADK-1	PEP-1	AP-1	ADA	MPI	PGM-1	PGM-2	PGM-3	Pop. Means
S. tridecemlineatus														
LUB	0	.167	.250	.167	.330	.330	0	0	.093	0	0	.167	0	.0420
POR	0	.167	0	0	0	.389	.056	.056	.167	.056	.056	.167	0	.0317
PLA	0	.083	.083	.083	.083	0	.167	.083	.417	0	.083	.250	.083	.0286
LOV	0	.182	0	0	0	.273	.182	0	.182	0	.091	.091	.091	.0312
LEV	0	.083	0	0	0	.330	.250	.083	.167	.083	.083	.167	.083	.0381
WAC	0	.286	0	0	.430	.214	.143	0	.143	0	0	.286	0	.0429
TAH	0	.375	0	0	.312	.187	.125	0	.312	.063	0	0	.063	.0411

Table 3. Continued.

Pop.	ALB	NSP	GOT-1	IDH-1	LAP	ADK-1	PEP-1	AP-1	ADA	MPI	PGM-1	PGM-2	PGM-3	Pop. Means
HOT	0	.158	0	.210	.210	.263	0	.263	.158	0	0	.105	.059	.0406
MAT	0	.295	.118	.176	.412	.295	.176	0	.353	0	0	.118	0	.0555
VER	0	.625	0	0	0	.063	0	.188	.063	0	.312	.250	0	.0429
HIL	0	.500	0	0	.083	.250	0	.083	0	0	.082	.167	0	.0333
DEN*	0	-	0	.111	-	-	-	-	-	-	.111	0	0	.0490
WIC*	0	-	0	.059	-	-	-	-	-	-	0	.235	0	.0510
PAR*	0	-	0	0	-	-	-	-	-	-	0	0	0	.0680
LEW*	0	-	0	0	-	-	-	-	-	-	0	.500	0	.0470
GRU*	0	-	0	0	-	-	-	-	-	-	0	.333	0	.0570
AMA*	0	-	0	0	-	-	-	-	-	-	0	0	0	.0550
COR*	0	-	0	.200	-	-	-	-	-	-	0	0	0	.0690
MEAN	0	.270	.038	.063	.176	.239	.094	.075	.189	.019	.063	.157	.031	.0395
S. mexicanus														
HOM	.470	.313	.177	0	.529	.235	.118	.177	.235	.059	.118	.177	0	.0741

Table 3. <u>Continued</u>.

Pop.	ALB	NSP	GOT-1	IDH-1	LAP	ADK-1	PEP-1	AP-1	ADA	MPI	PGM-1	PGM-2	PGM-3	Pop. Means
BIG	.200	0	.134	.200	.200	.134	.134	.200	.267	.067	.067	.067	0	.0476
ROS	.308	.154	0	.154	.154	.308	.077	.154	.385	.077	.077	.077	0	.0549
ART	.334	.267	.201	.067	.334	.267	.067	.067	.134	0	.067	.334	.267	.0686
KEN	.385	.154	0	.154	.231	.231	.231	.231	.385	0	0	.308	0	.0659
RAN	.267	.067	.267	.133	.200	.333	0	.267	.200	0	0	.333	0	.0590
SNY	.461	.231	0	.077	.154	.308	.231	0	.231	0	0	.231	.231	.0615
ABI	.400	.200	.067	.067	.400	.200	.133	.267	.333	0	0	.267	0	.0667
AUS	.336	.222	.222	.112	.112	.112	.166	.112	.056	0	0	.112	.112	.0492
AND	.300	.050	.250	.050	.100	.400	.150	.050	.050	0	.050	.250	.050	.0486
SEY	.333	.222	.111	0	.056	.389	0	.111	.222	.056	.111	.111	0	.0508
MUN	.333	0	.111	0	.111	.111	.111	0	.444	0	0	.111	0	.0381
SHE*	.467	-	.067	.200	-	-	-	-	-	-	0	.333	.133	.0890
CAR*	.571	-	.286	0	-	-	-	-	-	-	.143	0	0	.0640
NEW*	0	-	0	0	-	-	-	-	-	-	1.000	0	0	.0630

Table 3. Continued.

Pop.	ALB	NSP	GOT-1	IDH-1	LAP	ADK-1	PEP-1	AP-1	ADA	MPI	PGM-1	PGM-2	PGM-3	Pop. Means
MID*	.700	-	.100	.300	-	-	-	-	-	-	0	0	0	.0810
PEC*	.600	-	.400	0	-	-	-	-	-	-	.400	.200	0	.0910
HAR*	.429	-	0	.286	-	-	-	-	-	-	.286	0	0	.0680
CCH*	.444	-	0	.778	-	-	-	-	-	-	0	0	0	.0730
MEAN	.386	.160	.133	.142	.215	.252	.118	.136	.227	.022	.122	.199	.055	.0573

Table 4. Results of the analysis of F-statistics for each variable locus for S. tridecemlineatus, S. mexicanus with hybrids included in the sample, S. mexicanus with no hybrids in the sample, and with the data for S. tridecemlineatus and S. mexicanus combined.

	Locus	F_{IS}	F_{IT}	F_{ST}	Chi square	Degrees of freedom
S. tridecemlineatus	GOT-1	0.491	0.568	0.153	97.35***	20
	IDH-1	0.448	0.483	0.065	41.41***	20
	PGM-1	0.301	0.365	0.092	29.31***	10
	PGM-2	0.362	0.418	0.087	27.75***	10
	PGM-3	0.257	0.297	0.053	16.98	10
	LAP	0.325	0.429	0.154	98.27***	20
	MPI	0.830	0.838	0.046	14.68	10
	NSP	0.250	0.321	0.095	120.28***	40
	PEP-1	0.469	0.511	0.079	25.22***	10
	ADK	0.407	0.465	0.098	31.11***	10
	AP-1	0.628	0.662	0.094	29.78***	10
	ADA	0.424	0.475	0.089	56.82***	20
	TOTAL	0.432	0.486	0.092	588.16***	190

Table 4. Continued.

	Locus	F_{IS}	F_{IT}	F_{ST}	Chi square	Degrees of freedom
S. mexicanus	ALB	0.417	0.476	0.101	110.03***	33
(hybrids included)	GOT-1	0.555	0.575	0.046	32.20	22
	IDH-1	0.529	0.564	0.074	53.83***	22
	PGM-1	0.173	0.202	0.036	13.00	11
	PGM-2	0.288	0.322	0.048	17.38	11
	PGM-3	0.101	0.184	0.092	33.31***	11
	LAP	0.342	0.366	0.036	26.28	22
	MPI	0.556	0.578	0.050	18.12	11
	NSP	0.296	0.353	0.081	117.40***	44
	PEP-1	0.461	0.485	0.045	16.43	11
	ADK	0.414	0.440	0.044	16.12	11
	AP-1	0.505	0.546	0.084	30.57***	11
	ADA	0.499	0.532	0.066	48.17***	22
	TOTAL	0.395	0.433	0.062	532.84***	242

Table 4. Continued.

	Locus	F_{IS}	F_{IT}	F_{ST}	Chi square	Degrees of freedom
S. mexicanus (no hybrids)	ALB	0.471	0.515	0.083	71.99***	33
	GOT-1	0.565	0.594	0.067	38.76*	22
	IDH-1	0.524	0.569	0.094	54.81***	22
	PGM-1	0.304	0.352	0.068	19.85*	11
	PGM-2	0.284	0.313	0.042	12.05	11
	PGM-3	0.053	0.185	0.139	40.26***	11
	LAP	0.370	0.390	0.032	18.81	22
	MPI	0.368	0.418	0.079	22.78***	11
	NSP	0.084	0.120	0.040	45.77	44
	PEP-1	0.432	0.460	0.050	14.42	11
	ADK	0.421	0.461	0.069	19.94*	11
	AP-1	0.482	0.538	0.108	31.43***	11
	ADA	0.503	0.542	0.078	45.23***	22
	TOTAL	0.374	0.420	0.073	436.09***	242

Table 4. Continued.

	Locus	F_{IS}	F_{IT}	F_{ST}	Chi square	Degrees of freedom
S. tridecemlineatus and *S. mexicanus*	ALB	0.417	0.722	0.522	1065.25***	66
	GOT-1	0.543	0.587	0.096	130.22***	44
	IDH-1	0.499	0.540	0.080	109.00***	44
	PGM-1	0.249	0.304	0.074	49.96***	22
	PGM-2	0.321	0.366	0.066	44.91***	22
	PGM-3	0.164	0.229	0.078	52.73***	22
	LAP	0.335	0.425	0.136	185.14***	44
	MPI	0.754	0.768	0.058	39.29*	22
	NSP	0.270	0.611	0.467	1271.42***	88
	PEP-1	0.464	0.497	0.061	41.41***	22
	ADK	0.411	0.452	0.070	47.34***	22
	AP-1	0.554	0.595	0.092	62.27***	22

Table 4. Continued.

Locus	F_{IS}	F_{IT}	F_{ST}	Chi square	Degrees of freedom
ADA	0.469	0.518	0.092	125.49***	44
TOTAL	0.419	0.509	0.145	3224.43***	484

* $P < 0.05$; *** $P \leq 0.001$

Table 5. Values of Nei's (1971) identity coefficient (I, above diagonal) and Rogers' (1972) similarily coefficient (S, below diagonal) for the two ground squirrel species and hybrids between the two species.

	S. tridecemlineatus	Hybrids	*S. mexicanus*
S. tridecemlineatus	0.997 / 0.989	0.966	0.959
Hybrids	0.936	0.973 / 0.963	0.978
S. mexicanus	0.928	0.967	0.985 / 0.982

Table 6. Means (± standard deviations) of the differences between sides for the paired characters (Right-Left; upper value) and of the absolute values of asymmetry ([Right - Left]/[Right + Left], lower values) for each character for S. tridecemlineatus, S. mexicanus with hybrids included in the sample, S. mexicanus without hybrids in the sample, and the hybrid individuals. Cranial asymmetry, skeletal asymmetry and total asymmetry are explained in the text. An asterix beside a value of the difference between paired characters means that character mean was significantly different from zero for that group.

	S. tridecemlineatus	*S. mexicanus*	*S. mexicanus* without hybrids	Hybrids
UDL	.0276 ± .1178***	-.0168 ± .1130*	.0175 ± .1075*	.0138 ± .1354
	.0028 ± .0039	.0022 ± .0031	.0024 ± .0033	.0032 ± .0040
TRL	-.0032 ± .1010	.0003 ± .1053	.0000 ± .1050	.0043 ± .1078
	.0047 ± .0049	.0042 ± .0046	.0043 ± .0046	.0047 ± .0044
BUL	-.0019 ± .1050	.0075 ± .1055	.0063 ± .1038	.0128 ± .1135
	.0048 ± .0041	.0044 ± .0036	.0044 ± .0039	.0043 ± .0049
MOL	.0064 ± .0519*	.0055 ± .0603	.0029 ± .0583	.0170 ± .0678
	.0089 ± .0101	.0081 ± .0098	.0088 ± .0105	.0119 ± .0128

Table 6. Continued.

	S. tridecemlineatus	S. mexicanus	S. mexicanus without hybrids	Hybrids
MAN	-.0090 ± .1168	.0123 ± 1379	.0172 ± .1359	-.0085 ± .1453
	.0027 ± .0023	.0028 ± .1379	.0029 ± .0015	.0030 ± .0027
PPL	.0176 ± .0806***	.0128 ± .0808**	.0115 ± .0838	.0181 ± .0671
	.0023 ± .0022	.0021 ± .0019	.0020 ± .0019	.0016 ± .0017
FEL	-.0090 ± .1264	.0032 ± .1292	.0002 ± .1373	.0180 ± .0867
	.0018 ± .0018	.0013 ± .0015	.0014 ± .0016	.0008 ± .0011
FPW	.0056 ± .0910	.0105 ± .0808	.0070 ± .0811	.0255 ± .0786*
	.0056 ± .0059	.0038 ± .0043	.0039 ± .0042	.0033 ± .0047
HUL	-.0002 ± .1028	.0123 ± .1272	.0095 ± .1274	.0245 ± .1268
	.0019 ± .0017	.0018 ± .0018	.0018 ± .0018	.0018 ± .0018
HDW	.0028 ± .0800	.0067 ± .0780	.0032 ± .0780	.0213 ± .0771
	.0055 ± .0051	.0043 ± .0043	.0043 ± .0043	.0042 ± .0043
SCL	.0133 ± .1110	-.0008 ± .0978	.0005 ± .0935	-.0064 ± .1154
	.0026 ± .0025	.0016 ± .0017	.0016 ± .0016	.0016 ± .0021

Table 6. Continued.

	S. tridecemlineatus	*S. mexicanus*	*S. mexicanus* without hybrids	Hybrids
SCW	-.0047 ± .0677	.0047 ± .0780	.0032 ± .0740	.0081 ± .0100
	.0079 ± .0088	.0072 ± .0082	.0070 ± .0076	.0081 ± .0100
CRANIAL	.4052 ± .1760	.4221 ± .1823	.4168 ± .1813	.4447 ± .1869
	.0261 ± .0134	.0247 ± .0136	.0237 ± .0130	.0287 ± .0152
SKELETAL	.3639 ± .2778	.3800 ± .2552	.3818 ± .2603	.3723 ± .2345
	.0254 ± .0141	.0201 ± .0117	.0201 ± .0112	.0198 ± .0137
TOTAL	.7691 ± .3260	.8020 ± .3400	.7985 ± .3456	.8170 ± .3182
	.0513 ± .0179	.0453 ± .0184	.0445 ± .0179	.0485 ± .0203

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Figure 1. Map of sampling localities of ground squirrels. Explanation of the sample abbreviations are given in Table 1. The approximate ranges of the species in the study area is also indicated (the range of _S_. _mexicanus_ is the hatched area).

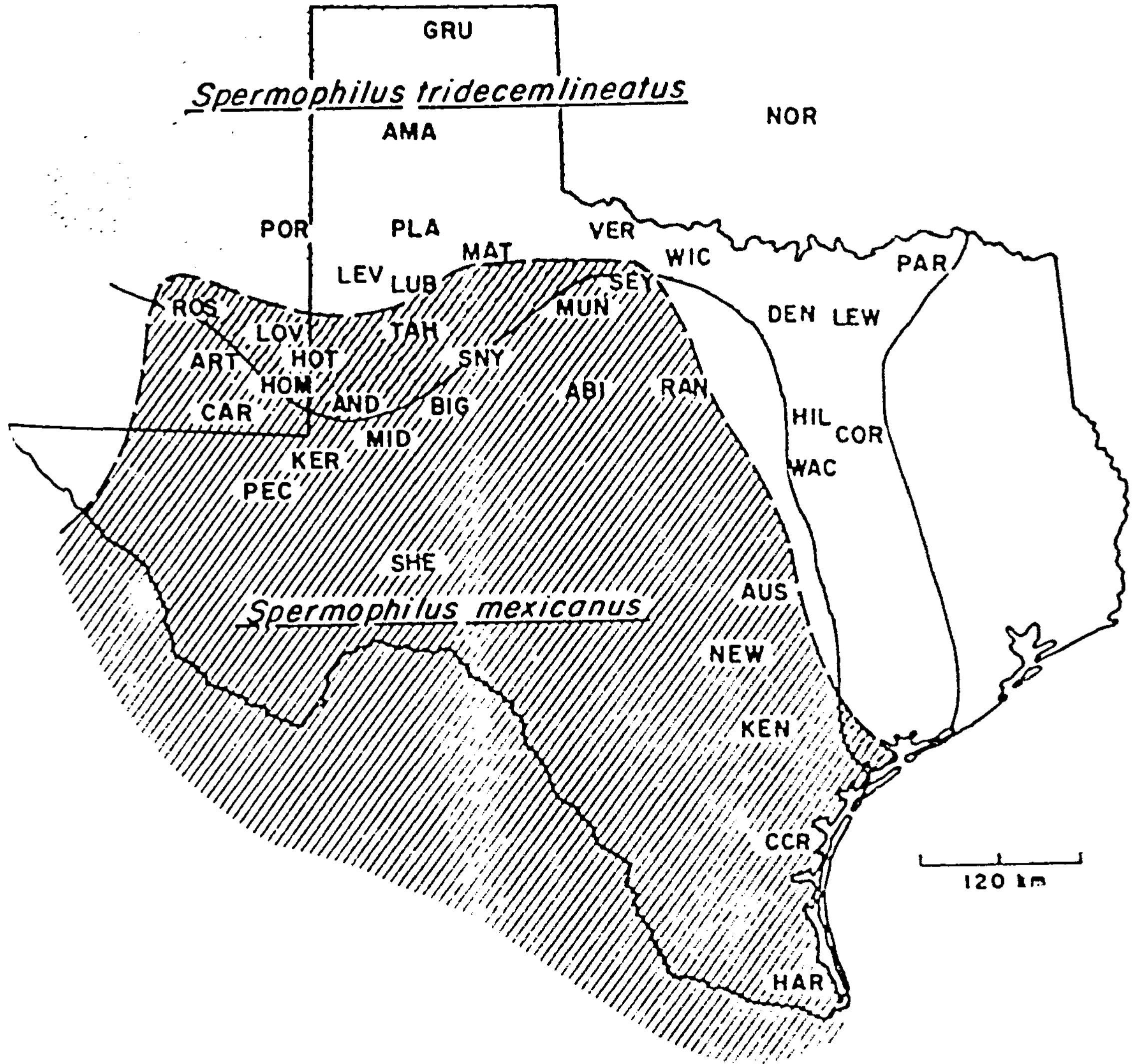

GRU
Spermophilus tridecemlineatus
NOR
AMA
POR
PLA
VER
MAT
WIC
PAR
LEV
LUB
SEY
ROS
MUN
DEN
LEW
LOV
TAH
ART
HOT
SNY
HOM
ABI
RAN
CAR
AND
BIG
HIL
COR
MID
KER
WAC
PEC
SHE
AUS
Spermophilus mexicanus
NEW
KEN
CCR
120 km
HAR

Figure 2. Geographic frequency of the ALB-*a* allele. The other alleles were the ALB-*b*, *c*, and *d*. The presence of the ALB-*a* allele in association with the other ALB alleles was an indication of hybridization.

