SYMPATRY AND HYBRIDIZATION OF THE EASTERN AND SOUTHERN PLAINS WOOD RATS

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CHAPTER I

INTRODUCTION

Two wood rat species of the genus Neotoma Say and Ord are widely distributed throughout the woodlands and grasslands of the eastern, central, and southwestern United States. Neotoma floridana (Ord), the eastern wood rat, ranges from Connecticut in the northeast, southward into Florida, to the southwest as far as southcentral Texas, and northwest into central Colorado and southwest South Dakota. N. micropus Baird, the southern plains wood rat, ranges from southcentral and southwestern Kansas and southeastern Colorado south across western Oklahoma, the western half of Texas, most of New Mexico, and south to central Mexico (Hall and Kelson, 1959).

The generalized distribution map (Fig. 1) by Hall and Kelson (1959), indicates a complete separation of the ranges of the two species. However, preliminary field collections by the writer and reports of other investigators (Finley, 1958; Davis, 1960; Glass, personal communication) have shown the possibility that the two species may be sympatric in certain localities in eastern Colorado, western Oklahoma and central Texas. Furthermore, successful crosses between the two species were made by me in the laboratory in the spring of 1964.

The possibility that these wood rats can and do survive sympatrically and that natural hybrids may exist in regions of sympatry provided the basis for this investigation.

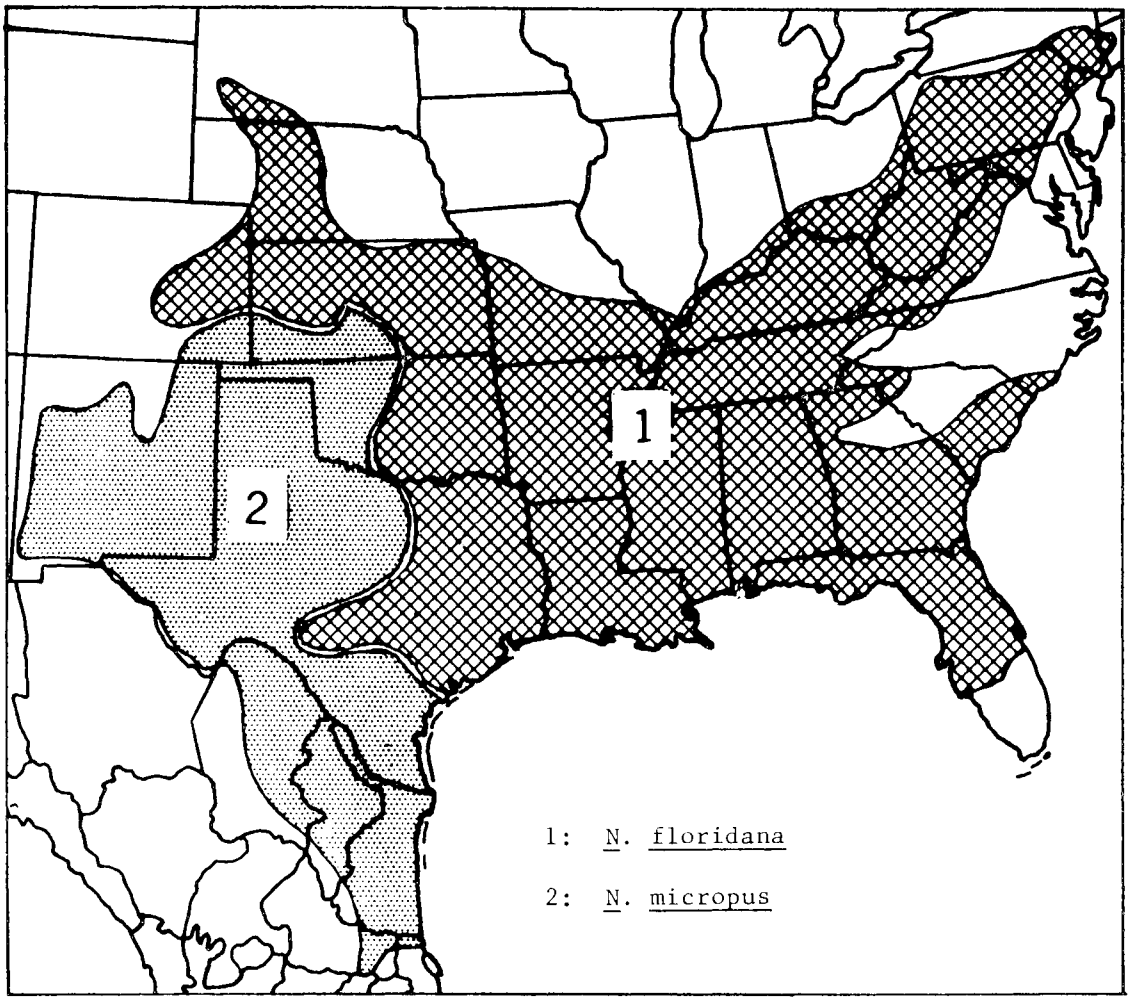

Figure 1. Distribution of the Eastern Wood Rat, N. floridana, and Southern Plains Wood Rat, N. micropus, in North America (After Hall and Kelson, 1959).

In view of the possibility that N. floridana and N. micropus are sympatric in certain localities and that there may be isolating mechanisms that prevent their interbreeding in regions of sympatry, the objectives of this study were to obtain more precise information about the distribution of the two species in Oklahoma and about the ecological, ethological, and taxonomic relationships between the species.

The study was divided into the following phases:

1. Determination of the present distribution of N. floridana and N. micropus in Oklahoma and the location of areas of sympatry and the presence of hybrid populations, if any.
2. Correlation of distribution with ecological factors and an attempt to explain the location of the present range boundaries of the two species.
3. Recording of the reproductive behavior of both species and hybrid offspring.
4. Determination of estrous cycles, gestation periods, and breeding seasons of both species and hybrids.
5. Determination of seasonal and annual reproductive capacities for each species and hybrids.
6. Recording of postnatal development of both species, and hybrids, and information pertaining to the inheritance by hybrids of parental morphological and behavioral characteristics.

Literature Review

Although several studies have been done on the ecology and life histories of wood rats, and others have dealt with taxonomy and reproduction, few have dealt with interspecific relationships. Finley

(1958), in his study of the wood rats of Colorado, speculated on interspecific relationships between N. floridana and N. micropus in eastern Colorado. Davis (1960) referred to the possibility that N. floridana and N. micropus may occur in the same area in Texas, but did not elaborate. Cockrum (1952), Hall (1955), and Hall and Kelson (1959) indicate a complete separation of the ranges of the two species in Kansas and, therefore, did not discuss interspecific relationships. Blair (1939) listed both species as occurring in the mixed-grass plains biotic district of Oklahoma but did not report regions of sympatry.