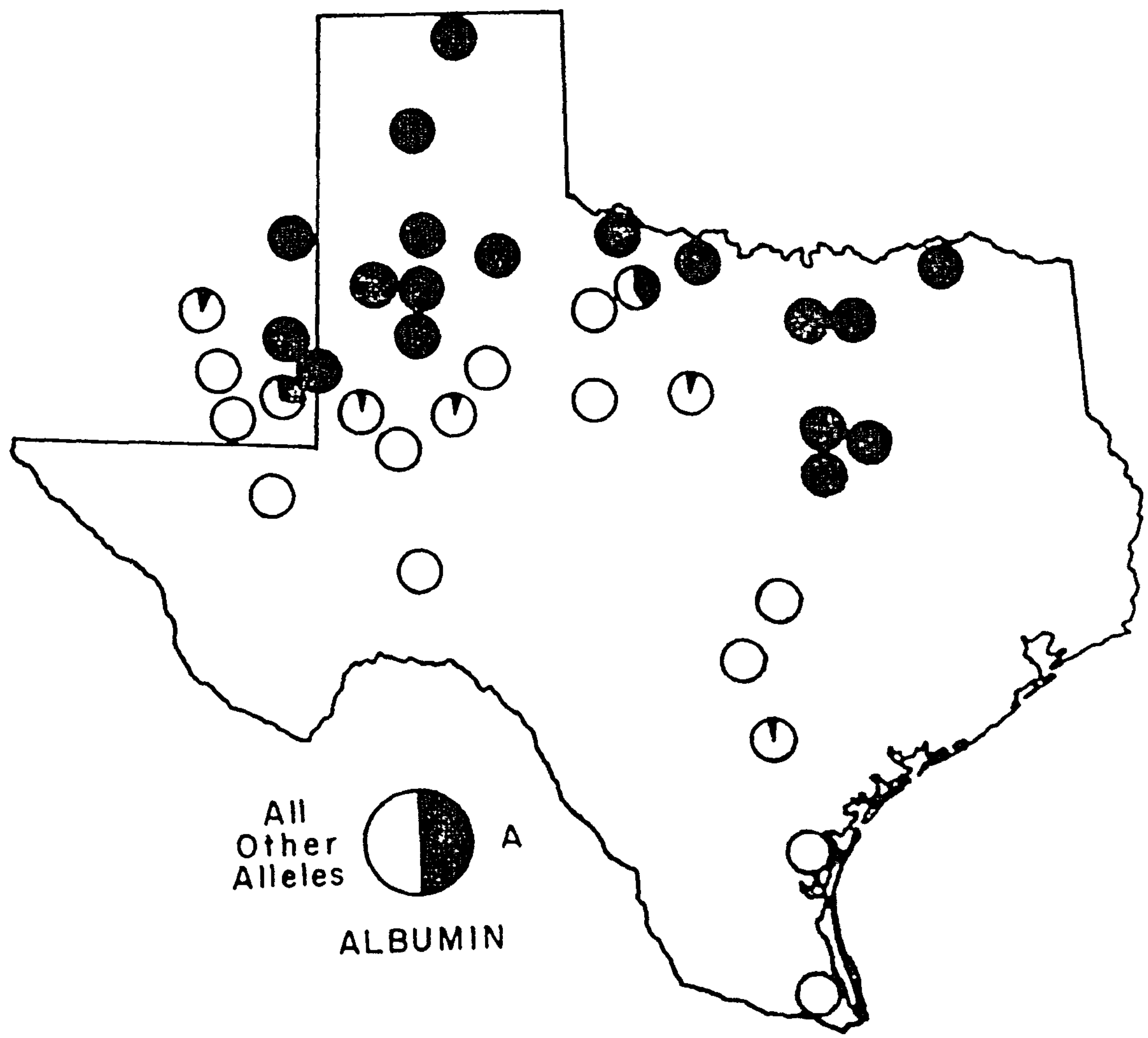
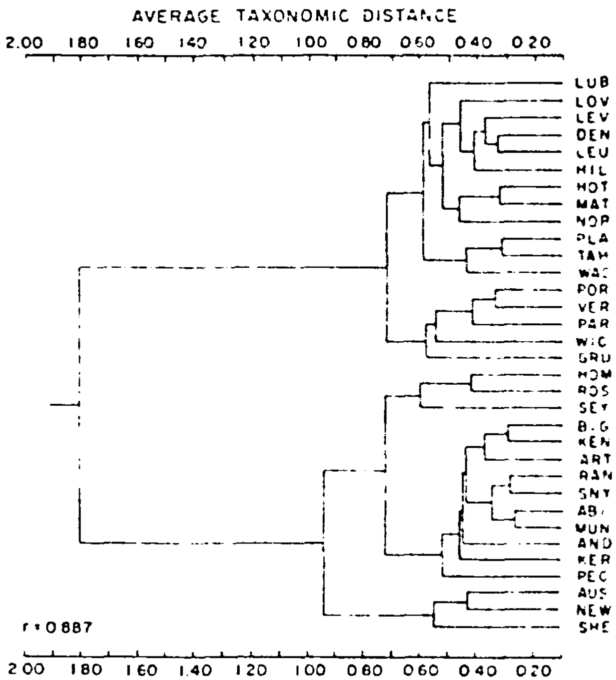
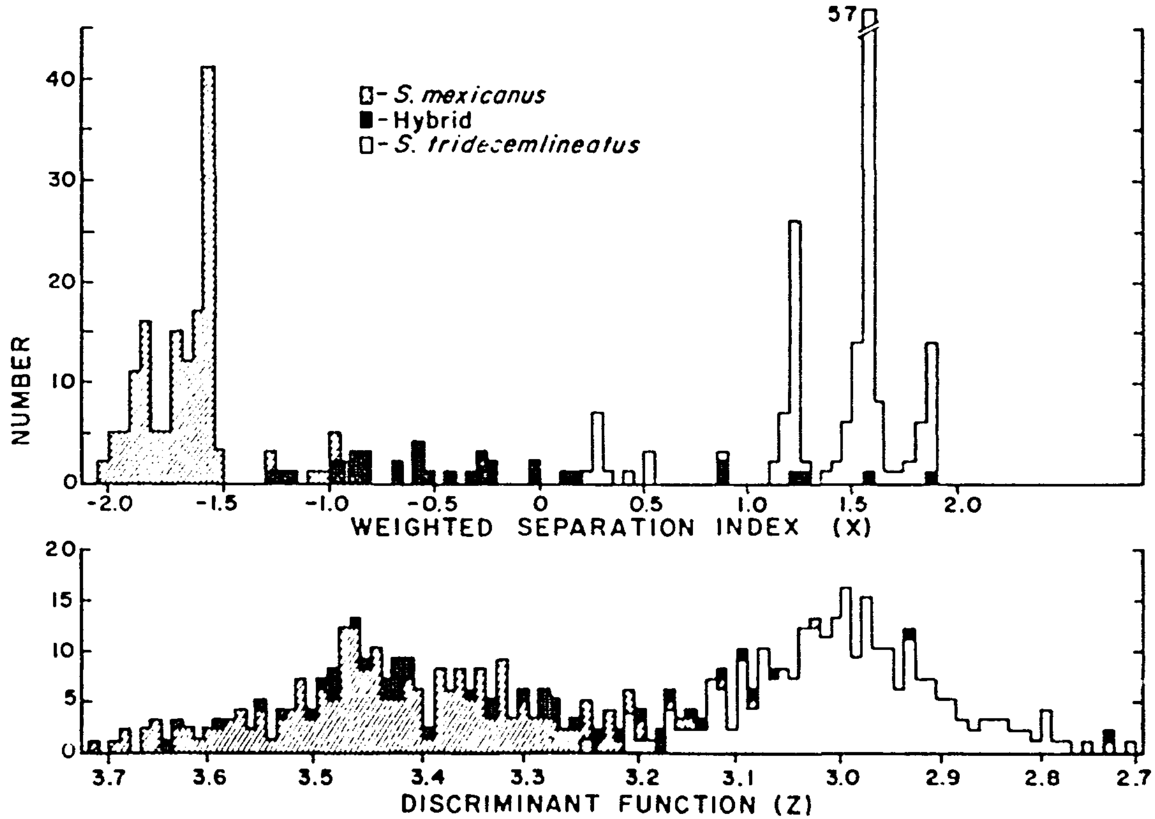

All
Other
Alleles
A
ALBUMIN

Figure 3. Dendrogram (UPGMA) of phenetic and genetic distance between populations of *S. mexicanus* and *S. tridecemlineatus*. Locality abbreviations are explained in Table 1. (A) Average taxonomic distance (Sokal, 1961). (B) Nei's (1971) genic identity (*I*) and distance (*D*).

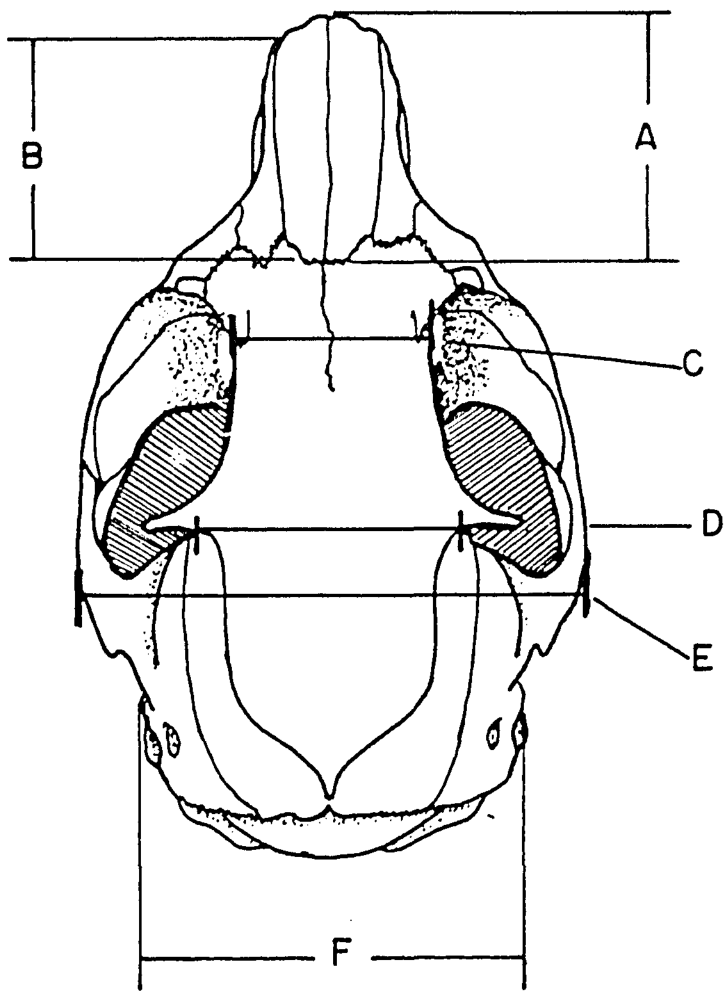

AVERAGE TAXONOMIC DISTANCE
2.00 1.80 1.60 1.40 1.20 1.00 0.80 0.60 0.40 0.20
LUB
LOV
LEV
DEN
LEU
HIL
HOT
MAT
NOR
PLA
TAH
WAI
POR
VER
PAR
WIC
GRU
HOM
ROS
SEY
BIG
KEN
ART
RAN
SNY
ABI
MUN
AND
KER
PEC
AUS
NEW
SHE
r = 0.887

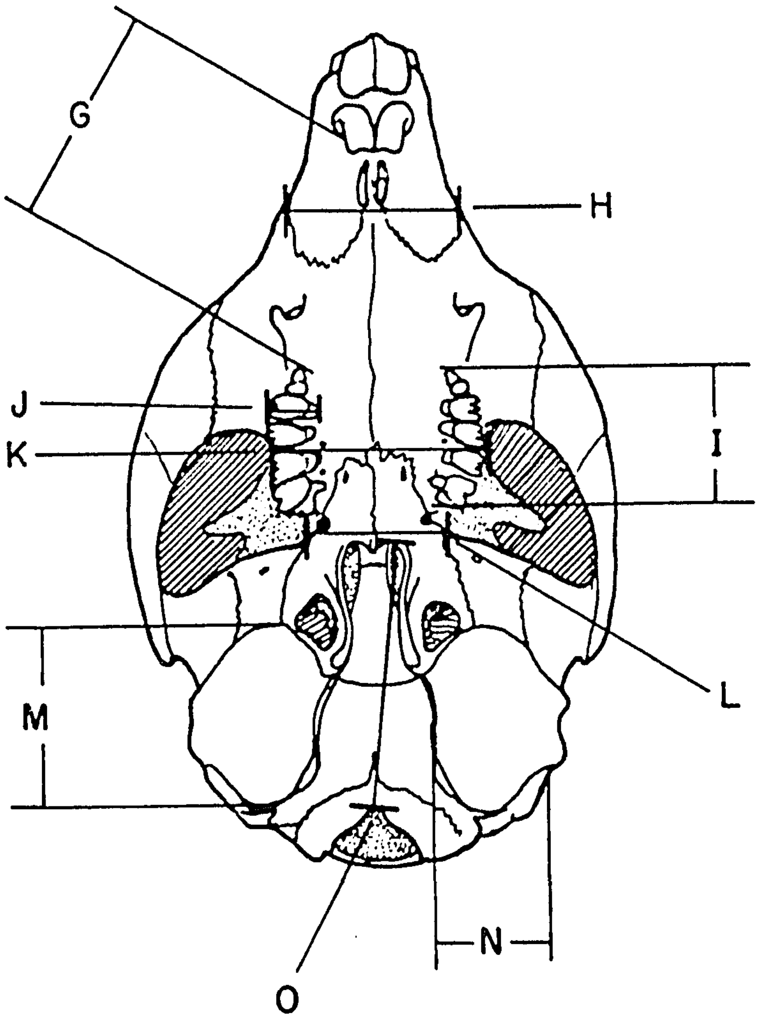

NEI'S D
0.04 0.03 0.02 0.01 0
r = 0.896
0.96 0.97 0.98 0.99 1.00
NEI'S I

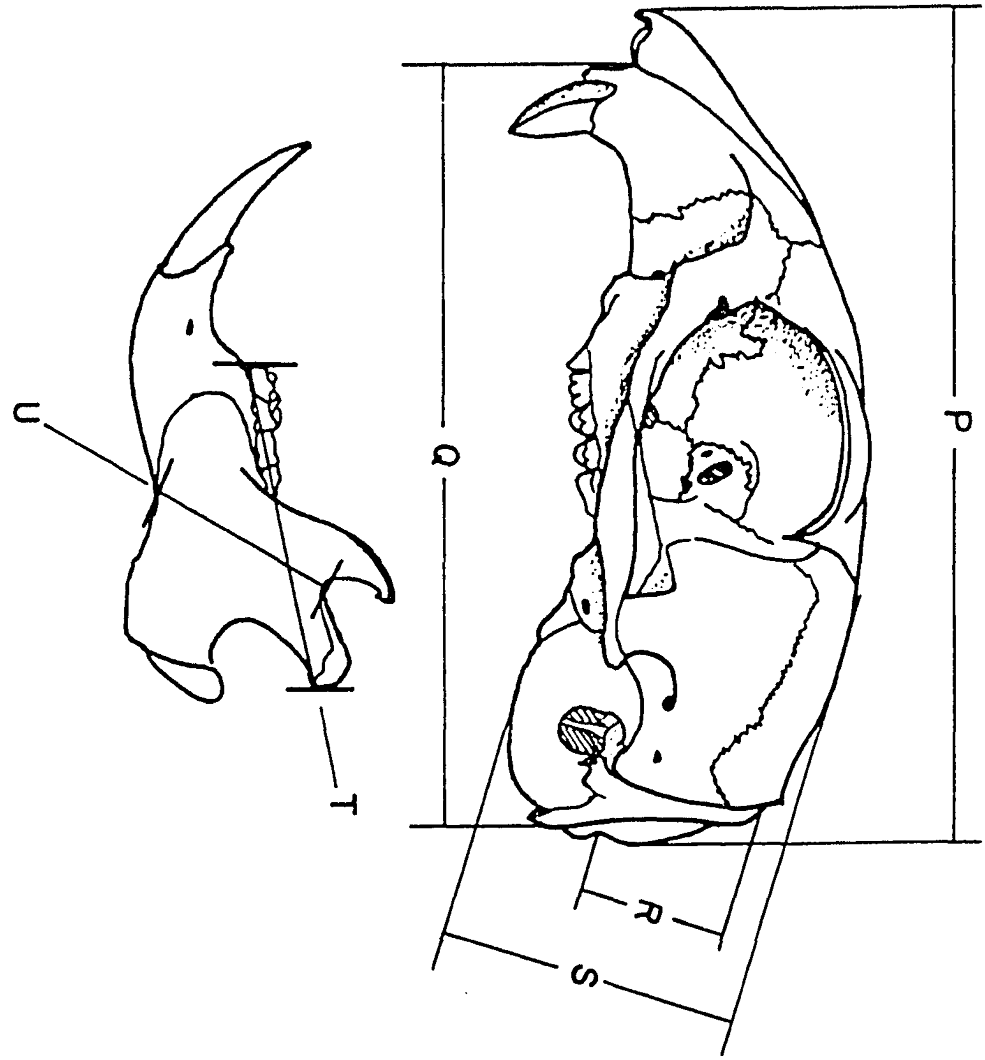
Figure 4. Frequency histograms of individual scores calculated from electrophoretic data (weighted separation index, X; Vogt and McPherson, 1972) and morphologic data (discriminant function, z).

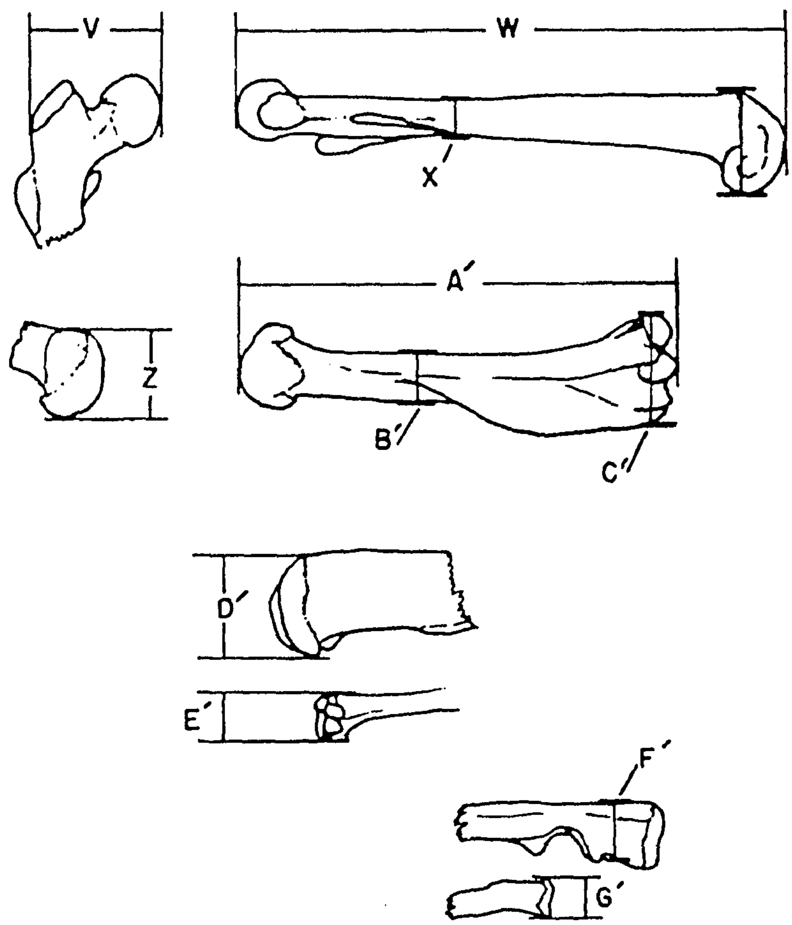

S. mexicanus
Hybrid
S. tridecemlineatus
57
NUMBER
WEIGHTED SEPARATION INDEX (X)
DISCRIMINANT FUNCTION (Z)
0 10 20 30 40
-2.0 -1.5 -1.0 -0.5 0 0.5 1.0 1.5 2.0
0 5 10 15 20
3.7 3.6 3.5 3.4 3.3 3.2 3.1 3.0 2.9 2.8 2.7

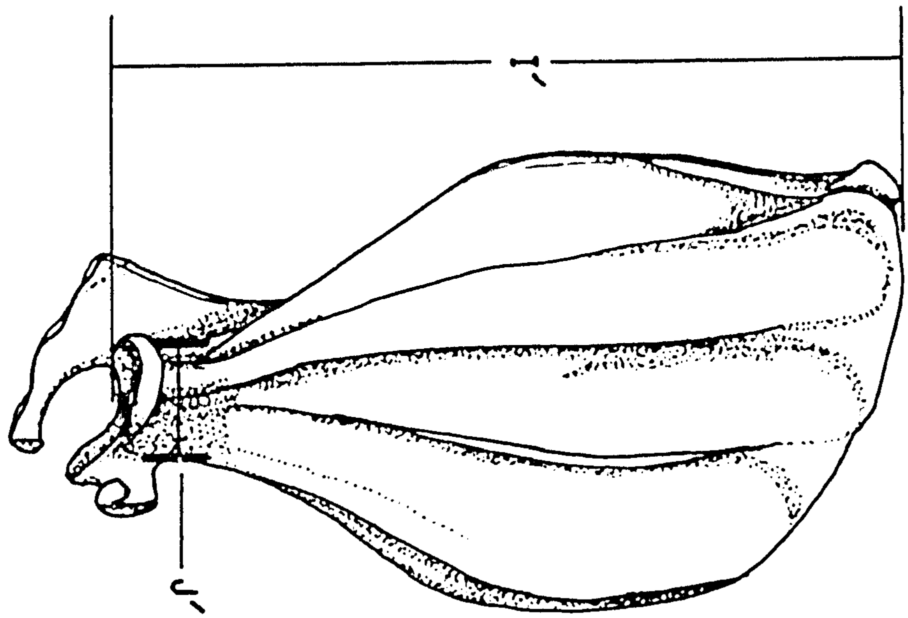
Appendix I. Cranial and skeletal measurements taken on adult ground squirrels were as follows: A. nasal length; B. rostral length; C. interorbital breadth; D. postorbital breadth; E. zygomatic breadth; F. brain case breadth; G. upper diastema length; H. premaxillary breadth; I. tooth row length; J. 2nd premolar breadth; K. breadth across tooth rows; L. palatal width; M. bular length; N. bular breadth; O. post-palatal length; P. greatest length of skull; Q. basal length of skull; R. occipital depth; S. skull depth; T. mandible length; U. mandible depth; V. femur proximal width; W. femur length; X. femur minimal width; Y. femur distal width; Z. humerus proximal width; A'. humerus length; B'. humerus minimal width; C'. humerus distal width; D'. tibia proximal width; E'. fibula proximal width; F'. ulna proximal width; G'. radius proximal width; H'. sacrum width; I'. scapula length; J'. scapula width; K'. pelvis length.

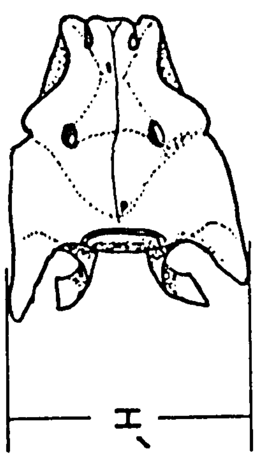

A
B
C
D
E
F

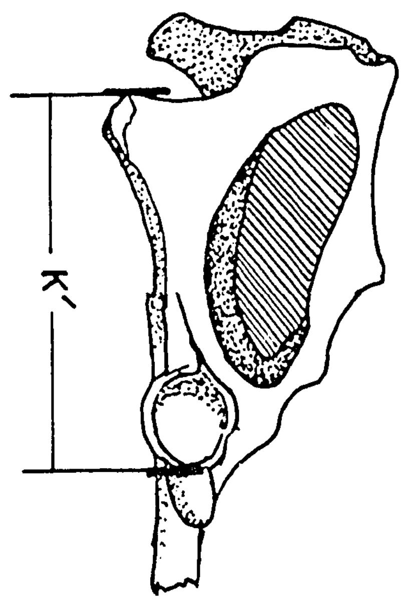

G
H
I
J
K
L
M
N
O


P
Q
R
S
T
U


V
W
X
A'
Z
B'
C'
D'
E'
F'
G'


I'
J'


H'


K'

Appendix II. Sample size (N), mean, standard error, variance, and coefficient of variation (C.V.) for morphometric measurements of adult ground squirrels from 33 localities. Measurement abbreviations are explained in the Materials and Methods section of the morphology paper. Descriptions of the measurements are shown in Appendix I. Skeletal measurements were not available for 10 localities.

SPECIES=MEXICANUS LOCATION=ABILENE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	17	44.75000000	0.36839776	2.30718750	3.394
BASL	17	39.42941176	0.39053740	2.59283088	4.084
ZYB	16	26.91875000	0.35586968	2.02629167	5.283
ROSL	16	17.56562500	0.22563423	0.81457292	5.138
NASL	16	15.25937500	0.19553446	0.61173958	5.126
PMXB	16	9.98750000	0.07739240	0.09583333	3.100
IOB	16	10.46250000	0.22580873	0.81583333	8.633
POB	16	13.08125000	0.18579082	0.55229167	5.631
PPL	17	15.09117647	0.18382353	0.57444853	5.022
BAT	17	11.95294118	0.05531836	0.05202206	1.908
TRL	17	8.88529412	0.07606652	0.09836397	3.530
BCB	17	19.56764706	0.11391602	0.22060662	2.400
BUL	17	9.47941176	0.08901615	0.13470588	3.872
BUB	17	7.85294118	0.05679403	0.05483456	2.982
MOLW	17	2.25882353	0.03409419	0.01976103	6.223
UDL	17	14.39705882	0.24270498	1.00139706	6.951
PALW	17	7.18823529	0.08591307	0.12547794	4.923
OCD	17	7.10882353	0.13600357	0.31444853	7.888
SKD	16	18.82187500	0.22257811	0.79265625	4.730
MANL	17	18.91764706	0.15368878	0.40154412	3.350
MAND	17	14.56176471	0.17612712	0.52735294	4.987
FEL	17	34.50000000	0.50300567	4.30125000	6.011
FMW	17	2.55588235	0.05248991	0.04683824	8.468
FDW	17	5.87352941	0.04757302	0.03847426	3.340
FPW	17	7.54411765	0.12535848	0.26715074	6.851
HUL	17	27.14705882	0.39050002	2.59233456	5.931
HMW	17	2.75000000	0.07053053	0.08468750	10.582
HPW	17	5.34705882	0.08579972	0.12514706	6.616
HDW	17	7.10294118	0.08569253	0.12483456	4.974
RPW	17	2.08529412	0.03503273	0.02086397	6.927
UPW	17	3.12647059	0.03324310	0.01878676	4.384
TPW	17	5.46176471	0.07506485	0.09579044	5.667
FIW	17	1.86470588	0.06135191	0.06393897	13.566
SCL	17	21.46176471	0.77023594	10.08547794	14.797
SCW	17	3.91764706	0.05986215	0.06091912	6.300
PEVL	17	13.95294118	0.23606262	0.94733456	6.976
SACW	17	11.94117647	0.20037810	0.68257353	6.919
BDYL	16	191.87500000	3.41549777	186.65000000	7.120
TL	16	120.06250000	2.95306162	139.52916667	9.838
HFL	16	42.56250000	0.63880585	6.52916667	6.003

SPECIES=MEXICANUS LOCATION=ANDREWS

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	20	45.47500000	0.34309926	2.35434211	3.374
BASL	20	40.24000000	0.34890053	2.43463158	3.878
ZYB	20	26.63250000	0.23589904	1.11296711	3.961
ROSL	20	17.92250000	0.16056950	0.51565132	4.007
NASL	20	15.92250000	0.16489530	0.54380921	4.631
PMXB	20	10.21500000	0.14212208	0.40397368	6.222
IOB	20	10.84250000	0.15244822	0.46480921	6.288
POB	20	12.77500000	0.12888694	0.33223684	4.512
PPL	20	15.66250000	0.19125193	0.73154605	5.461
BAT	20	12.00000000	0.09658648	0.18657895	3.600
TRL	20	8.50750000	0.06264720	0.07849342	3.293
BCB	20	19.31750000	0.14194490	0.40296711	3.286
BUL	20	9.47250000	0.09013696	0.16249342	4.256
BUB	20	7.92000000	0.07194662	0.10352632	4.063
MOLW	19	2.21842105	0.02892077	0.01589181	5.633
UDL	20	14.96500000	0.16335705	0.53371053	4.832
PALW	20	7.20000000	0.05677750	0.06447368	3.527
OCD	20	6.91750000	0.12205882	0.29796711	7.891
SKD	20	18.88250000	0.16504684	0.54480921	3.909
MANL	20	18.82000000	0.15842149	0.50194737	3.765
MAND	20	14.80500000	0.19149344	0.73339474	5.784
FEL	20	35.33250000	0.46967619	4.41191447	5.945
FMW	20	2.53000000	0.02497367	0.01247368	4.414
FDW	20	5.34500000	0.05948242	0.07076316	4.551
FPW	20	7.66250000	0.08794997	0.15470395	5.133
HUL	20	27.90250000	0.42742305	3.65380921	6.851
HMW	20	2.60750000	0.07239103	0.10480921	12.416
HPW	20	5.40500000	0.05583104	0.06234211	4.620
HDW	20	7.16750000	0.08631910	0.14901974	5.386
RPW	20	2.17000000	0.02389671	0.01142105	4.925
UPW	20	3.22000000	0.03616483	0.02615789	5.023
TPW	20	5.53750000	0.04891924	0.04786184	3.951
FIW	20	1.90500000	0.04336200	0.03760526	10.180
SCL	20	22.72000000	0.36181923	2.61826316	7.122
SCW	20	3.96000000	0.06183595	0.07647368	6.983
PEVL	20	14.12000000	0.25403246	1.29115789	8.047
SACW	20	12.06500000	0.24807416	1.23081579	9.195
BDYL	20	201.55000000	2.60614153	135.83947368	5.783
TL	17	116.76470588	1.97880202	66.56617647	6.987
HFL	20	41.70000000	0.42981024	3.69473684	4.610

SPECIES=MEXICANUS LOCATION=ARTESIA

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	17	45.03823529	0.31574868	1.69485294	2.891
BASL	17	39.79705882	0.33855963	1.94858456	3.508
ZYB	17	27.12941176	0.27600281	1.29501838	4.195
ROSL	17	17.58823529	0.14762391	0.37047794	3.461
NASL	17	15.49117647	0.13278931	0.29976103	3.534
PMXB	17	9.84705882	0.10383019	0.18327206	4.348
IOB	17	10.44411765	0.14238530	0.34465074	5.621
PCB	17	13.44705882	0.12894300	0.28264706	3.954
PPL	17	15.26470588	0.13406571	0.30555147	3.621
BAT	17	11.81470588	0.09755887	0.16180147	3.405
TRL	17	8.53235294	0.08122920	0.11216912	3.925
BCB	17	19.16176471	0.13473349	0.30860294	2.899
BUL	17	9.35882353	0.08789149	0.13132353	3.872
BUB	17	7.76470588	0.08742273	0.12992647	4.642
MOLW	17	2.18823529	0.03136872	0.01672794	5.911
UDL	17	14.80882353	0.16456467	0.46038603	4.582
PALW	17	7.03529412	0.07106913	0.08586397	4.165
OCD	17	7.19411765	0.13475757	0.30871324	7.723
SKD	17	18.96470588	0.10552431	0.18930147	2.294
MANL	17	18.50294118	0.15318137	0.39889706	3.413
MAND	17	14.77058824	0.18421429	0.57689338	5.142
FEL	17	35.36470588	0.45688694	3.54867647	5.327
FMW	17	2.57058824	0.04794659	0.03908088	7.690
FDW	17	5.97058824	0.13180442	0.29533088	9.102
FPW	17	7.58823529	0.10943785	0.20360294	5.946
HUL	17	27.95882353	0.33186293	1.87226103	4.894
HMW	17	2.97647059	0.12104915	0.24909926	16.768
HPW	17	5.31764706	0.06859155	0.07998162	5.318
HDW	17	6.99117647	0.09036642	0.13882353	5.329
RPW	17	2.17352941	0.04246920	0.03066176	8.056
UFW	17	3.22647059	0.05038777	0.04316176	6.439
TPW	17	5.51470588	0.09575212	0.15586397	7.159
FIW	17	1.88529412	0.04388419	0.03273397	9.597
SCL	17	22.62352941	0.43286659	3.18534926	7.889
SCW	17	3.95882353	0.07873486	0.10538603	8.200
PEVL	17	13.83235294	0.24468396	1.01779412	7.293
SACW	17	12.06176471	0.22288753	0.84454044	7.619
BDYL	17	198.35294118	3.03525992	156.61764706	6.309
TL	15	125.53333333	2.62926147	103.69523810	8.112
HFL	17	42.17647059	0.63149737	6.77941176	6.173

SPECIES=MEXICANUS LOCATION=AUSTIN

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	25	42.57600000	0.36730006	3.37273333	4.313
BASL	25	37.50200000	0.35491173	3.14905833	4.732
ZYB	25	26.06000000	0.20934421	1.09562500	4.017
ROSL	25	16.19000000	0.18191115	0.82729167	5.618
NASL	25	14.09000000	0.16950910	0.71833333	6.015
PMXB	25	9.30000000	0.10327956	0.26666667	5.553
IOB	25	11.11000000	0.13714348	0.47020833	6.172
POB	25	13.28600000	0.14984770	0.56135833	5.639
PPL	25	14.54200000	0.17099415	0.73097500	5.879
BAT	25	11.64600000	0.08679094	0.18831667	3.726
TRL	25	8.28400000	0.07442670	0.13848333	4.492
BCB	25	18.68200000	0.12506265	0.39101667	3.347
BUL	25	8.75800000	0.08820809	0.19451667	5.036
BUB	25	7.34600000	0.07696969	0.14810833	5.239
MOLW	25	2.18800000	0.03550587	0.03151667	8.114
UDL	25	13.67800000	0.15335362	0.58793333	5.606
PALW	25	7.26400000	0.08263973	0.17073333	5.683
OCD	25	6.38000000	0.09941496	0.24708333	7.791
SKD	25	17.90000000	0.12100275	0.36604167	3.380
MANL	25	18.00600000	0.16212958	0.65715000	4.502
MAND	25	13.85800000	0.14202934	0.50430833	5.124
FEL	18	32.87777778	0.37294584	2.50359477	4.813
FMW	18	2.34166667	0.04630991	0.03860294	8.390
FDW	18	5.35000000	0.09217772	0.15294118	7.310
FPW	18	7.06388889	0.11016962	0.21847222	6.617
HUL	18	26.04166667	0.36209832	2.36007353	5.899
HMW	18	2.36944444	0.04393602	0.03474673	7.867
HPW	18	5.01944444	0.07498790	0.10121732	6.338
HDW	18	6.78611111	0.08370560	0.12611928	5.233
RPW	18	2.02222222	0.03239418	0.01888889	6.796
UPW	18	2.94166667	0.03861364	0.02683824	5.569
TPW	18	5.07222222	0.09386597	0.15859477	7.851
FIW	18	1.64166667	0.05289804	0.05036765	13.671
SCL	18	20.92222222	0.39973893	2.87624183	8.106
SCW	18	3.36666667	0.06517949	0.07647059	8.214
PEVL	18	12.28888889	0.21315233	0.81781046	7.359
SACW	18	11.01666667	0.28660168	1.47852941	11.037
BDYL	25	180.04000000	2.07643925	107.79000000	5.767
TL	19	107.47368421	2.26899331	97.81871345	9.203
HFL	25	39.24000000	0.45195870	5.10666667	5.759