Studies which concern some aspect of the life history of either N. floridana or N. micropus are numerous, especially for the former. Murphy (1952) studied the ecology and helminth parasites of N. floridana, and Chapman (1951) investigated the estrous cycle of that species. Burt and Barkalow (1942) compared the bacula of wood rats and included N. floridana and N. micropus in their study. Pearson (1952) reported on life history and ecological observations of N. f. floridana. Lay and Baker (1938), and Poole (1936 and 1940) have published on studies of the Attwater wood rat, N. f. attwaterii. Svihla and Svihla (1933) raised N. f. rubida in captivity and described house construction, vocalization, food habits, and some aspects of reproduction for the subspecies. Howell (1926) reported on the anatomy of the genus Neotoma and Goldman (1910) revised the taxonomic status of the genus and of certain species.

A review of the literature yielded few published studies of N. micropus. Feldman (1935) maintained a laboratory colony of N. micropus and reported on reproductive success and some behavioral aspects of caged specimens. Raun (1966a, b) studied N. micropus on the Welder

Wildlife Foundation Refuge. Bailey (1931) discussed the distribution, habitat, and general habits of N. m. canescens in New Mexico.

Mayr (1963:114-117) reviewed the literature pertaining to significant studies of vertebrate hybridizations. He concluded that hybridization among fishes is frequent and cited the reviews by Hubbs (1955, 1961). He contrasted the rarity of hybridization among reptiles with its comparative frequency in amphibians, and estimated the occurrence of hybrids among wild birds to be perhaps one out of 60,000, whereas only a very few genuine hybrid mammals have been reported even though some hybridize readily in captivity.

Blair (1951) discussed intraspecific and interspecific interbreeding of natural populations of vertebrates and speculated on the effects of the breakdown of isolating mechanisms. He said, "Hybrids between sympatric species are rare, and they usually occur where there has been a breakdown of ecological isolation."

Sibley (1954) reviewed the literature on hybridization in his paper on the towhees of Mexico and concluded that the phenomenon of vertebrate hybridization is not as rare as once believed.

McCarley (1954) found hybridization had occurred between sympatric species of Peromyscus leucopus and P. gossypinus in Louisiana.

Most recent authors of hybridization studies are compelled to pass judgment on the comment by Anderson (1953:300) that introgressive hybridization is more important than all other factors combined in providing raw materials for natural selection to work upon.

Taxonomy of the Species

Goldman (1910), in his revision of the genus Neotoma, divided the

genus into the following subgenera: Neotoma, Homodontomys, and Teonoma. The subgenus Neotoma was subdivided into six groups, each of which he considered to be well-marked, yet closely related to each of the other five groups. One group was designated as the floridana group and to this category were assigned the species floridana and micropus. More recent authorities have revised the floridana group until it now is composed of two species and 13 subspecies (Miller and Kellogg, 1955), rather than the two species and 9 subspecies recognized by Goldman. However, the criteria Goldman used to separate the group into two species are still recognized as valid.

Goldman and others (Hall and Kelson, 1959; Finley, 1958; Blair, et al., 1957; and Cockrum, 1952) relying on differences in color, body measurements, and qualitative skull characters and skull descriptions of N. floridana and N. micropus, listed the following as characteristic of the species:

> N. floridana - Upper parts varying from pale cinnamon to buffy gray, sides fairly distinct from back; underparts white or grayish; tail shorter than head and body. External measurements in mm: total length, 310-441; tail length, 129-203; rear foot, 35-46. Skull large, elongated; sphenopalatine vacuities relatively small; palate lacking posterior median spine; first molar with moderately developed anterointernal re-entrant angle.
>
> N. micropus - Upper parts steely to slaty gray, sometimes washed with buff; underparts gray on belly, white on gular and pectoral regions. External measurements in mm: total length, 300-380; tail length, 120-185; rear foot length, 34-41. Skull generally similar to that of N. floridana, but more robust and sculptured; palate usually with posterior median projection; sphenopalatine vacuities large; anterointernal re-entrant angle of first molar shallow.

Except for the presence of a forked anterior palatal spine in N. floridana and an unforked anterior palatal spine in N. micropus, indicated by Finley (1958) as species characters, the ones listed by Hall

and Kelson are usually the same as those listed by other authors as characteristic of the two species.

CHAPTER II

STUDY AREAS

Faunal Areas of Kansas

Several systems have been devised for dividing the state of Kansas into biologically-significant regions. Among the systems are those of Brumwell (1941), Stevens (1948), and Cockrum (1952). Brumwell divided the state into six biotic districts using as a basis for division similarities of vegetation, and amphibian, reptilian and mammalian faunas. Stevens showed the state composed of eight physiographic regions with each region having characteristic surface configurations and geological structures. Cockrum divided the state into two major mammalian distributional areas and subdivided each area into provinces and subcenters on the basis of the presence or absence of certain kinds of mammals in each.

Cockrum's distributional areas and their provinces and subcenters are as follows:

A. Great Plains Distributional Area
   1. Short Grass Plains Provinces
      a. Central High Plains Subcenter
      b. Southern High Plains Subcenter
   2. Mixed Grass Plains Province
      a. Blue Hills Subcenter
      b. Red Hills Subcenter

B. Central Lowland Distributional Area
   1. Tall Grass Province
      a. Kansas River Valley Subcenter
      b. Osage Plains Subcenter
   2. Cherokee Prairie Province