SPECIES=MEXICANUS   LOCATION=BIG SPRING

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	18	44.70000000	0.47758584	4.10555824	4.533
BASL	18	38.95277778	0.41126841	3.04455065	4.479
ZYB	18	26.76111111	0.35843149	2.31251634	5.682
ROSL	18	17.34166667	0.25690624	1.18301471	6.285
NASL	18	15.63055556	0.27344746	1.34592320	7.422
PMXB	18	9.62777778	0.11027463	0.21888889	4.859
IOB	18	10.42777778	0.18691782	0.62888889	7.605
POB	18	13.14444444	0.18234533	0.59849673	5.886
PPL	18	15.06111111	0.18979502	0.64839869	5.346
BAT	18	11.88888889	0.11465746	0.23663399	4.092
TRL	18	8.58055556	0.10338541	0.19239379	5.112
BCB	18	19.21111111	0.18838889	0.64222222	4.171
BUL	18	9.38888889	0.09016647	0.14633987	4.074
BUB	18	7.56388889	0.07462384	0.10023693	4.186
MOLW	18	2.23611111	0.02582165	0.01200163	4.899
UDL	18	14.17222222	0.20659954	0.76830065	6.185
PALW	18	7.11388839	0.08311791	0.12435458	4.957
OCD	18	6.87500000	0.11577037	0.24125000	7.144
SKD	18	18.73611111	0.18659337	0.62670752	4.225
MANL	18	18.56388889	0.22951375	0.94817810	5.245
MAND	18	14.22777778	0.22920801	0.94565359	6.835
FEL	15	34.65666667	0.64053301	6.15423810	7.158
FMW	15	2.49000000	0.04932883	0.03650000	7.673
FDW	15	5.92000000	0.12400077	0.23064286	8.112
FPW	15	7.39666667	0.16391539	0.40302381	8.583
HUL	15	27.21666667	0.51537473	3.98416667	7.334
HMW	15	2.81333333	0.12319812	0.22766667	16.960
HPW	15	5.21666667	0.10686737	0.17130952	7.934
HDW	15	6.90333333	0.15503200	0.36052381	8.698
RPW	15	2.10333333	0.04096069	0.02516667	7.542
UPW	15	3.13333333	0.05577734	0.04666667	6.894
TPW	15	5.48666667	0.11937004	0.21373810	8.426
FIW	15	1.83333333	0.06448822	0.06238095	13.623
SCL	15	21.69333333	0.50598482	3.84030952	9.034
SCW	15	3.81666667	0.09996031	0.14988095	10.144
PEVL	15	13.64333333	0.30549985	1.39995238	8.672
SACW	15	11.93666667	0.26206445	1.03016667	8.503
BDYL	18	191.55555556	2.76913689	138.02614379	6.133
TL	16	121.68750000	2.48615961	98.89583333	8.172
HFL	18	40.33333333	0.70941382	9.05882353	7.462

SPECIES=MEXICANUS LOCATION=HOBBS-WEST

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	28	42.86964286	0.48583329	6.60895172	5.997
BASL	28	37.60714286	0.47041939	6.19624339	6.619
ZYB	28	25.76428571	0.29558991	2.44645503	6.071
ROSL	28	16.52500000	0.25136532	1.76916667	8.049
NASL	28	14.71607143	0.20878607	1.22056548	7.507
PMXB	28	9.67678571	0.07239671	0.14675595	3.959
IOB	28	9.96071429	0.16699090	0.78080688	8.871
POB	28	12.84821429	0.13878922	0.53934854	5.716
PPL	28	14.40535714	0.20232346	1.14617394	7.432
BAT	28	11.72321429	0.08523552	0.20342262	3.847
TRL	28	8.46250000	0.09468777	0.25104167	5.921
BCB	28	18.66607143	0.10724587	0.32204696	3.040
BUL	28	9.14821429	0.08105954	0.18397817	4.689
BUB	28	7.38214286	0.06751515	0.12763228	4.839
MOLW	28	2.11071429	0.03142947	0.02765873	7.879
UDL	28	13.67500000	0.23580746	1.55694444	9.125
PALW	28	7.01071429	0.07016407	0.13784392	5.296
OCD	28	6.96607143	0.12253389	0.42075066	9.312
SKD	28	18.07678571	0.13162301	0.48503929	3.853
MAHL	28	17.81964286	0.17550643	0.86247024	5.212
MAND	28	13.59642857	0.20538273	1.18109788	7.993
FEL	19	31.83947368	0.83695336	13.30932749	11.458
FMW	20	2.38000000	0.06828732	0.09326316	12.832
FDW	20	5.54250000	0.11021958	0.24296711	8.893
FPW	19	6.98157895	0.14917956	0.42283526	9.314
HUL	20	25.35000000	0.53654597	5.75763158	9.466
HMW	20	2.77250000	0.10732850	0.23038816	17.312
HPW	20	4.95250000	0.10159744	0.20644079	9.174
HDW	20	6.78500000	0.11442649	0.26186842	7.542
RPW	20	2.07000000	0.04029497	0.03247368	8.706
UPW	20	2.97000000	0.04282768	0.03668421	6.449
TPW	20	5.03500000	0.11681632	0.27292105	10.376
FIW	20	1.68750000	0.06165214	0.07601974	16.339
SCL	20	20.14000000	0.62855934	7.90173684	13.957
SCW	20	3.68750000	0.09211513	0.16970395	11.172
PEVL	20	12.62750000	0.32410758	2.10091447	11.479
SACW	19	10.96842105	0.45128489	3.86950292	17.934
BDYL	28	179.60714286	3.55729346	354.32142857	10.480
TL	26	109.00000000	2.11732778	116.56000000	9.905
HFL	28	38.60714286	0.41256484	4.76587302	5.655

SPECIES=MEXICANUS   LOCATION=KENNEDY

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	17	44.12647059	0.30525778	1.58409926	2.852
BASL	17	38.94117647	0.28304526	1.36194853	2.997
ZYB	17	26.54411765	0.23763086	0.95996324	3.691
ROSL	17	17.23823529	0.17018207	0.49235294	4.070
NASL	17	15.02941176	0.15724295	0.42033088	4.314
PMXB	17	9.85588235	0.10562162	0.13965074	4.419
IOB	17	10.80000000	0.11796373	0.23656250	4.503
POB	17	13.10000000	0.20841665	0.73843750	6.560
PPL	17	15.13235294	0.14213066	0.34341912	3.873
BAT	17	11.74705882	0.08483013	0.12233456	2.977
TRL	17	8.39705882	0.07394734	0.09295956	3.631
BCB	17	19.20588235	0.14980885	0.38152574	3.216
BUL	17	9.30882353	0.14045850	0.33538603	6.221
BUB	17	7.73235294	0.08910721	0.13498162	4.751
MOLW	17	2.14411765	0.04019309	0.02746324	7.729
UDL	17	14.31470588	0.12476188	0.26461397	3.594
PALW	17	7.21764706	0.09470748	0.15248162	5.410
OCD	17	6.96764706	0.09643853	0.15810662	5.707
SKD	17	18.40000000	0.18776941	0.59937500	4.208
MANL	17	18.27647059	0.14259399	0.34566176	3.217
MAND	17	14.27647059	0.16466977	0.46097426	4.756
FEL	17	33.47058824	0.35394465	2.12970588	4.360
FMW	17	2.37647059	0.03590163	0.02191176	6.229
FDW	17	5.57647059	0.09106373	0.14097426	6.733
FPW	17	7.11176471	0.10497981	0.18735294	6.086
HUL	17	26.62352941	0.28866827	1.41659926	4.471
HMW	17	2.55882353	0.07404233	0.09319853	11.931
HPW	17	5.17647059	0.06259076	0.06659926	4.985
HDW	17	6.82058824	0.09004276	0.13783088	5.443
RPW	17	1.98235294	0.05250021	0.04685662	10.920
UPW	17	3.06764706	0.05090020	0.04404412	6.841
TPW	17	5.18235294	0.06077641	0.06279412	4.835
FIW	17	1.80294118	0.03334054	0.01889706	7.625
SCL	17	21.92647059	0.37443874	2.38347426	7.041
SCW	17	3.62352941	0.07302770	0.09066176	8.310
PEVL	17	13.16176471	0.24380295	1.01047794	7.637
SACW	17	11.55294118	0.14886029	0.37670956	5.313
BDYL	17	189.94117647	2.16501357	79.68382353	4.700
TL	17	112.41176471	2.71983296	125.75735294	9.976
HFL	17	39.52941176	0.50815155	4.38970588	5.300

SPECIES=MEXICANUS LOCATION=KERMIT

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	11	44.76363636	0.56729385	3.54004545	4.203
BASL	11	39.35454545	0.57288959	3.61022727	4.828
ZYB	11	27.17272727	0.19275086	0.40868182	2.353
ROSL	11	17.45909091	0.27599557	0.83790909	5.243
NASL	11	15.45909091	0.24613542	0.66640909	5.281
PMXB	11	9.54545455	0.07460641	0.06122727	2.592
IOB	11	10.45454545	0.23649472	0.61522727	7.503
POB	11	12.98636364	0.12704525	0.17754545	3.245
PPL	11	15.26818182	0.25255717	0.70163636	5.486
BAT	11	12.17272727	0.11527904	0.14618182	3.141
TRL	11	8.80909091	0.07828218	0.06740909	2.947
BCB	11	19.59090909	0.18486090	0.37590909	3.130
BUL	11	9.67272727	0.15290574	0.25718182	5.243
BUD	11	8.00909091	0.09789098	0.10540909	4.054
MOLW	11	2.20454545	0.02734838	0.00822727	4.114
UDL	11	14.36363636	0.25540439	0.71754545	5.897
PALW	11	7.23636364	0.09344199	0.09604545	4.283
OCD	11	6.91363636	0.12882174	0.18254545	6.180
SKD	11	18.91818182	0.16324448	0.29313636	2.862
MANL	11	18.97272727	0.16724555	0.30768182	2.924
MAND	11	15.12272727	0.19474501	0.41718182	4.271
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TFW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	11	195.00000000	4.86919818	260.80000000	8.282
TL	11	122.45454545	2.75140835	83.27272727	7.452
HFL	11	37.63636364	0.49124568	2.65454545	4.329

SPECIES=MEXICANUS LOCATION=MUNDAY

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	14	44.69642857	0.36311625	1.84594780	3.040
BASL	14	39.38571429	0.41692980	2.43362637	3.961
ZYB	14	26.68571429	0.30442833	1.29747253	4.268
ROSL	14	17.57857143	0.20345331	0.57950549	4.331
NASL	14	15.30714286	0.19448842	0.52956044	4.754
PMXB	14	9.95357143	0.12518824	0.21940934	4.706
IOB	14	10.24642857	0.15312355	0.32825549	5.592
POB	14	12.78571429	0.22141085	0.68631868	6.479
PPL	14	15.00357143	0.15049956	0.31710165	3.753
BAT	14	11.98928571	0.13819664	0.26737637	4.313
TRL	14	8.85357143	0.08161560	0.09325549	3.449
BCB	14	19.49285714	0.14814393	0.30725275	2.844
BUL	14	9.57857143	0.07462623	0.07796703	2.915
BUD	14	7.92142857	0.09885530	0.13681319	4.669
MOLW	14	2.36071429	0.03363450	0.01583791	5.331
UDL	14	14.55357143	0.22686736	0.72056319	5.833
PALW	14	7.42142857	0.13431903	0.25253242	6.772
OCD	14	7.01785714	0.15214647	0.32407967	8.112
SKD	14	18.61071429	0.19966853	0.55814560	4.014
MANL	14	18.82142857	0.14701371	0.30258242	2.923
MAND	14	14.63214286	0.13172640	0.24292582	3.368
FEL	14	34.83928571	0.48759836	3.32853022	5.237
FMW	14	2.62142857	0.04852616	0.03296703	6.926
FDW	14	5.97857143	0.09885530	0.13681319	6.187
FPW	14	7.64285714	0.11671525	0.19071429	5.714
HUL	14	27.31071429	0.39718026	2.20853022	5.441
HMW	14	2.60000000	0.08941200	0.11192308	12.867
HPW	14	5.35357143	0.08603990	0.10364011	6.013
HDW	14	6.99285714	0.12826582	0.23032967	6.863
RPW	14	2.18571429	0.02938405	0.01208791	5.030
UPW	14	3.25642857	0.05647724	0.04465549	6.489
TPW	14	5.41428571	0.08490922	0.10093407	5.868
FIW	13	1.74615385	0.06341296	0.05227564	13.094
SCL	14	22.00357143	0.65541834	6.01402473	11.145
SCW	14	3.91071429	0.07132548	0.07122253	6.824
PEVL	14	13.81785714	0.25085607	0.88100275	6.793
SACW	14	11.48214286	0.29025411	1.17944429	9.458
BDYL	13	186.33461538	6.19505434	498.92307692	11.984
TL	13	126.23076923	6.27587347	512.02564103	17.926
HFL	13	43.00000000	0.42365927	2.33333333	3.552

SPECIES=MEXICANUS LOCATION=NEW BRAUNFELS

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	5	41.85000000	0.53525695	1.43250000	2.860
BASL	5	36.90000000	0.64865245	2.10375000	3.931
ZYB	5	24.71000000	0.55551778	1.54300000	5.027
ROSL	5	16.00000000	0.40957295	0.83875000	5.724
NASL	5	13.89000000	0.37060761	0.68675000	5.966
PMXB	5	9.33000000	0.28133610	0.39575000	6.743
IOB	5	9.90000000	0.25544080	0.32625000	5.770
POB	5	13.22000000	0.16015617	0.12825000	2.709
PPL	5	14.19000000	0.13453624	0.09050000	2.120
BAT	5	11.54000000	0.17421251	0.15175000	3.376
TRL	5	8.25000000	0.09082951	0.04125000	2.462
BCB	5	18.53000000	0.15937377	0.12700000	1.923
BUL	5	9.06000000	0.06964194	0.02425000	1.719
BUB	5	7.24000000	0.19646883	0.19300000	6.068
MOLW	5	2.25000000	0.05244044	0.01375000	5.212
UDL	5	13.31000000	0.33443953	0.55925000	5.619
PALW	5	7.18000000	0.25377155	0.32200000	7.903
OCD	5	6.07000000	0.16628289	0.13825000	6.125
SKD	5	17.28000000	0.08602325	0.03700000	1.113
MANL	5	17.97000000	0.25475478	0.32450000	3.170
MAND	5	13.83000000	0.23537205	0.27700000	3.306
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TPW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	5	174.60000000	3.84187454	73.80000000	4.920
TL	5	109.60000000	2.92574777	42.80000000	5.969
HFL	5	40.20000000	0.37416574	0.70000000	2.081

SPECIES=MEXICANUS LOCATION=PECOS

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	8	43.86875000	0.34133895	0.93209821	2.201
BASL	8	38.72500000	0.28831406	0.66500000	2.106
ZYB	8	26.55000000	0.22951813	0.42142857	2.445
ROSL	8	16.93750000	0.18582586	0.27625000	3.103
NASL	8	15.05625000	0.21264438	0.36174107	3.995
PMXB	8	9.23125000	0.19841729	0.31495536	6.079
IOB	8	10.45000000	0.16502164	0.21785714	4.467
POB	8	13.05000000	0.24275208	0.47142857	5.261
PPL	8	15.23750000	0.18340772	0.26910714	3.404
BAT	8	11.83125000	0.13293980	0.14138393	3.178
TRL	8	8.62500000	0.12500000	0.12500000	4.099
BCB	8	19.28750000	0.23636949	0.44696429	3.466
BUL	8	9.35625000	0.07223319	0.04174107	2.184
BUB	8	7.60625000	0.09422499	0.07102679	3.504
MOLW	8	2.25625000	0.03712611	0.01102679	4.654
UDL	8	13.85625000	0.15219745	0.18531250	3.107
PALW	8	7.21875000	0.14636595	0.17138393	5.735
OCD	8	6.51875000	0.18075672	0.26138393	7.843
SKD	8	18.47500000	0.18968960	0.28785714	2.904
MANL	8	13.35625000	0.17150528	0.23531250	2.643
MAND	8	14.18750000	0.13152607	0.13839286	2.622
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TFW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	8	185.00000000	4.02669663	129.71428571	6.156
TL	7	125.14285714	4.99251140	174.47619048	10.555
HFL	8	42.50000000	0.50000000	2.00000000	3.328

SPECIES=MEXICANUS LOCATION=RANGER

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	17	44.13823529	0.48710447	4.03360294	4.550
BASL	17	39.14705882	0.48744288	4.03920956	5.134
ZYB	17	26.44411765	0.28270887	1.35871324	4.408
ROSL	17	17.32352941	0.25928060	1.14284926	6.171
NASL	17	15.15294118	0.22127100	0.83233456	6.021
PMXB	17	9.77647059	0.09462753	0.15222426	3.991
IOB	17	10.16470588	0.19943692	0.67617647	8.090
POB	17	12.69705882	0.12685901	0.27353456	4.119
PPL	17	14.97352941	0.22430930	0.85534926	6.177
BAT	17	12.07058824	0.11679378	0.23189338	3.989
TRL	17	8.65000000	0.07058058	0.08468750	3.364
BCB	17	19.19705882	0.18798812	0.60077206	4.038
BUL	17	9.40000000	0.11139160	0.21093750	4.886
BUB	17	7.63235294	0.11022547	0.20654412	5.955
MOLW	17	2.24117647	0.02719594	0.01257353	5.003
UDL	17	14.58823529	0.24118768	0.98891544	6.817
PALW	17	7.44705882	0.06607018	0.07420956	3.658
OCD	17	7.32941176	0.13680028	0.31814338	7.696
SKD	17	18.38823529	0.13982193	0.33235294	3.135
MANL	17	18.25294118	0.20653259	0.72514706	4.665
MAND	17	13.73235294	0.20445143	0.71060662	6.139
FEL	17	34.24411765	0.68830678	8.05402574	8.287
FMW	17	2.42647059	0.05988924	0.06097426	10.176
FDW	17	5.94705882	0.11411992	0.22139706	7.912
FPW	17	7.50882353	0.16439703	0.45944853	9.027
HUL	17	26.52352941	0.47383987	3.81691176	7.366
HMW	17	2.50588235	0.09012678	0.13808824	14.829
HPW	17	5.28235294	0.07287948	0.09029412	5.689
HDW	17	6.99705882	0.09358766	0.14889706	5.515
RPW	17	2.10588235	0.02707640	0.01246324	5.301
UPW	17	3.10000000	0.06431197	0.07031250	8.554
TPW	17	5.60588235	0.09595518	0.15652574	7.057
FIW	17	1.87058824	0.04518321	0.03470588	9.959
SCL	17	21.33529412	0.46216730	3.63117647	8.932
SCW	17	3.63529412	0.09555995	0.15523897	10.838
PEVL	17	13.03823529	0.37932626	2.44610294	11.996
SACW	17	11.80294118	0.42094673	3.01233456	14.705
BDYL	16	192.56250000	4.59883460	338.39533333	9.553
TL	14	115.00000000	2.09918875	61.69230769	6.830
HFL	16	41.87500000	0.61829739	6.11666667	5.906

SPECIES=MEXICANUS LOCATION=ROSWELL

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	16	43.87812500	0.34299443	1.88232292	3.127
BASL	16	38.39062500	0.39222174	2.46140625	4.087
ZYB	16	26.46562500	0.27863951	1.24223958	4.211
ROSL	16	16.91562500	0.18324157	0.53723958	4.333
NASL	16	15.32812500	0.16482116	0.43465625	4.301
PMXB	16	9.64062500	0.08993270	0.12940625	3.731
IOB	16	9.73437500	0.24663226	0.97323958	10.134
POB	16	13.06875000	0.15922174	0.40562500	4.873
PPL	16	14.99062500	0.15911335	0.40507292	4.246
BAT	16	11.61562500	0.12116782	0.23490625	4.173
TRL	16	8.27812500	0.09842179	0.15498958	4.756
BCB	16	19.15312500	0.15834224	0.40115625	3.307
BUL	16	9.18125000	0.11936246	0.22795833	5.200
BUB	16	7.28125000	0.09206825	0.13562500	5.058
MOLW	16	2.13125000	0.03760402	0.02262500	7.058
UDL	16	14.15000000	0.22615445	0.81833333	6.393
PALW	16	6.83125000	0.10061012	0.16195833	5.891
OCD	16	6.95000000	0.15718835	0.39533333	9.047
SKD	16	18.58125000	0.12143886	0.23595833	2.614
MANL	16	18.28750000	0.17721809	0.50250000	3.876
MAND	16	14.12812500	0.18455852	0.54493958	5.225
FEL	16	33.88437500	0.47065377	3.54423958	5.556
FMW	16	2.45937500	0.05366151	0.04607292	8.728
FDW	16	5.65000000	0.09884753	0.15633333	6.998
FPW	16	7.24687500	0.13137643	0.27615625	7.251
HUL	16	26.83750000	0.38628843	2.38750000	5.757
HMW	16	2.81562500	0.06657057	0.07090625	9.457
HPW	16	5.07500000	0.08253787	0.10900000	6.505
HDW	16	6.84062500	0.11116980	0.19773958	6.501
RPW	16	2.05937500	0.04163801	0.02773958	8.088
UPW	16	3.09062500	0.05366151	0.04607292	6.945
TPW	16	5.16875000	0.08112169	0.10529167	6.278
FIW	15	1.81333333	0.05105242	0.03909524	10.904
SCL	16	21.43125000	0.44557722	3.17662500	8.316
SCW	16	3.84375000	0.04955531	0.03929167	5.157
PEVL	16	13.44062500	0.30765304	1.51440625	9.156
SACW	16	11.33125000	0.26148116	1.09395833	9.230
BDYL	15	184.40000000	2.94344592	130.40000000	6.193
TL	14	115.07142857	2.87173472	115.45604396	9.338
HFL	15	40.53333333	0.67518369	6.83809524	6.451

SPECIES=MEXICANUS LOCATION=SEYMOUR

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	19	42.90789474	0.40784097	3.16035088	4.143
BASL	19	37.78421053	0.37067294	2.61057018	4.276
ZYB	19	25.71315789	0.25734366	1.25828947	4.362
ROSL	19	16.82368421	0.17886780	0.60788012	4.634
NASL	19	14.77631579	0.19313391	0.70371345	5.697
PMXB	19	10.55263158	0.13341410	0.33818713	5.511
IOB	19	10.01052632	0.11707816	0.26043860	5.098
POB	19	12.18157895	0.07677319	0.11200292	2.747
PPL	19	14.76315789	0.18695944	0.66412281	5.520
BAT	19	11.63684211	0.10201494	0.19773392	3.821
TRL	19	8.23421053	0.08464344	0.13612573	4.481
BCB	19	18.80000000	0.15351629	0.44777778	3.559
BUL	19	9.10000000	0.09474496	0.17055556	4.538
BUB	19	7.56578947	0.08254475	0.12945906	4.756
MOLW	19	2.08684211	0.03603972	0.02467836	7.528
UDL	19	13.77631579	0.18230843	0.63149123	5.768
PALW	19	7.04736842	0.08773246	0.14624269	5.426
OCD	19	6.61842105	0.11083221	0.23339181	7.299
SKD	19	17.74736842	0.17907632	0.60929825	4.398
MANL	19	17.79210526	0.15858766	0.47785088	3.885
MAND	19	13.78421053	0.17975180	0.61390351	5.684
FEL	19	32.78157895	0.39232793	2.92450292	5.217
FMW	19	2.39473684	0.04221477	0.03385965	7.684
FDW	19	5.38947368	0.08016603	0.12210526	6.484
FPW	19	7.01578947	0.09072907	0.15640351	5.637
HUL	19	25.66842105	0.26842105	1.36894737	4.558
HMW	19	2.81052632	0.07690837	0.11238304	11.923
HPW	19	5.02894737	0.05964267	0.06758772	5.170
HDW	19	6.73157895	0.08653538	0.14228070	5.603
RPW	19	2.02631579	0.03573956	0.02426901	7.688
UPW	19	2.96052632	0.05856208	0.06516082	8.622
TPW	19	5.03421053	0.08652254	0.14223684	7.492
FIW	19	1.80000000	0.03726780	0.02638389	9.025
SCL	19	21.47105263	0.35964805	2.45758772	7.301
SCW	19	3.63421053	0.04867433	0.04501462	5.838
PEVL	19	13.22368421	0.18000846	0.61565789	5.934
SACW	19	11.17368421	0.17173727	0.56038012	6.700
BDYL	19	183.52631579	1.99174968	75.37426901	4.731
TL	17	111.70588235	2.31803147	91.34558824	8.556
HFL	19	39.21052632	0.57010796	6.17543860	6.335

SPECIES=MEXICANUS LOCATION=SHEFFIELD

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	16	41.73750000	0.32782427	1.71950000	3.142
BASL	16	36.90000000	0.34610933	1.91666667	3.752
ZYB	16	24.72187500	0.26731570	1.14332292	4.325
ROSL	16	15.69062500	0.25715668	1.05807292	6.556
NASL	16	13.73437500	0.27144362	1.17390625	7.906
PMXB	16	8.82500000	0.09287088	0.13800000	4.209
IOB	16	9.22500000	0.14874475	0.35400000	6.450
POB	16	13.07500000	0.11858541	0.22500000	3.628
PPL	16	14.39375000	0.12448854	0.24795833	3.460
BAT	16	11.38437500	0.10284685	0.16923958	3.614
TRL	16	8.32500000	0.08190442	0.10733333	3.935
BCB	16	18.83125000	0.10703144	0.18329167	2.273
BUL	16	9.27187500	0.09387145	0.14098958	4.050
BUB	16	7.35625000	0.04445855	0.03162500	2.417
MOLW	16	2.11250000	0.03430865	0.01883333	6.496
UDL	16	13.15937500	0.19386232	0.63273958	6.045
PALW	16	7.17812500	0.09735767	0.15165625	5.425
OCD	16	6.51562500	0.11829683	0.22390625	7.262
SKD	16	17.90937500	0.10706439	0.18340625	2.391
MANL	16	17.60625000	0.15691525	0.39395833	3.565
MAND	16	13.35000000	0.17865236	0.51066667	5.353
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TFW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	16	170.81250000	3.35437370	180.02916667	7.855
TL	16	123.06250000	2.15922199	74.59583333	7.013
HFL	16	40.87500000	0.31457643	1.58333333	3.078

SPECIES=MEXICANUS   LOCATION=SNYDER

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	17	44.87352941	0.42128824	3.01722426	3.871
BASL	17	40.00294118	0.45557153	3.52827206	4.696
ZYB	17	27.35882353	0.26624552	1.20507353	4.012
ROSL	17	17.21764706	0.20273594	0.69873162	4.855
NASL	17	15.03823529	0.18813761	0.60172794	5.158
PMXB	17	9.95000000	0.10752907	0.19656250	4.456
IOB	17	10.46764706	0.21234602	0.76654412	8.364
POB	17	12.73823529	0.18343783	0.57204044	5.938
PPL	17	15.34705882	0.17312390	0.50952206	4.651
BAT	17	12.21764706	0.08806970	0.13185662	2.972
TRL	17	8.66176471	0.09270540	0.14610294	4.413
BCB	17	19.37058824	0.18525910	0.58345588	3.943
BUL	17	9.52058824	0.10872412	0.20095588	4.709
BUB	17	7.68529412	0.10143861	0.17492647	5.442
MOLW	17	2.27941176	0.03404658	0.01970588	6.159
UDL	17	14.96470588	0.26609115	1.20367647	7.331
PALW	17	7.33529412	0.08475361	0.12211397	4.764
OCD	17	7.21176471	0.11250240	0.21516544	6.432
SKD	17	18.55882353	0.19503183	0.64663603	4.333
MANL	17	18.76470583	0.17051849	0.49430147	3.747
MAND	17	14.28235294	0.18629225	0.53998162	5.378
FEL	16	34.93750000	0.39648192	2.51516667	4.539
FMW	16	2.47812500	0.05203539	0.04332292	8.399
FDW	16	5.99687500	0.10200784	0.16648958	6.804
FPW	16	7.64062500	0.13580154	0.29507292	7.109
HUL	17	27.90588235	0.31239358	1.65902574	4.616
HMW	17	2.69411765	0.08961543	0.13652574	13.715
HPW	17	5.35294118	0.06998826	0.08327206	5.391
HDW	17	7.08235294	0.08817400	0.13216912	5.133
RPW	17	2.16470588	0.03114385	0.01648897	5.932
UPW	17	3.20294118	0.04607191	0.03608456	5.931
TPW	17	5.60294118	0.08590678	0.12545956	6.322
FIW	17	1.90882353	0.03327561	0.01882353	7.188
SCL	17	22.27647059	0.39360975	2.63378676	7.285
SCW	17	3.81176471	0.07025811	0.08391544	7.600
PEVL	17	13.93823529	0.21028383	0.75172794	6.220
SACW	17	11.87352941	0.26936464	1.23347426	9.354
BDYL	16	191.18750000	3.17833650	161.62916667	6.650
TL	16	114.18750000	2.78869556	124.42916667	9.769
HFL	16	41.75000000	0.42323084	2.86666667	4.055

SPECIES=TRIDECEMLINEATUS LOCATION=DENTON

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	16	40.17500000	0.24824383	0.98600000	2.472
BASL	16	34.70000000	0.23197521	0.86100000	2.674
ZYB	16	23.15937500	0.20862740	0.69640625	3.603
ROSL	16	15.59687500	0.16108155	0.41515625	4.131
NASL	16	13.47187500	0.16182351	0.41893958	4.805
PMXB	16	9.27500000	0.09082951	0.13200000	3.917
IOB	16	8.81250000	0.12661457	0.25650000	5.747
FOB	16	12.57812500	0.11465244	0.21032292	3.646
PPL	16	13.18437500	0.15510203	0.38490625	4.706
BAT	16	10.90000000	0.06373774	0.06500000	2.339
TRL	16	7.71875000	0.06596637	0.06962500	3.419
BCB	16	17.41250000	0.10863739	0.18883333	2.496
BUL	16	8.52500000	0.08152198	0.10633333	3.825
BUB	16	6.92812500	0.06291011	0.06332292	3.632
MOLW	16	1.92187500	0.02456656	0.00965625	5.113
UDL	16	12.85625000	0.10427078	0.17395833	3.244
PALW	16	6.68437500	0.08584370	0.11790625	5.137
OCD	16	6.07500000	0.12306841	0.24233333	8.103
SKD	16	17.05937500	0.09652491	0.14907292	2.263
MANL	16	16.65937500	0.10136760	0.16440625	2.434
MAND	16	12.57187500	0.15538720	0.38632292	4.944
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TPW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	16	165.62500000	1.91240468	58.51666667	4.619
TL	16	82.87500000	1.88165486	56.65000000	9.082
HFL	16	34.06250000	0.44223627	3.12916667	5.193

SPECIES=TRIDECEMLINEATUS LOCATION=GRUVER

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	8	38.49375000	0.25327101	0.51316964	1.861
BASL	8	33.61250000	0.28469125	0.64839286	2.396
ZYB	8	22.82500000	0.25997939	0.54071429	3.222
ROSL	8	15.01875000	0.15865999	0.20138393	2.988
NASL	8	12.93750000	0.18726175	0.28053571	4.094
PMXB	8	8.60625000	0.10833047	0.09388393	3.560
IOB	8	8.06875000	0.17241393	0.23781250	6.044
POB	8	11.73125000	0.34225323	0.93709821	8.252
PPL	8	13.06250000	0.19882467	0.31625000	4.305
BAT	8	10.45625000	0.07345887	0.04316964	1.987
TRL	8	7.38750000	0.08059489	0.05196429	3.086
BCB	8	17.11875000	0.16954179	0.22995536	2.801
BUL	8	8.26250000	0.18267604	0.26696429	6.253
BUB	8	6.80625000	0.12079997	0.11674107	5.020
MOLW	8	1.93125000	0.03398726	0.00924107	4.978
UDL	8	12.46250000	0.17971952	0.25839286	4.079
PALW	8	6.28750000	0.14600330	0.17053571	6.568
OCD	8	5.42500000	0.12210944	0.11928571	6.366
SKD	8	16.56875000	0.17111439	0.23424107	2.921
MANL	8	15.99375000	0.08835677	0.06245536	1.563
MAND	7	12.19285714	0.13819783	0.13369048	2.999
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TPW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	8	155.12500000	2.83118791	64.12500000	5.162
TL	7	86.42857143	2.38903390	39.95238095	7.313
HFL	8	32.25000000	0.31339159	0.78571429	2.749

SPECIES=TRIDECEMLINEATUS LOCATION=HILLSBORO

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	16	40.01562500	0.33806184	1.82857292	3.379
BASL	16	35.03437500	0.41635113	2.77357292	4.754
ZYB	16	23.19375000	0.25128317	1.01029167	4.334
ROSL	16	15.50000000	0.19055839	0.58100000	4.918
NASL	16	13.46875000	0.17811952	0.50762500	5.290
PMXB	16	9.68437500	0.13012164	0.27090625	5.374
IOB	16	8.60937500	0.18930893	0.57340625	8.795
POB	16	12.47187500	0.12058613	0.23265625	3.867
PPL	16	13.38750000	0.17809759	0.50750000	5.321
BAT	16	10.92812500	0.08611629	0.11865625	3.152
TRL	16	7.70937500	0.06195071	0.06140625	3.214
BCB	16	17.10625000	0.10326695	0.17062500	2.415
BUL	16	8.10000000	0.08660254	0.12000000	4.277
BUB	16	6.43750000	0.10282469	0.16916667	6.389
MOLW	16	1.92812500	0.02885623	0.01332292	5.986
UDL	16	12.89062500	0.21297588	0.72573958	6.609
PALW	16	6.70312500	0.09224839	0.13615625	5.505
OCD	16	5.80312500	0.10968409	0.19248958	7.560
SKD	16	16.95312500	0.07394660	0.08748958	1.745
MANL	16	16.65000000	0.15227442	0.37100000	3.653
MAND	16	12.20312500	0.13161408	0.27715625	4.314
FEL	16	28.11875000	0.44475824	3.16495333	6.327
FMW	16	1.97187500	0.03290414	0.01732292	6.675
FDW	16	4.78125000	0.06018634	0.05795833	5.035
FPW	16	6.14375000	0.08658750	0.11995833	5.637
HUL	16	23.00625000	0.30611392	1.49929167	5.322
HMW	16	2.16250000	0.05293471	0.04483333	9.791
HPW	16	4.39375000	0.03923089	0.02462500	3.572
HDW	16	5.91875000	0.06706263	0.07195833	4.532
RPW	16	1.85312500	0.02756385	0.01215625	5.950
UPW	16	2.66250000	0.03579455	0.02050000	5.378
TPW	16	4.45312500	0.05799942	0.05382292	5.210
FIW	16	1.53125000	0.04515598	0.03262500	11.796
SCL	16	17.89062500	0.36954980	2.18507292	8.262
SCW	16	3.26250000	0.04069705	0.02650000	4.990
PEVL	16	10.83437500	0.19799615	0.62723958	7.276
SACW	16	9.90312500	0.23204116	0.86148958	9.372
BDYL	16	161.62500000	3.62155008	209.85000000	8.963
TL	16	89.87500000	1.99138771	63.45000000	8.863
HFL	16	33.81250000	0.26170515	1.09533333	3.096

SPECIES=TRIDECEMLINEATUS LOCATION=HOBBS-NORTH

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	18	39.27222222	0.26340599	1.24888389	2.846
BASL	18	34.32500000	0.28754795	1.48830382	3.554
ZYB	17	23.56470588	0.16763738	0.47773897	2.933
ROSL	18	15.07222222	0.14891883	0.39918301	4.192
NASL	18	13.30000000	0.12413097	0.27735294	3.960
FMXB	18	9.29444444	0.07647129	0.10526144	3.491
IOB	18	8.52222222	0.12288835	0.27183007	6.118
POB	18	12.16944444	0.10440767	0.19621732	3.640
PPL	18	13.15000000	0.15328644	0.42294118	4.946
BAT	18	10.74166667	0.04905146	0.04330882	1.937
TRL	18	7.51111111	0.05416562	0.05281046	3.060
BCB	17	17.56764706	0.10413696	0.18435662	2.444
BUL	18	8.56944444	0.04750970	0.04062908	2.352
BUB	18	6.90555556	0.06870522	0.08496732	4.221
MOLW	18	1.91944444	0.02946663	0.01562908	6.513
UDL	18	12.58333333	0.14411093	0.37382353	4.859
PALW	18	6.40833333	0.06213127	0.06948529	4.113
OCD	18	5.63888889	0.14866264	0.39781046	11.185
SKD	18	17.14166667	0.07799049	0.10948529	1.930
MANL	18	16.86111111	0.09789914	0.17251634	2.463
MAND	18	12.40555556	0.09478983	0.16173203	3.242
FEL	18	28.44444444	0.28098476	1.42114379	4.191
FMW	18	2.01666667	0.02681332	0.01294118	5.641
FDW	18	4.85000000	0.06076850	0.06647059	5.316
FPW	18	6.41666667	0.05871722	0.06205882	3.882
HUL	18	22.81944444	0.19445495	0.68062908	3.615
HMW	18	2.13333333	0.05081043	0.04647059	10.105
HPW	18	4.51944444	0.02592690	0.01209967	2.434
HDW	18	6.16944444	0.05002269	0.04504085	3.440
RPW	18	1.89166667	0.01819017	0.00595588	4.080
UPW	18	2.54444444	0.03521384	0.02232026	5.872
TPW	18	4.39722222	0.05460378	0.05366830	5.268
FIW	18	1.50833333	0.02596189	0.01213235	7.303
SCL	18	17.76666667	0.32315338	1.87970588	7.717
SCW	18	3.23333333	0.05716620	0.05882353	7.501
PEVL	18	11.12500000	0.12282420	0.27154412	4.684
SACW	18	9.13611111	0.18689951	0.62876634	8.679
BDYL	18	159.44444444	2.67061255	128.37908497	7.106
TL	18	84.44444444	1.29660749	30.26143791	6.514
HFL	18	34.94444444	0.20567476	0.76143791	2.497