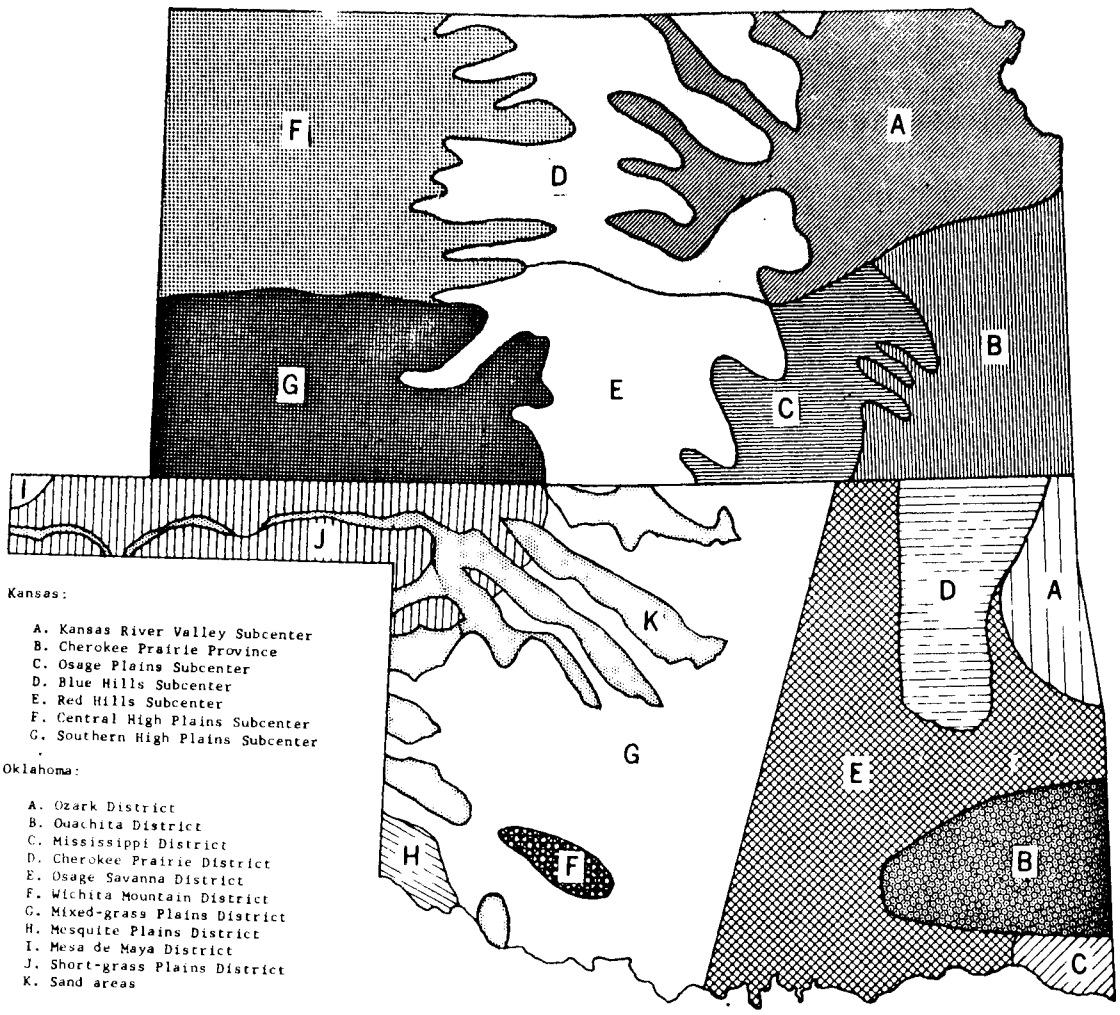

Figure 2 Mammalian Distributionsl Areas and Subdivisions of Kansas (After Cockrum, 1952) and Biotic Districts of Oklahoma (After Blair, 1939).

Figure 2 shows Kansas subcenter boundaries.

Biotic Areas and Districts of Oklahoma

Blair (1939) considered the biotic district to be the most natural geographic unit in mammalian distribution and, after Blair and Hubbell (1938), divided the state of Oklahoma into three major biotic areas, then subdivided each major biotic area into biotic districts.

Blair and Hubbell's major biotic areas and districts of Oklahoma are as follows:

A. Eastern Deciduous Forest Biotic Area
   1. Mississippi Biotic District
   2. Ouachita Biotic District
   3. Ozark Biotic District
   4. Cherokee Prairie Biotic District
   5. Osage Savanna Biotic District

B. Great Plains Grassland Biotic Area
   1. Mixed-grass Plains Biotic District
   2. Short-grass Plains Biotic District
   3. Mesquite Plains Biotic District
   4. Wichita Mountains Biotic District

C. Southern Rocky Mountains Biotic Area
   1. Mesa de Maya Biotic District

In addition to the listed biotic districts, extensive sand areas are recognized as occurring in the Great Plains Grassland Biotic Area. Figure 2 shows Oklahoma biotic district boundaries.

Distribution of Neotoma floridana

The Kansas range of Neotoma floridana, as given by Hall and Kelson (1959), includes all of the Osage Plains, Kansas River Valley, and Blue Hills subcenters plus all of the Cherokee Prairie Province and the eastern portion of the Red Hills Subcenter and all but the extreme southern edge of the Central High Plains Subcenter. The range of the species in Oklahoma includes the entire Eastern Deciduous Forest Biotic

Area plus most of the eastern one-half of the Mixed-grass Plains District and the eastern part of the Wichita Mountains.

The habitat type of N. floridana is listed as rocky bluffs and wooded, rocky ravines, as well as the oak-elm flood plain forest in eastern Oklahoma.

Distribution of N. micropus

Hall and Kelson (1959) gave the Kansas range of N. micropus as the southwest portion of the Red Hills Subcenter and most of the Southern High Plains Subcenter. The range of the species in Oklahoma was given as all of the Short-grass Plains, Wichita Mountains, Mesa de Maya, and Mesquite Plains districts and approximately the west one-half of the Mixed-grass Plains District.

Distribution of both species in Oklahoma as described by Blair (1939) is in general agreement with Hall and Kelson. Blair listed both as occurring in the Mixed-grass District and possibly in the Wichita Mountains District. No reference was made to their occurrence in sand areas that are continuous from the Mixed-grass Plains District into the Short-grass Plains District.

N. micropus habitat is given as rocky canyons and open grassland.

Selection of Primary Study Areas

A review of the literature and personal communication with Glass (1964) seemed to indicate certain areas in Blaine, Dewey, Major and Woodward counties, Oklahoma, as the areas most likely to support sympatric populations of N. floridana and N. micropus. Duck and Fletcher (1943) classified and mapped habitat types in the state of Oklahoma and

show the following types occurring in the four-county region:

1. post oak - blackjack forest
2. stabilized dune
3. tall grass prairie
4. mixed-grass eroded plains
5. sand-sage grassland
6. shinnery oak-grassland
7. shortgrass highplains
8. bottomland (flood plain)

Except for the Shinnery oak-grassland and shortgrass highplains types, all types occur in each of the four counties (Fig. 3).

Preliminary field collecting and examination of museum specimens at Oklahoma State University revealed that N. floridana had been collected in the post oak-blackjack forest, stabilized dune, and bottomland types in Blaine, Major, and Dewey counties and that N. micropus had been collected in the mixed-grass eroded plains, stabilized dune, and bottomland types in Major and Woodward counties.