SPECIES=TRIDECEMLINEATUS LOCATION=LEVELLAND

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	14	39.93571429	0.33403250	1.56208791	3.130
BASL	14	35.05000000	0.25832299	0.93423077	2.758
ZYB	14	23.62857143	0.18580936	0.48335165	2.942
ROSL	15	15.50000000	0.16980381	0.43250000	4.243
NASL	15	13.34333333	0.19699327	0.58209524	5.718
PMXB	14	9.35714286	0.07629057	0.08148352	3.051
IOB	14	8.41785714	0.14244790	0.28407967	6.332
PCB	14	12.02500000	0.15107218	0.31951923	4.701
PPL	14	13.46428571	0.17172593	0.41285714	4.772
BAT	15	10.98333333	0.10450184	0.16380952	3.685
TRL	15	7.46666667	0.05641400	0.04773810	2.926
BCB	14	17.37500000	0.13132357	0.24144231	2.823
BUL	14	8.45714286	0.09562650	0.12802198	4.231
BUB	14	6.91428571	0.05066280	0.03593407	2.742
MOLW	15	1.93333333	0.03297426	0.01630952	6.606
UDL	15	12.95000000	0.16917165	0.42928571	5.059
PALW	14	6.75714286	0.07428360	0.07725275	4.113
OCD	14	6.10357143	0.11062563	0.17133242	6.782
SKD	14	16.92142857	0.12422444	0.21604396	2.747
MANL	15	16.50333333	0.13205939	0.26159524	3.099
MAND	15	12.04333333	0.16292466	0.39816667	5.239
FEL	15	28.58666667	0.33038458	1.63730952	4.476
FMW	15	2.11333333	0.04537323	0.03088095	8.315
FDW	15	4.94666667	0.08287493	0.10302381	6.489
FPW	15	6.33000000	0.05429198	0.04421429	3.322
HUL	15	23.04000000	0.19689253	0.58150000	3.310
HMW	15	2.31333333	0.04717411	0.03338095	7.893
HPW	15	4.45666667	0.04078593	0.02495238	3.544
HDW	15	6.09333333	0.08740528	0.11459524	5.556
RPW	15	1.83333333	0.02745348	0.01130952	5.801
UPW	15	2.65000000	0.04705620	0.03321429	6.877
TPW	15	4.52333333	0.06340848	0.06030952	5.429
FIW	15	1.48000000	0.03408672	0.01742857	8.920
SCL	15	18.30666667	0.36170452	1.96245238	7.652
SCW	15	3.16000000	0.08269278	0.10257143	10.135
PEVL	14	11.16785714	0.21576640	0.65177198	7.229
SACW	15	9.93666667	0.28185046	1.19159524	10.936
BDYL	15	161.53333333	3.62381891	196.98095238	8.689
TL	14	82.57142857	1.40920945	27.80219780	6.386
HFL	15	33.93333333	0.39601186	2.35238095	4.520

SPECIES=TRIDECEMLINEATUS LOCATION=LEWISVILLE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	7	39.55714286	0.58273050	2.37702381	3.898
BASL	7	34.42142857	0.54367107	2.06904762	4.179
ZYB	7	23.39285714	0.26377041	0.48702381	2.983
ROSL	7	15.32857143	0.23473824	0.38571429	4.052
NASL	7	13.10714286	0.15638345	0.17119048	3.157
PMXB	7	9.37142857	0.09184429	0.05904762	2.593
IOB	7	8.60000000	0.09940293	0.06916667	3.058
POB	7	12.56428571	0.16822402	0.19809524	3.542
PPL	7	12.82857143	0.32693693	0.74821429	6.743
BAT	7	10.96428571	0.13527498	0.12809524	3.264
TRL	7	7.55714286	0.07190319	0.03619048	2.517
DCB	7	17.58571429	0.10449099	0.07642857	1.572
BUL	7	8.24285714	0.13470805	0.12702381	4.324
DUB	7	6.73571429	0.06335302	0.02809524	2.488
MOLW	7	1.95000000	0.03086067	0.00666667	4.187
UDL	7	12.67857143	0.23901015	0.39988095	4.988
PALW	7	6.95714286	0.10202041	0.07285714	3.880
OCD	7	6.24285714	0.19161860	0.25702381	8.121
SKD	7	16.72142857	0.15463365	0.16738095	2.447
MANL	7	16.52857143	0.25445019	0.45321429	4.073
MAND	7	12.62142857	0.20926662	0.30654762	4.387
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TPW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	7	161.14285714	2.44392903	41.80952381	4.013
TL	4	88.25000000	1.65201897	10.91666667	3.744
HFL	7	33.85714286	1.05624157	7.80952381	8.254

SPECIES=TRIDECEMLINEATUS LOCATION=LOVINGTON

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	15	39.97333333	0.26235502	1.03245238	2.542
BASL	15	35.00000000	0.27641411	1.14607143	3.059
ZYB	15	23.89000000	0.18278272	0.50114286	2.963
ROSL	15	15.49666667	0.16536156	0.41016667	4.133
NASL	15	13.36000000	0.13113061	0.25792857	3.801
PMXB	15	9.73000000	0.12778330	0.24492857	5.086
IOB	15	8.53666667	0.09056262	0.12302381	4.109
POB	15	12.71666667	0.16609426	0.41380952	5.059
PPL	15	13.33666667	0.14560765	0.31802381	4.228
BAT	15	10.57333333	0.09950672	0.14852381	3.645
TRL	15	7.51000000	0.05122313	0.03935714	2.642
BCB	15	17.64666667	0.13985253	0.29338095	3.069
BUL	15	8.65000000	0.08864053	0.11785714	3.969
BUB	15	7.18333333	0.09520237	0.13595238	5.133
MOLW	15	1.91333333	0.03104017	0.01445238	6.283
UDL	15	12.93000000	0.14790602	0.32814286	4.430
PALW	15	6.66333333	0.08301845	0.10338095	4.825
OCD	15	6.06333333	0.11099836	0.18480952	7.090
SKD	15	17.19333333	0.13980145	0.29316667	3.149
MANL	15	16.56000000	0.13444772	0.27114286	3.144
MAND	15	12.29333333	0.14115735	0.29888095	4.447
FEL	13	29.70000000	0.35355339	1.62500000	4.292
FMW	13	2.22307692	0.05083135	0.03358974	8.244
FDW	13	4.94615385	0.08329338	0.09019231	6.072
FPW	13	6.28076923	0.07327907	0.06980769	4.207
HUL	14	23.71785714	0.26979882	1.01907967	4.256
HMW	14	2.30714286	0.06688869	0.06263736	10.848
HPW	14	4.52857143	0.04708955	0.03104396	3.891
HDW	14	6.25714286	0.06086762	0.05186813	3.640
RPW	14	1.92500000	0.02269603	0.00721154	4.411
UPW	14	2.74642857	0.04845534	0.03287088	6.601
TPW	14	4.62500000	0.04796691	0.03221154	3.881
FIW	14	1.53571429	0.02058791	0.00593407	5.016
SCL	14	19.00357143	0.32885350	1.51402473	6.475
SCW	14	3.23214286	0.04877824	0.03331044	5.647
PEVL	15	11.57666667	0.17278301	0.44780952	5.780
SACW	14	10.73571429	0.15076987	0.31824176	5.255
BDYL	15	164.73333333	3.50844785	184.63809524	8.249
TL	12	86.50000000	1.40615530	23.72727273	5.631
HFL	15	35.80000000	0.22253946	0.74285714	2.408

SPECIES=TRIDECEMLINEATUS   LOCATION=LUBBOCK

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	15	39.44000000	0.43646851	2.85757143	4.286
BASL	15	34.03000000	0.44069210	2.91314286	5.016
ZYB	14	23.59642857	0.33816182	1.60094780	5.362
ROSL	15	15.22000000	0.25805131	0.99885714	6.567
NASL	15	13.36333333	0.27431589	1.12873810	7.950
PMXB	15	9.73000000	0.18662414	0.52242857	7.428
IOB	15	8.16333333	0.18057228	0.48909524	8.567
POB	15	12.11333333	0.17296206	0.44873810	5.530
PPL	15	13.28333333	0.25145608	0.94845238	7.332
BAT	15	10.97000000	0.09609024	0.13850000	3.392
TRL	15	7.69000000	0.16541434	0.41042857	8.331
BCB	15	17.67333333	0.13765612	0.28423810	3.017
BUL	15	9.14333333	0.17028454	0.43495238	7.213
BUB	15	7.18333333	0.10149674	0.15452381	5.472
MOLW	15	1.96333333	0.01419814	0.00302381	2.801
UDL	15	12.53000000	0.24450144	0.89671429	7.557
PALW	15	6.63333333	0.11879020	0.21166667	6.936
OCD	15	5.83000000	0.13343449	0.26707143	8.864
SKD	15	17.21666667	0.14397972	0.31095238	3.239
MANL	15	16.16666667	0.15838971	0.37630952	3.794
MAND	15	12.31333333	0.21058121	0.66516667	6.624
FEL	15	28.01333333	0.64391782	6.21945238	8.902
FMW	15	2.06666667	0.04013865	0.02416667	7.522
FDW	15	4.92333333	0.14815265	0.32923810	11.655
FPW	15	6.06666667	0.11899046	0.21233095	7.596
HUL	15	22.28333333	0.31921282	1.52845238	5.548
HMW	15	2.28666667	0.07691471	0.08873810	13.027
HPW	15	4.52333333	0.07557189	0.08566667	6.471
HDW	15	6.07000000	0.08671244	0.11278571	5.533
RPW	15	1.91000000	0.03015831	0.01364286	6.115
UPW	15	2.61000000	0.05736267	0.04935714	8.512
TPW	15	4.46666667	0.09032569	0.12238095	7.832
FIW	15	1.55000000	0.06305704	0.05964286	15.756
SCL	15	17.76000000	0.47479820	3.38150000	10.354
SCW	15	3.21333333	0.09617279	0.13873810	11.592
PEVL	15	11.34666667	0.21594017	0.69945238	7.371
SACW	15	9.97333333	0.32300179	1.56495238	12.543
BDYL	13	155.53846154	4.71714737	289.26923077	10.935
TL	12	87.41666667	2.15483366	55.71969697	8.539
HFL	13	34.15384615	0.42132504	2.30769231	4.448

SPECIES=TRIDECEMLINEATUS LOCATION=MATADOR

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	19	39.35263158	0.23670724	1.06457602	2.622
BASL	19	34.21052632	0.24910891	1.17904971	3.174
ZYB	18	23.19722222	0.21770011	0.85308007	3.982
ROSL	19	15.44473684	0.15582711	0.46135965	4.398
NASL	19	13.58684211	0.19771510	0.74273392	6.343
PMXB	19	8.94473684	0.07750634	0.11413743	3.777
IOB	19	8.40526316	0.07636619	0.11080409	3.960
POB	19	12.24210526	0.10473185	0.20840643	3.729
PPL	19	12.99473684	0.08137117	0.12580409	2.729
BAT	19	10.53684211	0.08118657	0.12523392	3.359
TRL	19	7.57105263	0.05988730	0.06814327	3.448
BCB	17	17.42647059	0.11890413	0.24034926	2.813
BUL	19	8.29210526	0.08220847	0.12840643	4.321
BUB	19	6.83157895	0.05699730	0.06172515	3.637
MOLW	19	1.99736842	0.02145091	0.00874269	4.681
UDL	19	12.77368421	0.12648928	0.30399123	4.316
PALW	19	6.38421053	0.08685982	0.14334795	5.930
OCD	18	5.73055556	0.08633221	0.13415850	6.392
SKD	19	17.17368421	0.14884391	0.42093567	3.778
MANL	19	16.49473684	0.12965850	0.31941520	3.426
MAND	19	12.32368421	0.11978101	0.27260234	4.237
FEL	19	28.65526316	0.31381203	1.87108187	4.774
FMW	19	2.15526316	0.03417677	0.02219298	6.912
FDW	19	4.83157895	0.06096333	0.07061404	5.500
FPW	19	6.32631579	0.07258474	0.10010234	5.001
HUL	18	23.04166667	0.37643516	2.55066176	6.931
HMW	18	2.17777778	0.03944513	0.02800654	7.685
HPW	19	4.44210526	0.04718124	0.04229532	4.630
HDW	19	6.05526316	0.07111217	0.09608187	5.119
RPW	19	1.87894737	0.02516489	0.01203216	5.838
UPW	19	2.61315789	0.02907997	0.01606725	4.851
TPW	19	4.43947368	0.04128402	0.03238304	4.053
FIW	19	1.50526316	0.02807018	0.01497076	8.128
SCL	19	17.74736842	0.23060668	1.01040936	5.664
SCW	19	3.17105263	0.05233101	0.05203216	7.193
PEVL	19	11.02105263	0.13541769	0.34842105	5.356
SACW	19	9.72631579	0.21141989	0.84926901	9.475
BDYL	19	164.21052632	2.25505144	96.61988304	5.986
TL	17	83.41176471	1.52445464	39.50735294	7.535
HFL	19	34.52631579	0.26894228	1.37426901	3.395

SPECIES=TRIDECEMLINEATUS LOCATION=NORMAN

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	17	40.30000000	0.37271362	2.36156250	3.813
BASL	17	35.28823529	0.33031651	1.85485294	3.859
ZYB	17	23.69705882	0.20971228	0.74764706	3.649
ROSL	17	15.55588235	0.22613612	0.86933824	5.994
NASL	17	13.62352941	0.17926103	0.54623676	5.425
PMXB	17	8.66176471	0.08957923	0.13641544	4.264
IOB	17	8.66764706	0.12276990	0.25623162	5.840
POB	17	12.07352941	0.16168447	0.44441176	5.522
PPL	17	13.64705882	0.11200632	0.21327206	3.334
BAT	17	10.80000000	0.10684307	0.19406250	4.079
TRL	17	7.83235294	0.10008647	0.17029412	5.269
BCB	17	17.35588235	0.11228594	0.21433824	2.667
BUL	17	8.22058824	0.06403394	0.06970588	3.212
BUB	17	6.59117647	0.06969409	0.08257353	4.360
MOLW	17	1.95294118	0.02922736	0.01452206	6.171
UDL	17	13.05588235	0.18727351	0.59621324	5.914
PALW	17	6.42647059	0.06698843	0.07628676	4.298
OCD	17	6.06764706	0.07313128	0.09091912	4.969
SKD	17	16.93235294	0.15302953	0.39810662	3.726
MANL	17	16.60000000	0.15164539	0.39093750	3.767
MAND	17	12.34117647	0.12942430	0.28476103	4.324
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TPW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	17	166.29411765	3.00461007	153.47058824	7.450
TL	15	89.46666667	1.90704625	54.55238095	8.256
HFL	17	33.58823529	0.46224217	3.63235294	5.674

SPECIES=TRIDECEMLINEATUS   LOCATION=PARIS

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	10	38.93500000	0.42183791	1.77947222	3.426
BASL	10	34.26000000	0.41397799	1.71377778	3.821
ZYB	10	23.07500000	0.39484526	1.55902778	5.411
ROSL	10	14.96500000	0.29824021	0.88947222	6.302
NASL	10	12.69000000	0.24080882	0.57988889	6.001
PMXB	10	8.76500000	0.13885444	0.19280556	5.010
IOB	10	8.94000000	0.15434449	0.23822222	5.460
POB	10	12.02500000	0.17276349	0.29847222	4.543
PPL	10	12.64500000	0.21543883	0.46413889	5.383
BAT	10	10.95500000	0.09558301	0.09136111	2.759
TRL	10	7.94000000	0.05953524	0.03544444	2.371
BCB	10	17.33500000	0.13479408	0.18169444	2.459
BUL	10	8.03500000	0.06057594	0.03669444	2.384
BUB	10	6.68000000	0.11527744	0.13288889	5.457
MOLW	10	1.97000000	0.04027682	0.01622222	6.465
UDL	10	12.07000000	0.24417662	0.59622222	6.397
PALW	10	6.98000000	0.09723963	0.09455556	4.405
OCD	10	5.63000000	0.12521093	0.15677778	7.033
SKD	10	16.65000000	0.11055416	0.12222222	2.100
MANL	10	16.36500000	0.17528548	0.30725000	3.387
MAND	10	12.42000000	0.20939065	0.43844444	5.331
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TPW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	10	157.60000000	3.71244154	137.82222222	7.449
TL	10	91.20000000	2.73170683	74.62222222	9.472
HFL	10	35.50000000	0.37267800	1.38888889	3.320