Because both species had been taken in the stabilized dune and bottomland types on the north side of the North Canadian River in adjoining Major and Woodward counties, and because these vegetation types were also present on the north side of the Cimarron River in Major County, the two vegetation types on the north side of the North Canadian River between the Longdale Campsite, Canton Reservoir, Blaine County, and Boiling Springs State Park in Woodward County, and the north side of the Cimarron River approximately ten miles northwest and southeast of the point where U. S. Highway 60 crosses the Cimarron River, were chosen as primary study areas. Primary study areas were

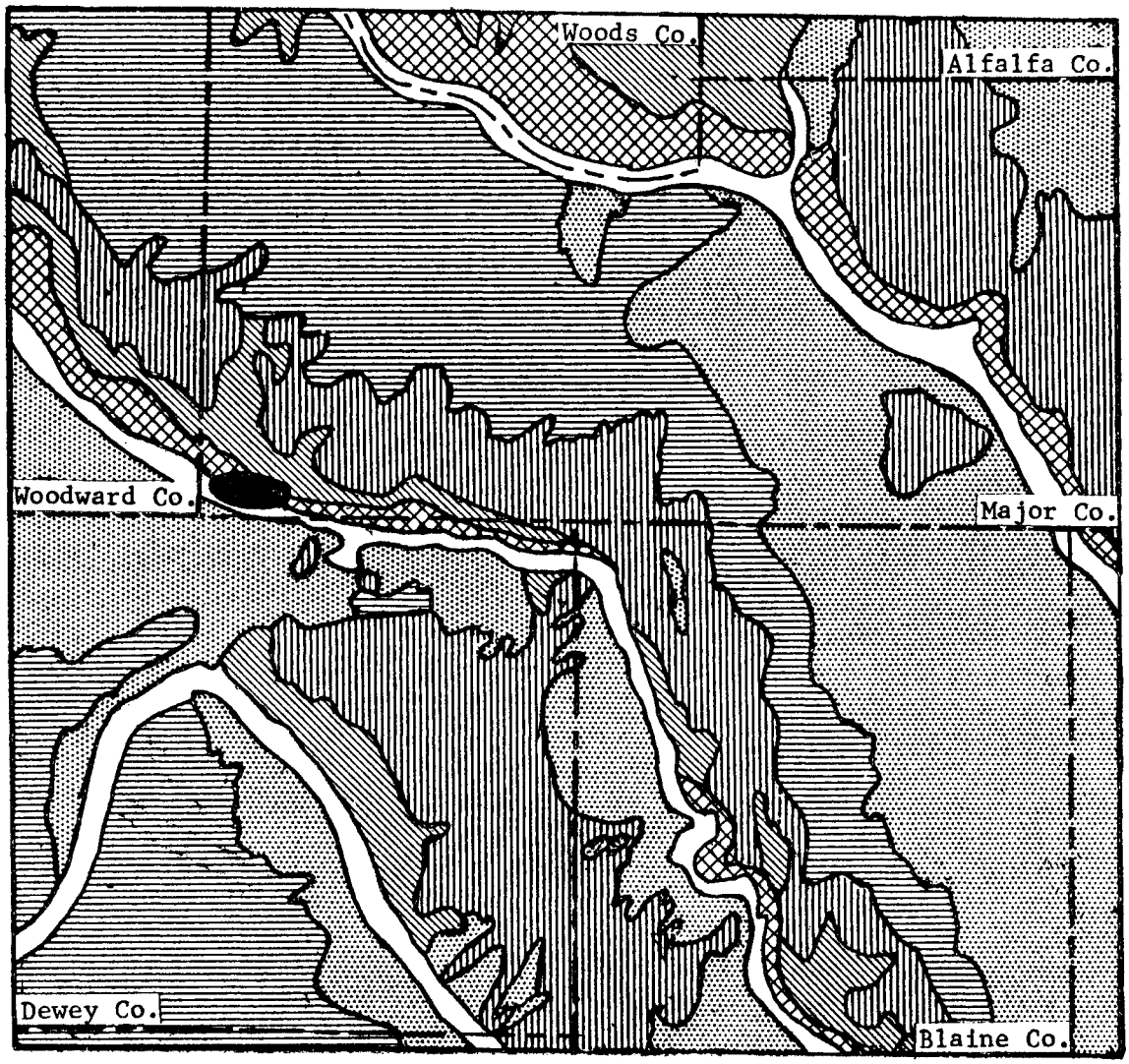

Fig. 3. Habitat types within and surrounding the primary study areas in Oklahoma (after Duck and Fletcher, 1943).

: post oak-blackjack forest
: stabilized dune
: tall grass prairie
: region of sympatry of N. floridana and N. micropus
: mixed grass eroded plains
: bottomland (flood plain)
: sand-sage grassland

designated as those in which sympatric populations of N. floridana and N. micropus would most probably be found.

Vegetation of Primary Study Areas

The two wood rats with which this study was concerned are herbivorous, and their distribution is influenced by the availability of suitable food plants. A second consideration, also vegetation-dependent, is availability of plant material for construction and support of the characteristic houses built by both species in the absence of suitable homesites in rock ledges. Also, plant growth sufficiently abundant to provide protective cover appears to be a necessary requirement.

The stabilized dune and bottomland habitat types are contiguous and parallel along the north side of the North Canadian River in Blaine, Dewey, Major, and Woodward counties and along the north side of the Cimarron River in Major and Woods counties (Fig. 3). The two habitat types appear to serve as avenues of dispersal along which the southern plains wood rat, N. micropus, has moved east and south from the more xeric shortgrass highplains, mixed-grass eroded plains, and sand-sage grassland types; while the eastern wood rat, N. floridana, has extended its range north and west from the more mesic black-jack forest and tall grass prairie types. Blair (1939:96) had the following to say about the overlap in zonation of the mammalian fauna of Oklahoma:

> This extension of certain mammals beyond their respective biotic districts is made possible by the existence of highways for distribution, of which the most important are the stream systems that cross the state in an east-west direction.

Vegetation of the stabilized dune habitat type in the primary study areas varies from savanna-like to woodland. Penfound (1962)

suggested that the vegetation type be called savanna when woody plants are separated by more than one crown diameter, whereas in woodland the woody plants are less than one crown diameter apart. Woodland occurs in protected pockets on north-facing slopes and in places along dune ridges; savanna type vegetation occurs on most south-facing slopes and on ridges and north-facing slopes that are not woodland as defined above.

Trees, shrubs, herbs, and grasses compose the stabilized dune vegetation. Predominant species present on the dunes follows: eastern red cedar, Juniperus virginiana; sugar hackberry, Celtis laevigata; western soapberry, Sapindus drummondii; woollybucket bumelia, Bumelia lanuginosa; American elm, Ulmus americana; Oklahoma plum, Prunus gracilis; sandsage, Artemisia filifolia; prickly pear, Opuntia sp.; horse nettle, Solanum carolinensis; little bluestem, Andropogon scoparius; sand bluestem, A. halli; sandbur, Cenchrus ssp.

Trees, shrubs, and woody vines are the principal plant forms of which the primary-study-area bottomland forest is composed. The predominant species follow: eastern cottonwood, Populus deltoides; American elm, Ulmus americana; common hackberry, Celtis occidentalis; western soapberry, Sapindus drummondii; black locust, Robinia pseudoacacia; eastern black walnut, Juglans nigra; black willow, Salix nigra; eastern redbud, Cercis canadensis; poison ivy, Toxicodendron radicans; wild grape, Vitis ssp.; coralberry, Symphoricarpos orbiculatus.

Secondary Study Areas

Secondary study areas are those in Kansas and Oklahoma containing allopatric populations of N. floridana or N. micropus and from which

specimens were collected for this study.

Secondary study areas from which N. floridana was collected were Osage orange, Maclura pomifera, hedge rows in Chase and Lyon counties, Kansas; wooded rock ledges in Riley County, Kansas; and bottomland forest in Russell County, Kansas. Black jack-post oak and mixed-grass eroded plains habitats in Payne and Blaine counties, Oklahoma, respectively, harbor the species. Specimens were collected in these areas.

N. micropus was collected from short grass-prickly pear associations in Hamilton, Morton, and Stevens counties, Kansas; from wooded, rocky canyons in Comanche and Barber counties, Kansas; from mesquite (Prosopis juliflora) - prickly pear-grassland and sand-sage grassland in Blaine and Harmon counties, Oklahoma, respectively.

CHAPTER III

METHODS

Field Collections for Laboratory Hybridization

Four subspecies of two species of the genus Neotoma were collected from 15 counties in two states for the purpose of making laboratory crosses. N. m. canescens was collected from Hamilton, Morton, and Stevens counties, Kansas. N. m. micropus was collected from Comanche and Barber counties, Kansas, and from Woodward, Major, Dewey, and Harmon counties, Oklahoma. N. f. osagensis was collected from Lyon, Chase, and Riley counties, Kansas, and from Payne, Blaine, and Dewey counties, Oklahoma. N. f. campestris was collected from Russell County, Kansas.

Specimens were collected in live traps and by hand. Live specimens were maintained in laboratory cages and in an outside enclosure. Most laboratory cages were constructed of one-half inch mesh hardware cloth over a wood frame and each cage provided approximately three square feet of floor space per rat. Rats were housed in separate cages. All captive specimens were fed Purina lab chow and had water available at all times.

An outside enclosure was utilized as a holding and breeding area. The enclosure was constructed of three by eight foot sheets of corrugated roofing metal attached to metal fence posts. Overall dimensions of the enclosure were approximately 100 feet by 100 feet by three feet.

Metal sides extended into the soil to a depth of three feet. A wire was attached to porcelain insulators on fence posts approximately two inches above the metal sides. The wire was connected to a fence charger and the charger was turned on at all times to discourage egress by the enclosed rats and ingress by house cats and other potential predators.

Twelve cylindrical cages of hardware cloth were constructed and placed in the east half of the enclosure. The cages were bottomless, and the sides extended into the ground approximately twelve inches, leaving a cylinder three feet high and two feet in diameter. The cylindrical cages were used as outside holding cages, as were numerous wood-wire cages placed in the enclosure.

Thirteen artificial wood rat houses were constructed of rocks and brush in the west half of the enclosure. These artificial houses, plus a drain tile buried in the ground, and a pile of decomposing baled straw were utilized as home sites by wood rats released inside the enclosure.

During the spring and summer of 1965 various sex combinations of N. floridana and N. micropus were released in the enclosure for the purpose of bringing about matings of the two species to produce hybrid offspring under semi-natural conditions. On 1 February 1965, eight female N. floridana from Lyon County, Kansas, and two male N. micropus from Major County, Oklahoma, were released within the enclosure. Subsequent live-trapping indicated the animals had taken up residence at various rock houses in the enclosure. All evidence of pregnancy and births of young was recorded and all adults and young were removed by live-trapping during the first week of May 1965.

On 16 May 1965, six female N. micropus from Major County, Oklahoma, and two male N. floridana from Blaine County, Oklahoma, were released within the enclosure. From 16 May to the first week of August 1965 the rats were recovered by live-trapping approximately once a week. Evidence of pregnancy and births was recorded. During the first week of August 1965, all remaining rats were captured and removed from the enclosure.

Laboratory Mating and Behavior

In order to produce hybrids of known parentage, selected crosses were made by controlled matings. Animals that were to be crossed were placed in a six foot by three foot by one and a half-foot wood-frame, glass-sided observation box. The box was covered with a hinged, one-half inch mesh, hardware cloth top. Visual observations of agonistic and reproductive behavior were made while specimens were confined in the observation box, and behavioral data were recorded in writing.

The following behavioral data were recorded:

1. Response of males and females to males and females of the same and different species and to hybrid males and females.
2. Response of both males and females to the observation box environment during the absence of other wood rats.
3. Time of day, frequency, and duration of copulations.

Estrous Cycles

An attempt was made to determine the estrus cycle of females of both species and hybrids. The vaginal smear technique of Chapman (1951) was first used but was abandoned when it became obvious that

visual observation of the behavior of estrous and anestrous females toward males when placed in the observation box with a male were an easier and more reliable method than Chapman's.

Reproductive Season of Males

Two criteria were relied upon to provide seasonal reproductive data for males. Smears of testis and epididymis and response of males toward estrous females were used. Responses were recorded from visual observations, and presence or absence of sperm in smears was determined using the technique described by Christian (1949).

Gestation Periods

Because the time of most copulations was recorded by visual observation, and time of parturition was recorded usually from the onset to not more than 12 to 24 hours following birth, gestation periods and litter size were noted with considerable accuracy.

Postnatal Development of Young

The following data were recorded for young of litters within 12 hours following parturition:

1. weight, total length, tail length, rear foot length
2. extent and color of pelage
3. description of vibrissae, teeth, eyes, ears, urogenital and anal regions, and tail
4. vocalization and degree of mobility

Changes in weight, body measurements, pelage, vocalization and mobility were recorded at daily, then weekly and monthly intervals

until sexual maturity was attained. Changes in incisor tooth form and dates of jaw tooth eruption were recorded as they occurred. Ages at which the ears unfolded were also recorded as were dates of weaning and ages at which young ate solid food.

Disposal of Laboratory Animals

All breeding stock and young were sacrificed during or at the end of the study. The following data were recorded for each specimen:

1. weight and standard body measurements
2. pelage
3. skull measurements which included condylonasal length, nasal length, zygomatic breadth, and length of left upper tooth row
4. skull characteristics which included characteristics of anterior projection of hard palate, shape of posterior border of hard palate, and relative size of sphenopalatine vacuities.
5. number of placental scars and/or embryos in females
6. breeding condition and dimensions of baculum for males

Skull and body measurements were taken for all specimens. Selected specimens were made into museum study skins. Hairs from various parts of the study skins were removed for the purpose of studying pigment location, color, and pattern of deposition.

Field Collections

In order to obtain a sufficient number of specimens to provide valid data for a comparative study of the structural and reproductive characteristics of *N. floridana* and *N. micropus* and to locate regions of sympatry, if any, specimens were collected by live and snap trapping,

shooting with 22 calibre shot, and by hand. The two types of live traps used were Model 2 Havahart and Style A-1 Johnson Live Catch traps baited with apple or a mixture of peanut butter and rolled oats.