SPECIES=TRIDECEMLINEATUS LOCATION=PLAINVIEW

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	16	40.27812500	0.26020700	1.08332292	2.584
BASL	16	35.48437500	0.22600326	0.81723958	2.548
ZYB	16	24.06875000	0.18285211	0.53495833	3.039
ROSL	16	15.48750000	0.14828885	0.35183333	3.830
NASL	16	13.72500000	0.21539692	0.74233333	6.278
PMXB	16	9.32500000	0.07799573	0.09733333	3.346
IOB	16	8.82812500	0.12877376	0.26532292	5.835
POB	16	11.98437500	0.12956005	0.26857292	4.324
PPL	16	13.85625000	0.16354631	0.42795833	4.721
BAT	16	10.86250000	0.07806247	0.09750000	2.875
TRL	16	7.72500000	0.05322906	0.04533333	2.756
BCB	16	17.51562500	0.11714652	0.21957292	2.675
BUL	16	8.45625000	0.07039694	0.07929167	3.330
BUB	16	7.19375000	0.04934466	0.03895833	2.744
MOLW	16	1.99375000	0.02695482	0.01162500	5.408
UDL	16	12.99687500	0.10767125	0.18548958	3.314
PALW	16	6.41562500	0.10865837	0.18890625	6.775
OCD	16	6.34062500	0.11539955	0.21307292	7.280
SKD	16	17.09687500	0.13256042	0.28115625	3.101
MANL	16	16.85625000	0.09605500	0.14762500	2.279
MAND	16	12.76250000	0.10844545	0.18816667	3.399
FEL	16	29.58750000	0.22250936	0.79216667	3.008
FMW	16	2.13437500	0.03218396	0.01657292	6.032
FDW	16	5.09375000	0.06452955	0.06662500	5.067
FPW	16	6.55312500	0.05233481	0.04382292	3.194
HUL	16	23.90312500	0.16262615	0.42315625	2.721
HMW	16	2.59062500	0.11070030	0.19607292	17.092
HPW	16	4.67187500	0.04280984	0.02932292	3.665
HDW	16	6.31562500	0.07849031	0.09857292	4.971
RPW	16	1.93750000	0.02393568	0.00916667	4.942
UPW	16	2.86250000	0.04170831	0.02783333	5.828
TPW	16	4.60625000	0.04180186	0.02795833	3.630
FIW	16	1.55000000	0.01369306	0.00300000	3.534
SCL	16	19.64062500	0.28530754	1.30240625	5.811
SCW	16	3.33750000	0.04621057	0.03416667	5.533
PEVL	16	11.96562500	0.13012164	0.27090625	4.350
SACW	16	10.83750000	0.25151624	1.01216667	9.283
BDYL	16	169.87500000	1.61728940	41.85000000	3.808
TL	15	90.80000000	1.81842423	49.60000000	7.756
HFL	16	35.18750000	0.26170515	1.09583333	2.975

SPECIES=TRIDECEMLINEATUS LOCATION=PORTALES

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	31	38.86451613	0.25296302	1.98369892	3.624
BASL	31	33.95645161	0.26702001	2.21029032	4.378
ZYB	31	23.43709677	0.21477630	1.42999462	5.102
ROSL	31	14.86290323	0.16487153	0.84266129	6.176
NASL	31	13.14516129	0.19511996	1.18022581	8.265
PMXB	31	8.86290323	0.07633992	0.18066129	4.796
IOB	31	8.28387097	0.09255591	0.26556452	6.221
POB	31	12.08548387	0.07822608	0.18969892	3.604
PPL	31	13.08064516	0.14373432	0.64044624	6.118
BAT	31	10.73225806	0.06782125	0.14259140	3.518
TRL	31	7.68387097	0.04937170	0.07556452	3.577
BCB	31	17.53870968	0.10217289	0.32361828	3.244
BUL	31	8.49838710	0.04833151	0.07241398	3.166
BUB	31	6.75645161	0.04403945	0.06012366	3.629
MOLW	31	1.93387097	0.02026532	0.01273118	5.835
UDL	31	12.37580645	0.14208265	0.62581183	6.392
PALW	31	6.74516129	0.06351508	0.12505914	5.243
OCD	31	5.79516129	0.07366572	0.16822581	7.078
SKD	31	16.89838710	0.08225596	0.20974731	2.710
MANL	31	16.40483871	0.11762330	0.42889247	3.992
MAND	31	12.08709677	0.10803643	0.36182796	4.977
FEL	16	27.78125000	0.54405643	4.73595833	7.833
FMW	16	1.95312500	0.03337562	0.01782292	6.835
FDW	16	4.98437500	0.10435504	0.17423958	8.375
FPW	16	6.04687500	0.13840375	0.30648958	9.155
HUL	16	22.33437500	0.40663043	2.64557292	7.283
HMW	16	2.47500000	0.09128709	0.13333333	14.753
HPW	16	4.42187500	0.08967171	0.12865625	8.112
HDW	16	6.08437500	0.10028280	0.16090625	6.593
RPW	16	1.77812500	0.03534613	0.01998958	7.951
UPW	16	2.59687500	0.03274547	0.01715625	5.044
TPW	16	4.47500000	0.07500000	0.09000000	6.704
FIW	16	1.46875000	0.03647916	0.02129167	9.935
SCL	16	17.07812500	0.43277132	2.99665625	10.136
SCW	16	3.20312500	0.07077970	0.08015625	8.839
PEVL	16	10.60000000	0.22794371	0.83133333	8.602
SACW	16	9.31875000	0.24676553	0.97429167	10.592
BDYL	31	160.38709677	2.10154957	136.91182796	7.295
TL	28	86.00000000	1.81920967	92.66666667	11.193
HFL	31	33.51612903	0.30363733	2.85806452	5.044

SPECIES=TRIDECEMLINEATUS LOCATION=TAHOKA

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	18	40.20000000	0.34638658	2.15970588	3.656
BASL	18	35.28888889	0.31076954	1.73839869	3.736
ZYB	18	24.10000000	0.23115227	0.96176471	4.069
ROSL	18	15.76111111	0.17299531	0.53869281	4.657
NASL	18	13.66388889	0.18518696	0.61729575	5.750
PMXB	18	9.39722222	0.08842044	0.14072712	3.992
IOB	18	8.90833333	0.13904730	0.34801471	6.622
POB	18	12.03055556	0.13352553	0.32092320	4.709
PPL	18	13.56666667	0.13117119	0.30970588	4.102
BAT	18	11.06666667	0.08938790	0.14382353	3.427
TRL	18	7.41111111	0.06574803	0.07781046	3.764
BCB	18	17.73611111	0.12159114	0.26611928	2.900
BUL	18	8.41111111	0.08120373	0.11869281	4.096
BUB	18	7.01944444	0.07026315	0.08886438	4.247
MOLW	18	2.01111111	0.02410338	0.01045752	5.085
UDL	18	13.39722222	0.14034692	0.35455065	4.445
PALW	18	6.52777778	0.07882120	0.11183007	5.123
OCD	18	5.93888889	0.10729560	0.20722222	7.665
SKD	18	17.18333333	0.12025300	0.26029412	2.969
MANL	18	16.54166667	0.12394984	0.27654412	3.179
MAND	18	12.66111111	0.11169780	0.22457516	3.743
FEL	18	29.41944444	0.21765006	0.85268791	3.139
FMW	18	2.28333333	0.04884282	0.04294118	9.075
FDW	18	4.91666667	0.05571871	0.05588235	4.808
FPW	18	6.38333333	0.08650815	0.13470588	5.750
HUL	18	23.25833333	0.24635413	1.09242647	4.494
HMW	18	2.41944444	0.07400085	0.09857026	12.976
HPW	18	4.58888889	0.05340613	0.05133987	4.938
HDW	18	6.20833333	0.08756417	0.13801471	5.984
RPW	18	1.89444444	0.03635538	0.02379085	8.142
UPW	18	2.73611111	0.04098572	0.03023693	6.355
TPW	18	4.52777778	0.06874484	0.08506536	6.442
FIW	18	1.56111111	0.02443999	0.01075163	6.642
SCL	18	19.15277778	0.31924831	1.83455065	7.072
SCW	18	3.30000000	0.05176619	0.04823529	6.655
PEVL	18	11.76944444	0.15483171	0.43151144	5.581
SACW	18	10.05000000	0.19938631	0.71558824	8.417
BDYL	17	172.64705882	2.49697048	105.99264706	5.963
TL	16	80.87500000	1.79089131	51.31666667	3.858
HFL	17	35.23529412	0.25043215	1.06617647	2.930

SPECIES=TRIDECEMLINEATUS   LOCATION=VERNON

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	17	38.37352941	0.35084241	2.09253676	3.770
BASL	17	33.47352941	0.30980063	1.63159926	3.816
ZYB	17	22.74411765	0.23258784	0.91965074	4.216
ROSL	17	14.61764706	0.18285628	0.56841912	5.158
NASL	17	12.86470588	0.24054796	0.98367647	7.710
PMXB	17	8.96176471	0.08264130	0.11610294	3.802
IOB	17	8.42058824	0.10370515	0.18283088	5.078
POB	17	12.02352941	0.11545288	0.22659926	3.959
PPL	17	12.86470588	0.14512702	0.35805147	4.651
BAT	17	10.61176471	0.06146637	0.06422794	2.388
TRL	17	7.75000000	0.07847349	0.10468750	4.175
BCB	17	16.87647059	0.14201269	0.34284926	3.470
BUL	17	8.18235294	0.08279817	0.11654412	4.172
BUB	17	6.77058824	0.06860731	0.08001838	4.178
MOLW	17	1.92352941	0.02815322	0.01347426	6.035
UDL	17	12.17941176	0.18446359	0.57845588	6.245
PALW	17	6.68529412	0.07926184	0.10680147	4.888
OCD	17	5.76470588	0.07926184	0.10680147	5.669
SKD	17	16.43823529	0.13064668	0.29016544	3.277
MANL	17	16.02941176	0.11820182	0.23751838	3.040
MAND	17	11.69705882	0.16033459	0.43702206	5.652
FEL	17	27.34705882	0.40532917	2.79295956	6.111
FMW	17	1.97941176	0.03788014	0.02439338	7.890
FDW	17	4.46470588	0.06802961	0.07867647	6.282
FPW	17	6.00294118	0.09109935	0.14108456	6.257
HUL	17	22.03823529	0.28896778	1.41954044	5.406
HMW	17	2.22941176	0.05941795	0.06001838	10.939
HPW	17	4.14705882	0.05823232	0.05764706	5.790
HDW	17	5.75294118	0.07711129	0.10108456	5.527
RPW	17	1.72352941	0.02782484	0.01316176	6.656
UPW	17	2.49411765	0.04615398	0.03621324	7.630
TPW	17	4.15882353	0.05527925	0.05194853	5.480
FIW	17	1.40000000	0.04200840	0.03000000	12.372
SCL	17	17.12058824	0.44844623	3.41876838	10.800
SCW	17	3.11764706	0.06832303	0.07935662	9.036
PEVL	17	10.63235294	0.18205027	0.56341912	7.060
SACW	17	9.10588235	0.20641737	0.72433824	9.346
BDYL	17	157.00000000	2.47487373	104.12500000	6.499
TL	13	87.84615385	2.11480178	58.14102564	8.680
HFL	17	34.05882353	0.30281265	1.55882353	3.666

SPECIES=TRIDECEMLINEATUS LOCATION=WACO

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	15	41.56333333	0.26001221	1.01409524	2.423
BASL	15	36.42000000	0.27506709	1.13492857	2.925
ZYB	15	23.98000000	0.18424880	0.50921429	2.976
ROSL	15	16.12333333	0.16710894	0.41888095	4.014
NASL	15	13.64666667	0.13570510	0.27623810	3.851
PMXB	15	9.59333333	0.11940992	0.21383095	4.821
IOB	15	9.00666667	0.10463846	0.16423810	4.500
POB	15	12.04666667	0.16913412	0.42909524	5.438
PPL	15	13.79333333	0.12657265	0.24030952	3.554
BAT	15	11.21000000	0.13364844	0.26792857	4.617
TRL	15	7.71000000	0.06271629	0.05900000	3.150
BCB	15	17.78666667	0.10298713	0.15909524	2.243
BUL	15	8.73666667	0.08829963	0.11695238	3.914
BUB	15	7.24333333	0.07971178	0.09530952	4.262
MOLW	15	2.13666667	0.03253813	0.01588095	5.898
UDL	15	13.59000000	0.16593910	0.41328571	4.730
PALW	15	6.73333333	0.11491888	0.19809524	6.610
OCD	15	6.30666667	0.09781745	0.14352381	6.007
SKD	15	17.07000000	0.09496867	0.13528571	2.155
MANL	15	16.99000000	0.12865606	0.24828571	2.933
MAND	15	12.69000000	0.12268815	0.22578571	3.744
FEL	14	30.33928571	0.31558330	1.39429945	3.892
FMW	14	2.13214286	0.03380907	0.01600275	5.933
FDW	14	5.01071429	0.07562534	0.08006868	5.647
FPW	14	6.49642857	0.07835259	0.08594780	4.513
HUL	14	24.40714286	0.26534537	0.98571429	4.068
HMW	14	2.38571429	0.06680062	0.06247253	10.477
HPW	14	4.65714286	0.05856741	0.04802198	4.705
HDW	14	6.23571429	0.05482955	0.04208791	3.290
RPW	14	1.96785714	0.03038541	0.01292582	5.777
UPW	14	2.75714286	0.04713120	0.03109890	6.396
TPW	14	4.63928571	0.07113263	0.07083791	5.737
FIW	14	1.66428571	0.02590588	0.00939560	5.824
SCL	14	19.21071429	0.29441591	1.21353022	5.734
SCW	14	3.46785714	0.06259216	0.05484890	6.753
PEVL	14	11.63928571	0.11965823	0.20045330	3.847
SACW	14	10.50357143	0.16545511	0.38325549	5.894
BDYL	15	170.06666667	2.01297379	60.78095238	4.584
TL	14	88.78571429	2.99849517	125.87362637	12.636
HFL	15	34.80000000	0.45981363	3.17142857	5.117

SPECIES=TRIDECEMLINEATUS LOCATION=WICHITA FALLS

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
GLS	14	38.45000000	0.43253660	2.61923077	4.209
BASL	14	33.58214286	0.41092923	2.36407967	4.578
ZYB	14	23.12142857	0.24660966	0.85142857	3.991
ROSL	14	14.94642857	0.21702688	0.65940934	5.433
NASL	14	13.10000000	0.30278016	1.28346154	8.648
PMXB	14	8.85357143	0.09024757	0.11402473	3.814
IOB	14	8.61428571	0.14271971	0.28516484	6.199
POB	14	12.60714286	0.14753655	0.30494505	4.380
PPL	14	12.69285714	0.20047040	0.56263736	5.910
BAT	14	10.57500000	0.11516233	0.18567308	4.075
TRL	14	7.57142857	0.05992539	0.05027473	2.961
BCB	14	17.22857143	0.12565371	0.22104396	2.729
BUL	14	7.96785714	0.10451446	0.15292582	4.908
BUB	14	6.55357143	0.08603990	0.10364011	4.912
MOLW	14	2.03214286	0.01785714	0.00446429	3.288
UDL	14	12.47142857	0.28447534	1.13296703	8.535
PALW	14	6.56071429	0.07247178	0.07353022	4.133
OCD	14	5.23214286	0.18793317	0.49446429	13.440
SKD	14	16.95357143	0.11074973	0.17171703	2.444
MANL	14	15.93571429	0.19218442	0.51708791	4.512
MAND	14	11.27142857	0.22266581	0.69412088	7.392
FEL	0	.	.	.	.
FMW	0	.	.	.	.
FDW	0	.	.	.	.
FPW	0	.	.	.	.
HUL	0	.	.	.	.
HMW	0	.	.	.	.
HPW	0	.	.	.	.
HDW	0	.	.	.	.
RPW	0	.	.	.	.
UPW	0	.	.	.	.
TPW	0	.	.	.	.
FIW	0	.	.	.	.
SCL	0	.	.	.	.
SCW	0	.	.	.	.
PEVL	0	.	.	.	.
SACW	0	.	.	.	.
BDYL	14	161.42857143	3.87966562	210.72527473	8.992
TL	13	92.53846154	2.56603897	85.60256410	9.998
HFL	14	33.35714286	0.70013455	6.86263736	7.853

Appendix III. Results of SS-STP (sums of squares-simultaneous test procedure) tests for 38 cranial, skeletal, and external characters of *S. mexicanus* and *S. tridecemlineatus* from 33 (for cranial and external measures) or 23 (for skeletal measures) localities. Locality abbreviations are as in Table 1 of section III. Nonsignificant subsets of localities are indicated by vertical columns of I's.

ZYB

```
SNY  I
KER  II
ART  II
ABI  II
BIG  II
MUN  II
AND  III
PEC  IIII
KEN  IIII
ROS  IIII
RAN  IIII
AUS  IIII
HOM  IIIII
SEY   IIIII
SHE    IIIII
NEW     IIIII
TAH      IIII
PLA       III
WAC       III
LOV       III
NOR       III
LEV        II
LUB        II
HOT        II
POR        II
LEW        II
MAT        II
HIL        II
DEN        II
WIC        II
PAR        II
GRU         I
VER         I
```

NAS

```
AND  I
BIG  I
ART  I
KER  II
ROS  III
MUN  III
ABI  III
RAN  III
PER  IIII
SNY  IIII
KEN  IIIII
SEY  IIIIII
HOM  IIIIIII
AUS   IIIIIII
NEW    IIIIIII
SHE     IIIIII
PLA      IIIII
TAH       IIII
WAC       IIII
NOR        III
MAT        III
DEN        III
HIL        III
LUB         II
LOV         II
LEV         II
HOT         II
POR         II
LEW         II
WIC         II
GRU         II
VER         II
PAR          I
```

IOB

```
AUS  I
AND  II
KEN  III
SNY  III
ABI  III
KER  III
PEC  III
ART  IIII
BIG  IIII
MUN  IIII
RAN  IIIII
SEY   IIII
HOM   IIIII
NEW   IIIIII
ROS    IIIIII
SHW     IIIIII
WAC      IIIIII
PAR       IIIII
TAH        IIII
PLA        IIII
DEN        IIII
NOR        IIII
WIC        IIII
HIL         III
LEW         III
LOV          II
HOT          II
VER          II
LEV          II
MAT          II
POR          II
LUB           I
GRU           I
```

GLS		BAS		OCD	
AND	I	AND	I	RAN	I
ART	I	SNY	I	SNY	II
SNY	II	ART	II	ART	II
KER	II	ABI	III	ABI	III
ABI	II	MUN	IIII	MUN	III
BIG	III	KER	IIII	KEN	III
MUN	IIII	RAN	IIII	HOM	IIII
RAN	IIIII	BIG	IIIII	ROS	IIIII
KEN	IIIIII	KEN	IIIII	AND	IIIII
ROS	IIIIII	PEC	IIIII	KER	IIIIII
PEC	IIIIII	ROS	IIIIII	BIG	IIIIIII
SEY	IIIIIII	SEY	IIIIII	SEY	IIIIIIII
HOM	IIIIII	HOM	IIIIII	PEC	IIIIIIIII
AUS	IIIIII	AUS	IIIIII	SHE	IIIIIIII
NEW	IIIIII	NEW	IIIIII	AUS	IIIIIIII
SHE	IIIIII	SHE	IIIIII	PLA	IIIIIIII
WAC	IIIIII	WAC	IIIIIII	WAC	IIIIIIII
NOR	IIIIII	PLA	IIIIIII	LEW	IIIIIIII
PLA	IIIII	TAH	IIIIII	LEV	IIIIIII
TAH	IIIII	NOR	IIIII	DEN	IIIIIIII
DEN	IIII	LEV	IIIII	NEW	IIIIIII
HIL	IIII	HIL	IIII	NOR	IIIIIII
LOV	IIII	LOV	IIII	LOV	IIIIII
LEV	IIII	DEN	IIII	TAH	IIIIII
LEW	IIII	LEW	IIII	LUB	IIIIII
LUB	IIII	HOT	IIII	HIL	IIIII
MAT	IIII	PAR	III	POR	IIII
HOT	III	MAT	II	VER	IIII
PAR	II	LUB	II	MAT	III
POR	II	POR	II	HOT	III
GRU	I	GRU	I	PAR	II
WIC	I	WIC	I	GRU	II
VER	I	VER	I	WIC	I