When specimens were collected by shooting or by hand, houses were either pierced at various levels and angles with a wood probe until the animal fled from the house, or if the animal did not attempt to escape when probing occurred, the house was torn apart and the specimen was either shot or caught by hand, when it became exposed or attempted to flee.

On numerous occasions animals did not attempt escape but retired to underground passages. When this occurred, the specimen was unearthed whenever possible with a shovel.

Collecting along the North Canadian River was begun in the vicinity of Canton Reservoir, Blaine County, where the presence of N. floridana had been established by Glass and others (personal communication). Following the establishment of the presence of N. floridana in the vicinity of Canton Reservoir, collecting for N. micropus was begun at Boiling Springs State Part in Woodward County. Each succeeding collection for N. floridana was northwest along the river and for N. micropus southeast along the river until collections of both species were made in the area between Chester and Seiling, Oklahoma. A similar procedure was employed along the Cimarron River with collecting for N. floridana beginning in Blaine County and for N. micropus in Woods County until collections for both species were made in the vicinity of Cleo Springs, Major County.

Museum Specimens

Data from museum specimens were obtained from three sources. The sources were the University of Kansas Museum of Natural History, The Oklahoma State University Museum of Zoology, and the vertebrate museum of Kansas State Teachers College, Emporia. Species and distribution data were obtained from all three sources. Skull measurements were taken from specimens in the Oklahoma State University and Kansas State Teachers College museums. Weights and body measurements were taken from specimens in the Kansas State Teachers College museum.

Identification of Specimens

Wood rats were identified after Hall and Kelson (1959). Plants from the primary study areas were identified from keys in Pohl (1954) and from Vines (1960).

CHAPTER IV

RESULTS

Hybridization

Laboratory Hybridization

Seventeen different combinations of males and females were placed together and copulations occurred. Fifteen of the 17 combinations involved either copulation between males and females of different species, between male or female hybrids and males or females of the two parental types (N. floridana and N. micropus), or between hybrid males and females. Crosses between males and females of the same species were also made. Table I shows the pairings that were made, matings that yielded offspring and those in which copulation occurred but no young were produced, number of litters, number of young and gestation periods for each successful cross.

A total of 103 offspring from 37 litters was produced by the 17 laboratory crosses and nine of the 15 crosses involving hybridization yielded a total of 91 hybrid offspring. Six hybrid crosses, Types I, K, L, N, P, and Q, failed to yield viable young, but some mating without young being produced occurred in all crosses.

Litter sizes varied from one to five with a mean of 2.8 young per litter, and gestation periods ranged from 33 to 55 days with a mean of 35.1 days. Where gestation periods were expressed over a range of days,

TABLE I

TYPES OF CROSSES, NUMBER OF LITTERS FROM EACH CROSS, NUMBER OF YOUNG AND MEAN SIZE FOR EACH LITTER, AND GESTATION PERIODS AND MEAN GESTATION PERIOD FOR 17 CROSSES. COPULATIONS FAILED TO YIELD YOUNG IN SOME CROSSES

Cross	Females	Males	Litters	Litter Sizes and Means	Gest. Periods and Means in Days
A	Nf	Nf	2	4,5,(4.5)	35,35,(35.0)
B	Nm	Nm	2	2,2,(2)	38,33,(35.5)
C	Nf	Nm	3	4,2,3,(3)	35,35,36,(35.3)
D	Nm	Nf	6	1,2,2,2,3, 3,(2.6)	35-36,34,35, 35-39,34,35, (35.1)
E	Nf	F_1(Cross C)	5	2,3,3,3,4, (3)	36,35,51*, 35,34,(35.0)
F	Nm	F_1(Cross C)	8	1,1,2,2,3, 3,4,4,(2.5)	55*,35,33, 34-39,36,36, 35,34,(35.1)
G	F_1(Cross D)	F_1(Cross C)	2	2,4,(3)	35,35,(35.0)
H	Nm	F_2(Cross F)	2	3,3,(3)	35,36,(35.5)
I	Nm	F_2(Cross G)			
J	Nf	F_2(Cross G)	2	3,3,(3)	35,35,(35.0)
K	Nf	F_2(Cross F)			
L	F_2(Cross E)	Nf			
M	F_2(Cross F)	Nf	3	2,3,3,(2.7)	34,35,35-37, (35.0)
N	F_2(Cross F)	Nm			
O	F_2(Cross F)	F_2(Cross F)	2	2,5,(3.5)	35,35-36,(35.2)
P	F_2(Cross E)	F_2(Cross G)			
Q	F_2(Cross E)	Nm			
TOTALS			37	103 (2.8)	(35.1)

N.f. = N. floridana; N.m. = N. micropus

* = litters from postpartum copulations not used in calculation of means.

the midpoint of the range was used in calculation of the mean.

In two instances known gestation periods exceeded 40 days. Both, cross E - 51 days, and cross F - 55 days, were recorded for females who had copulated within 24 hours following parturition of an earlier litter and who were nursing young throughout the extended gestation period. These periods were omitted when mean gestation periods were calculated.

Enclosure Hybridization

Nine young were known to have been born to eight N. floridana females released on 1 February 1965 in the enclosure with two N. micropus males. No young were recorded for six N. micropus females released on 16 May 1965 in the enclosure with two N. floridana males.

Gestation periods and litter sizes for enclosure females could not be determined because of the impossibility of observing copulation and parturition and because females were not accompanied by young when captured in traps. Young, if present, remained in the house when females left to forage.

Data from young raised in the enclosure were not included in this study even though much time and effort were spent in an attempt to produce enclosure hybrids. A cross D, F_1 hybrid male, being held in an individual cage, escaped into the enclosure during the winter of 1964-65. The specimen was observed at intervals during December 1964 and early January 1965. All attempts to catch the animal were unsuccessful and, because it had not been seen since the first week of January, N. floridana females and N. micropus males were released in the enclosure on 1 February 1964. Subsequent examination of young raised in the enclosure revealed the possibility that some may have been sired by a

male other than a N. micropus. Because of this uncertainty, data from enclosure young were not used.

Mating Behavior

No significant differences were noted in the mating behaviors of males and females of the same or different species or hybrids. All pairings of estrous females with males that were capable of mating resulted in copulation. Some captive females entered estrum each year, as early as late January or early February, before males were sexually active and some females continued estrous cycles through July and early August of each year when most males seemed to be sexually inactive. However, each type of cross that was attempted eventually resulted in copulation at one time or another.

When sexually-active males and estrous females are placed together in the observation cage a somewhat stereotyped pattern of behavior follows. The rats approach each other cautiously in a crouched position with legs partially flexed. The first physical contact is usually a touching of vibrissae followed by what appears to be a mutual smelling of the nose, mouth, and cheek areas. A brief sparring or boxing encounter usually follows with both standing on their rear legs and either touching or patting the forefeet of the other. An audible tooth chattering by one or both accompanies the action. Considerable headbobbing from side to side and toward and away from the potential mate is exhibited by both. The sparring is usually terminated by one or both dropping back to the quadruped position or, not infrequently, by one being pushed or falling backward. The sparring bouts are usually repeated four or five times.

Following sparring, the male remains in place and the female begins a vigorous display. It appears as if behavior to this point has resulted in sex recognition by both, and recognition of the female's estrus condition by the male.

Sexual display by the female is similar in most females. While the male remains in place she passes rapidly back and forth in front of him in a crouched position with her pelvic region lowered below the pectoral and moves in short hops with rapid drumming of both rear feet on the substrate. Her posterior is directed toward the male and she appears to drag the vaginal-anal area on the substrate while she emits a low-pitched raspy squeak. This action is repeated or continued while the male moves toward her to mount. Not infrequently, when the male moves toward her she will move rapidly away and continue to display at a greater distance but gradually work back toward the male while displaying.

Copulation is accomplished by the male approaching the female from the rear, mounting, then penetrating by rapid, vigorous thrusts of the hind quarters. The female remains in a crouched position with her tail flexed to the side and emits a raspy, squeaking sound during this time. After a few seconds, the female attempts to move away and the male is usually dragged along with her for a distance that varies among pairs. The male does not grasp the female with his fore feet during copulation and his ability to remain mounted is probably due in part to recurved spines approximately one-half mm in length arranged over the surface of the glans penis. Histological preparations by Stalling (personal communication) of a penis inserted into the vagina and enlarged by injection of an alcohol solution show some of the recurved spines fitted into

invaginations along the vaginal wall. Howell (1926) did not describe the penial spines in the text of his publication on wood rat anatomy or indicate their presence in figures of the male reproductive organs.

Frequency and Duration of Mating

No relationship was established between the type of cross and frequency and duration of mating. Both frequency and duration of mating were highly variable among pairs. When vigorous specimens were involved, copulation usually occurred at intervals of from two to 10 minutes with the female displaying prior to each copulation. Intervals between mating generally increased with mating frequency. The highest frequency observed was six matings in 19 minutes.

Duration of copulation ranged from two to 90 seconds but usually varied from 10 to 20 seconds. No apparent relationship existed between duration and impregnation success. However, an increase in pregnancies seemed to occur with increased copulations. Females became pregnant after as few as two copulations but the incidence was greater when four or five occurred and the pair was allowed to remain together overnight, during which time additional copulations probably took place.

Development of Young

Weights

Weights of the young of 16 litters were recorded within 24 hours following parturition. Individual weights ranged from 10 to 18 g; the mean weight for 42 young from crosses A, B, C, D, E, F, and G was 14.7 g. Too few young from any given cross were available to provide valid comparisons of cross differences by weight.

Weights of 39 young were recorded at two-day intervals for 10 days following parturition and for 35 young at four-day intervals until the age of one month. Weights for fewer than 35 young were recorded at six, 14, and 30 day intervals until the weights for some were recorded over a one-year period. Table II shows weights of young of crosses A, B, C, D, E, F, and G for periods ranging from 10 to 64 days. Too few young of each cross were available to provide valid comparisons of cross differences. The differences evident in Table II can probably be attributed to individual and litter differences.

Body Measurements

Because of the difficulty in obtaining accurate measurements of living, non-anesthesized specimens, few body measurements were taken of young. The following are measurements and means in mm for two male and two female young of cross C sacrificed at one day of age:

total length (males) - 96, 97, (96.5)
total length (females) - 91, 96, (93.5)
tail length (males) - 26, 29, (27.5)
tail length (females) - 25, 26, (25.5)
rear foot length (males) - 14, 15, (14.5)
rear foot length (females) - 14, 14, (14.0)
ear length (males) - 6, 6, (6.0)
ear length (females) - 6, 6, (6.0)

Average weight of the four young was 15.6 grams, only 0.4 grams heavier than the average weight of 39 young at 0 to 2 days of age (Table II).

Attempts to measure living specimens of all crosses resulted in values similar to measurements of the four sacrificed young. Variations among individuals and litters were greater than among crosses. Figures 4 and 5 show relative size and length of one-day old wood rats.

Figure 4. Young of Cross G at One Day of Age.

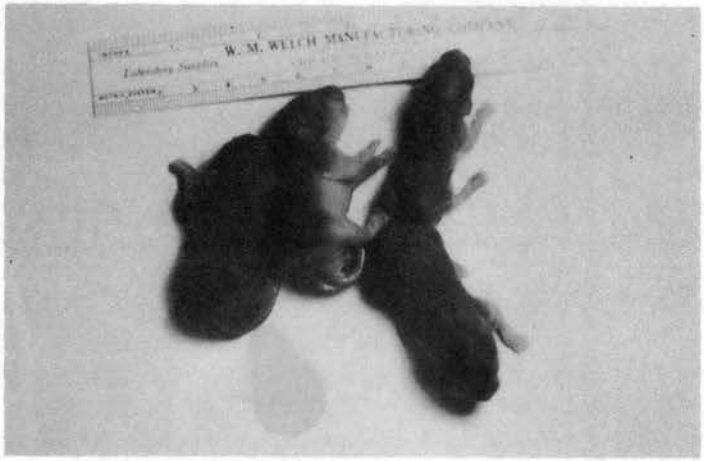

Figure 5. A Litter of Cross E Young at One Day of Age.

TABLE II

MEAN WEIGHTS IN GRAMS OF YOUNG OF FIVE CROSSES AT VARIOUS AGES FROM 0-2 TO 58-64 DAYS

Cross	No. of Young	Age in Days 0-2	4-6	8-10	12-14	16-18	20-22	24-28	30-34	36-40	42-48	50-56	58-64
A	3	14.7	21.3	31.0	33.3	46.0		63.5					
B	5	16.6	26.2	28.8	34.0	38.6	58.3	74.5	107.5			140.6	156.6
C	4	16.0	26.0	31.0									
D	5	18.1	28.0	32.2	40.0	42.5		61.5	86.0		99.2	121.0	
E	5	14.8	23.6	26.0	34.0	42.6	54.0	79.4	108.0	118.0	145.7		174.5
F	13	14.0	19.0	25.0	29.3	41.1	51.2	77.6	90.3	107.2	113.8	130.8	135.3
G	4	13.6	18.0	23.5	35.0	44.5	62.7	74.4	102.0	123.5		164.8	
Mean Weights		15.2	22.4	27.7	37.4	42.0	54.7	73.5	96.5	112.6	112.6	135.8	148.5