PMB		BCB		BUB	
SEY	I	KER	I	KER	I
AND	II	ABI	I	MUN	I
ABI	III	MUN	II	AND	II
MUN	IIII	SNY	III	ABI	III
SNY	IIIII	AND	IIII	ART	IIII
KEN	IIIII	PEC	IIII	KEN	IIIII
ART	IIIIII	BIG	IIII	SNY	IIIIII
RAN	IIIIIII	KEN	IIII	RAN	IIIIIII
LUB	IIIIIII	RAN	IIII	PEC	IIIIIIII
LOV	IIIIIII	ART	IIII	SEY	IIIIIIIII
HIL	IIIIIII	ROS	IIII	BIG	IIIIIIIII
HOM	IIIIIII	SHE	IIIII	HOM	IIIIIIIII
ROS	IIIIIIII	SEY	IIIII	SHE	IIIIIIII
BIG	IIIIIIIII	AUS	IIII	AUS	IIIIIIII
WAC	IIIIIIIII	HOM	IIII	ROS	IIIIIIII
KER	IIIIIIIII	NEW	IIII	WAC	IIIIIIII
TAH	IIIIIIIII	WAC	III	NEW	IIIIIIII
LEW	IIIIIIIIII	TAH	III	PLA	IIIIIIII
LEV	IIIIIIIIII	LUB	II	LOV	IIIIIIIII
NEW	IIIIIIIIII	LOV	II	LUB	IIIIIIIII
PLA	IIIIIIIII	LEW	II	TAH	IIIIIIIII
AUS	IIIIIIII	HOT	II	DON	IIIIIIIII
HOT	IIIIIIII	POR	II	LEV	IIIIIIIII
DEN	IIIIIIII	PLA	II	HOT	IIIIIIII
PEC	IIIIIII	MAT	II	MAT	IIIIIII
VER	IIIIII	DEN	II	GRU	IIIIIII
MAT	IIIII	LEV	II	VER	IIIIII
POR	IIII	NOR	II	POR	IIIII
WIC	III	PAR	II	LEW	IIII
SHE	II	WIC	II	PAR	IIII
PAR	II	GRU	II	NOR	III
NOR	I	HIL	II	WIC	II
GRU	I	VER	I	HIL	I

ROS

```
AND I
ART II
MUN II
ABI II
KER III
BIG III
RAN IIII
KEN IIII
SNY IIIII
PEC IIIIII
ROS IIIIIII
SEY IIIIIIII
HOM  IIIIIIII
AUS   IIIIIIII
WAC    IIIIIIII
NEW    IIIIIIIII
TAH     IIIIIIII
SHE      IIIIIII
DEN       IIIIII
NOR        IIIII
LEV         IIII
HIL         IIII
LOV         IIII
PLA         IIII
MAT         IIII
LEW         IIII
LUB          III
HOT          III
GRU          III
PAR          III
WIC           II
POR           II
VER            I
```

POB

```
ART I
AUS II
NEW III
BIG III
KEN III
SHE IIII
ROS IIII
PEC IIIII
KER IIIIII
HOM IIIIII
MUN IIIIII
AND IIIIIII
ABI IIIIIIII
SNY IIIIIIIII
LOV IIIIIIIIII
RAN IIIIIIIIIII
WIC IIIIIIIIIII
DEN IIIIIIIIIII
LEW IIIIIIIIIII
HIL  IIIIIIIIII
MAT   IIIIIIIII
SEY    IIIIIIII
HOT     IIIIIII
LUB      IIIIII
POR       IIIII
NOR        IIII
WAC        IIII
TAH         III
PAR         III
LEV          II
VER          II
PLA          II
GRU           I
```

PPL

```
AND I
SNY II
KER III
ART III
PEC III
KEN III
ABI III
BIG IIII
MUN IIII
ROS IIIII
RAN IIIII
SEY IIIIII
AUS IIIIIII
HOM  IIIIIII
SHE   IIIIIII
NEW   IIIIIIII
PLA    IIIIIIII
WAC     IIIIIIII
NOR      IIIIIII
TAH       IIIIII
LEV        IIIII
HIL        IIIII
LEV         IIII
LUB         IIII
DEN         IIII
HOT         IIII
POR          III
GRU          III
MAT          III
VER          III
LEW           II
WIC            I
PAR            I
```

MAL		BUL		MOL	
KER	I	KER	I	MUN	I
ABI	II	MUN	I	SNY	II
MUN	II	SNY	I	ABI	III
AND	II	ABI	I	PEC	IIII
SNY	III	AND	I	NEW	IIII
BIG	IIII	RAN	I	RAN	IIII
ART	IIII	BIG	II	BIG	IIIII
PEC	IIII	ART	II	AND	IIIII
ROS	IIII	PEC	III	KER	IIIIII
KEN	IIII	KEN	III	ART	IIIIII
RAN	IIII	SHE	III	AUS	IIIIIII
AUS	IIII	ROS	IIII	KEN	IIIIIIII
NEW	IIII	HOM	IIII	WAC	IIIIIIIII
HOM	IIII	LUB	IIIII	ROS	IIIIIIII
SEY	IIIII	SEY	IIIIII	SHE	IIIIIIIII
SHE	IIIII	NEW	IIIIIII	HOM	IIIIIIIII
WAC	IIIII	AUS	IIIIIII	SEY	IIIIIIIII
HOT	IIIII	WAC	IIIIIII	WIC	IIIIIIII
PLA	IIII	LOV	IIIIIII	TAH	IIIIIII
DEN	IIII	HOT	IIIIII	MAT	IIIIII
HIL	III	DEN	IIIIIII	PLA	IIIII
NOR	III	PAR	IIIIII	PAR	IIIII
LOV	III	LEV	IIIIII	LUB	IIII
TAH	III	PLA	IIIII	NOR	III
LEW	III	TAH	IIIII	LEW	III
LEV	III	MAT	IIIII	POR	II
MAT	III	GRU	IIIII	LEV	I
POR	II	LEW	IIIII	GRU	I
PAR	II	NOR	IIII	HIL	I
LUB	II	VER	III	VER	I
VER	II	HIL	II	DEN	I
GRU	II	PAR	II	HOT	I
WIC	I	WIC	I	LOV	I

PAW

```
RAN  I
MUN  II
SNY  III
AUS  III
KER  III
PEC  III
KEN  III
AND  IIII
ABI  IIIII
NEW  IIIIII
SHE  IIIIII
BIG  IIIIIII
SEY  IIIIIIII
ART  IIIIIIIII
HOM  IIIIIIIII
PAR  IIIIIIIIII
LEW  IIIIIIIIII
ROS   IIIIIIIIII
LEV    IIIIIIIIII
POR     IIIIIIIII
WAC      IIIIIIII
HIL       IIIIIII
VER        IIIIII
DEN        IIIIII
LOV        IIIIII
LUB         IIIII
WIC          IIII
TAH          IIII
NOR           III
PLA           III
HOT           III
MAT            II
GRU             I
```

MAD

```
KER  I
AND  II
ART  III
MUN  IIII
ABI  IIII
SNY  IIIII
KEN  IIIII
BIG  IIIII
PEC  IIIIII
ROS  IIIIII
AUS  IIIIII
NEW   IIIIII
SEY    IIIII
RAN    IIIIII
HOM     IIIIII
SHE      IIIIII
PLA       IIIIII
WAC        IIIII
TAH         IIII
LEW          III
DEN          IIII
PAR           III
HOT           III
NOR           III
MAT           III
LUB           III
LOV           III
HIL           III
GRU           III
POR            II
LEV            II
VER            II
WIC             I
```

SKD

```
ART  I
KER  I
AND  I
ABI  II
BIG  III
MUN  III
ROS  IIII
SNY  IIIII
PEC  IIIII
KEN  IIIII
RAN  IIIIII
HOM  IIIIIII
SHE   IIIIIII
AUS    IIIIIII
SEY     IIIIIII
NEW      IIIIIII
LUB       IIIIII
LOV        IIIII
TAH         IIII
MAT         IIII
HOT          III
PLA          III
WAC          III
DEN           II
WIC           II
HIL           II
NOR           II
LEV           II
POR           II
LEW           II
PAR           II
GRU            I
VER            I
```

<u>HFL</u>

```
MUN  I
ABI  II
PEC  II
ART  III
RAN  III
SNY  IIII
AND  IIII
SHE  IIIII
ROS  IIIII
BIG  IIIII
NEW  IIIIII
KEN  IIIIII
AUS   IIIIII
SEY    IIIIII
KER     IIIIII
HOM      IIIIII
LOV       IIIIII
PAR        IIIII
TAH         IIII
PLA          III
HOT          III
WAC          III
MAT          III
LUB          III
DEN           II
VER           II
LEV            I
LEW            I
HIL            I
NOR            I
POR            I
WIC            I
GRU            I
```

<u>UDL</u>

```
SNY  I
AND  I
ART  II
RAN  III
MUN  IIII
ABI  IIIII
KEN  IIIII
KER  IIIIII
BIG  IIIIIII
ROS  IIIIIIII
PEC  IIIIIIIII
AUS  IIIIIIIII
SEY   IIIIIIIII
HOM   IIIIIIIIII
WAC    IIIIIIIIII
NEW    IIIIIIIIIII
TAH     IIIIIIIIIII
SHE      IIIIIIIIII
PLA       IIIIIIIII
LOV        IIIIIIII
NOR         IIIIIII
DEN         IIIIIII
LEW         IIIIIII
LEV          IIIIII
HIL          IIIIII
HOT           IIIII
MAT           IIIII
WIC            IIII
LUB             III
POR             III
GRU             III
VER              II
PAR               I
```

<u>BAT</u>

```
SNY  I
KER  II
RAN  II
AND  III
MUN  III
ABI  III
BIG  IIII
PEC  IIII
ART  IIII
KEN  IIII
HOM  IIII
AUS  IIIII
SEY   IIIII
ROS   IIIIII
NEW   IIIIIII
SHE    IIIIIII
WAC     IIIIIII
TAH      IIIIIII
LEV       IIIIIII
LUB        IIIIII
LEW        IIIIII
PAR        IIIIII
HIL         IIIII
DEN         IIIII
PLA         IIIII
NOR         IIIII
HOT         IIIII
POR          IIII
VER           III
WIC           III
LOV            II
MAT            II
GRU             I
```

<u>TRL</u>

```
ABI  I
MUN  II
KER  III
SNY  IIII
RAN  IIII
PEC  IIIII
BIG  IIIII
ART  IIIII
AND  IIIII
HOM  IIIII
KEN  IIIIII
SHE   IIIII
AUS    IIII
ROS    IIIII
NEW    IIIIII
SEY     IIIIII
PAR      IIIIII
NOR       IIIII
VER        IIII
PLA         III
DEN         III
WAC         III
HIL         III
LUB          II
POR          II
WIC           I
MAT           I
LEW           I
HOT           I
LOV           I
LEV           I
TAH           I
GRU           I
```

UPW		TPW		FIW		FEL	
MUN	I	RAN	I	SNY	I	RAN	I
ART	II	SNY	II	AND	II	ART	II
AND	II	AND	II	ART	II	AND	II
SNY	III	ART	III	RAN	III	SNY	II
BIG	III	BIG	III	ABI	III	MUN	II
ABI	IIII	ABI	IIII	BIG	III	BIG	II
RAN	IIII	MUN	IIII	ROS	IIII	ABI	II
ROS	IIII	KEN	IIIII	KEN	IIII	ROS	II
KEN	IIIII	ROS	IIII	SEY	IIIII	KEN	II
HOM	IIIII	AUS	IIII	MUN	IIIIII	AUS	II
SEY	IIII	HOM	III	HOM	IIIIIII	SEY	II
AUS	IIIII	SEY	IIII	WAC	IIIIIII	HOM	II
PLA	IIIII	WAC	IIII	AUS	IIIIII	WAC	II
WAC	IIIII	LOV	III	TAH	IIIII	LOV	II
LOV	IIII	PLA	II	LUB	IIII	PLA	II
TAH	IIII	TAH	II	PLA	IIII	TAH	II
HIL	III	LEV	II	LOV	III	MAT	II
LEV	III	POR	I	HIL	III	LEV	I
MAT	II	LUB	I	HOT	III	HOT	I
LUB	II	HIL	I	MAT	III	HIL	I
POR	II	MAT	I	LEV	II	LUB	I
HOT	I	HOT	I	POR	II	POR	I
VER	I	VER	I	VER	I	VER	I

<u>FMW</u>

```
MUN  I
ART  II
ABI  II
AND  III
BIG  IIII
SNY  IIII
ROS  IIII
RAN  IIIII
SEY  IIIII
HOM  IIIIII
KEN   IIIIII
AUS   IIIIIII
TAH    IIIIIII
LOV     IIIIIII
MAT      IIIIIII
PLA       IIIIII
WAC        IIIII
LEV         IIII
LUB         IIII
HOT          III
VER           II
HIL           II
POR            I
```

<u>FDW</u>

```
SNY  I
MUN  II
ART  II
RAN  II
BIG  III
ART  III
AND  IIII
ROS  IIIII
KEN  IIIIII
HOM   IIIII
SEY    IIIII
AUS     IIIII
PLA      IIIII
WAC       IIII
POR        III
LEV        III
LOV        III
LUB        III
TAH         II
HOT         II
MAT         II
HIL         II
VER          I
```

<u>RPW</u>

```
MUN  I
ART  II
AND  III
SNY  IIII
RAN  IIIII
BIG  IIIIII
ABI  IIIIIII
HOM  IIIIIIII
ROS  IIIIIIIII
SEY  IIIIIIIIII
AUS   IIIIIIIIII
KEN    IIIIIIIIII
WAC     IIIIIIIII
PLA      IIIIIIII
LOV       IIIIIIII
LUB        IIIIIII
TAH         IIIIII
HOT          IIIII
MAT           IIII
HIL           IIII
LEV            III
POR             II
VER              I
```

SCL		SCW		PEV	
AND	I	AND	I	AND	I
ART	I	ART	II	ABI	I
SNY	II	ABI	II	SNY	II
MUN	II	MUN	III	ART	II
KEN	II	ROS	III	MUN	II
BIG	III	BIG	III	BIG	III
SEY	III	SNY	IIII	ROS	IIII
ABI	III	HOM	IIIII	SEY	IIII
ROS	IIII	RAN	IIIIII	KEN	IIIII
RAN	IIIII	SEY	IIIIIII	RAN	IIIIII
AUS	IIIIII	KEN	IIIIIII	HOM	IIIIII
HOM	IIIIIII	WAC	IIIIIII	AUS	IIIIII
PLA	IIIIIII	AUS	IIIIII	PLA	IIIIII
WAC	IIIIIII	PLA	IIIII	TAH	IIIIII
TAH	IIIIII	TAH	IIII	WAC	IIIII
LOV	IIIII	HIL	III	LOV	IIII
LEV	IIII	HOT	II	LUB	IIII
HIL	III	LOV	II	LEV	IIII
HOT	III	LUB	II	HOT	III
LUB	III	POR	II	MAT	III
MAT	II	MAT	I	HIL	II
VER	II	LEV	I	VER	II
POR	I	VER	I	POR	I

FPW

```
AND  I
MUN  I
SNY  II
ART  III
ABI  IIII
RAN  IIII
BIG  IIIII
ROS  IIIII
KEN  IIIIII
AUS   IIIII
SEY    IIIII
HOM     IIIII
PLA      IIIII
WAC       IIII
HOT        III
TAH         II
LEV         II
MAT         II
LOV         II
HIL          I
LUB          I
POR          I
VER          I
```

HUL

```
SNY  I
ART  II
AND  II
MUN  II
BIG  II
ABI  II
ROS  II
KEN  II
RAN  II
AUS  II
SEY  II
HOM  II
WAC  II
PLA  II
LOV  II
TAH  II
MAT  II
LEV   I
HIL   I
HOT   I
POR   I
LUB   I
VER   I
```

HMW

```
ART  I
ROS  II
BIG  III
SEY  III
HOM  IIII
ABI  IIIII
SNY  IIIIII
AND  IIIIIII
MUN  IIIIIII
PLA  IIIIIIII
KEN  IIIIIIIII
RAN  IIIIIIIIII
POR   IIIIIIIII
TAH    IIIIIIII
WAC     IIIIIII
AUS     IIIIIII
LEV      IIIIII
LOV       IIIII
LUB       IIIII
VER        IIII
MAT         III
HIL          II
HOT           I
```

SAW		HDW		HPW	
AND	I	AND	I	AND	I
ART	I	ABI	I	MUN	I
ABI	II	SNY	I	SNY	II
BIG	II	RAN	I	ABI	II
SNY	III	MUN	I	ART	III
RAN	III	ART	II	RAN	III
KEN	IIII	BIG	II	BIG	III
MUN	IIIII	ROS	II	KEN	IIII
ROS	IIIIII	KEN	II	ROS	IIII
SEY	IIIIIII	AUS	III	SEY	IIIII
AUS	IIIIIIII	HOM	III	AUS	IIII
PLA	IIIIIIIII	SEY	IIII	HOM	IIII
LOV	IIIIIIIIII	PLA	IIII	PLA	IIII
WAC	IIIIIIIII	LOV	III	WAC	III
HOM	IIIIIIII	WAC	II	TAH	III
TAH	IIIIIII	TAH	II	LOV	III
LUB	IIIIIII	HOT	II	LUB	III
LEV	IIIIII	LEV	I	HOT	II
HIL	IIIII	POR	I	LEV	II
MAT	IIII	LUB	I	MAT	II
POR	III	MAT	I	POR	II
HOT	II	HIL	I	HIL	II
VER	I	VER	I	VER	I