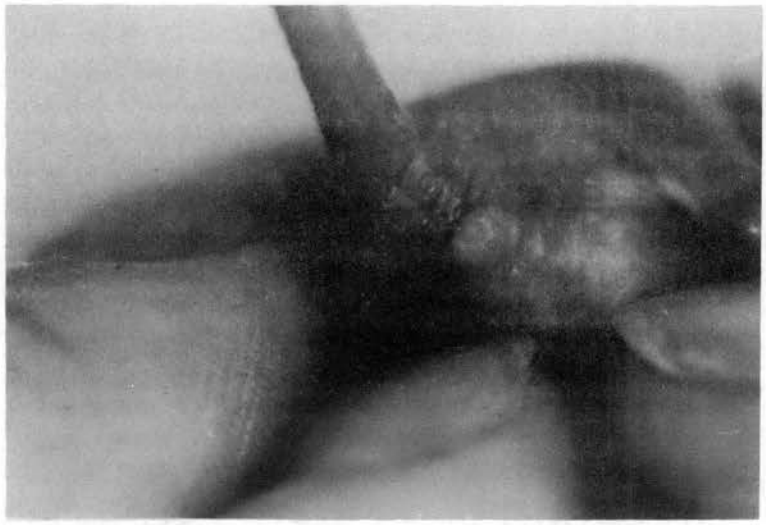

Figure 6. Anal Region of Cross E Young at One Day of Age.

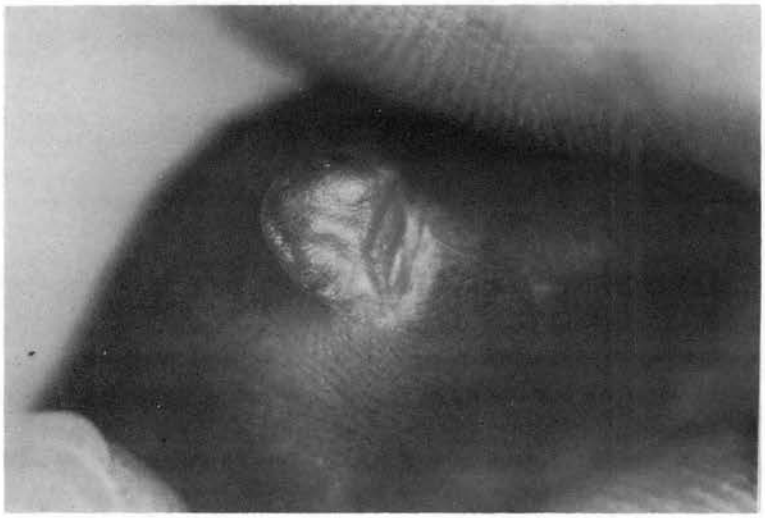

Figure 7. Ear of Cross E Young at One Day of Age.

Postpartum Development of Young

The stage of development of parturition was similar for young of all crosses. Greater variation occurred within litters than among litters of the same or different crosses. Description of a representative one-day old wood rat is as follows: eyes, external auditory canal, urogenital orifice, and anus closed; pinnae either folded over from base with distal end in contact with the side of the head or unfolded and erect; toes fused to tip and with well developed claws; tail naked with pronounced annuli that produce a segmented appearance; sparse, light grey hair prominent on dorsum and sides, venter and appendages nearly naked, vibrissae pronounced; dorsum and sides dark gray to black, venter and appendages pink to red in color; two recurved incisor teeth in each jaw separated at base and forming a V-shape: Figures 6, 7, 8, 9, and 10 show, respectively, the anal region, ear, tail, ventral abdomen, and teeth of a one-day old wood rat.

Eyes of most young were open by the 15th day, however, some opened as early as the 14th day and some as late as the 17th day.

The external auditory canal formed first as a slight depression and continued to deepen at least through the 14th day at which time observations were terminated.

The urogenital orifice which appeared closed at birth was open sufficiently by the second day to allow urination if young were placed under stress by handling or photographing.

Attempts to determine opening time of the anus by noting the first appearance of fecal pellets of young in cage dropping pans indicated that defecation does occur by the sixth or seventh day, and possibly earlier.

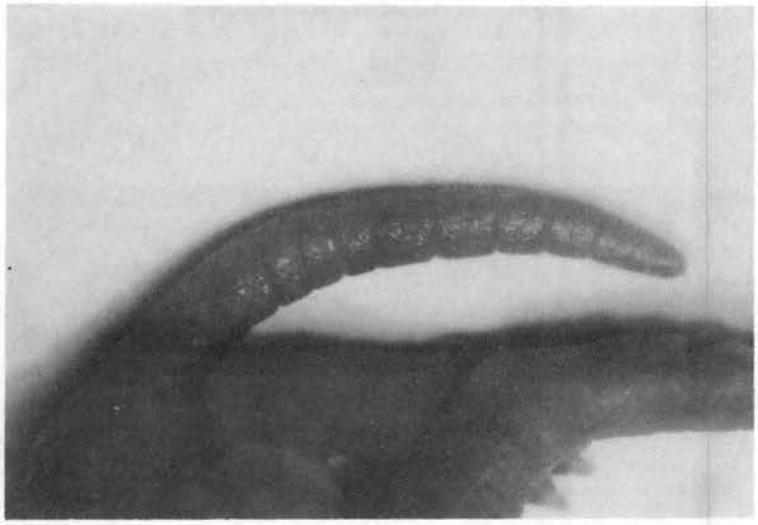

Figure 8. Tail of Cross E Young at One Day of Age.

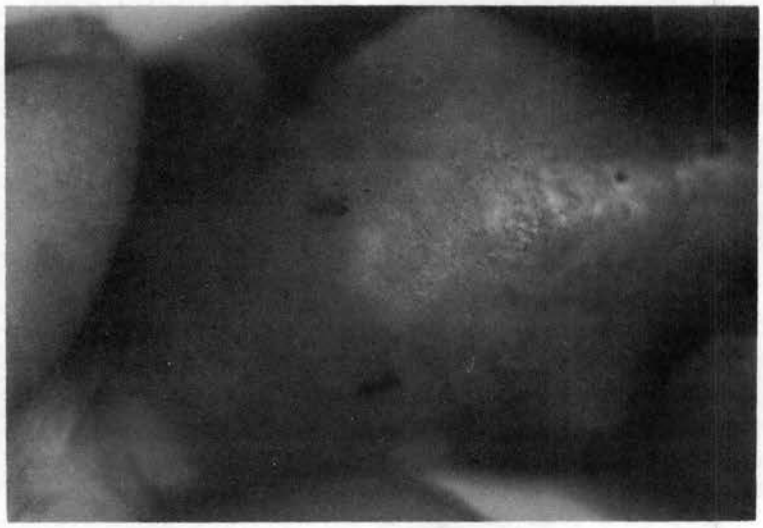

Figure 9. Ventral Abdomen of Cross E Young at One Day of Age.

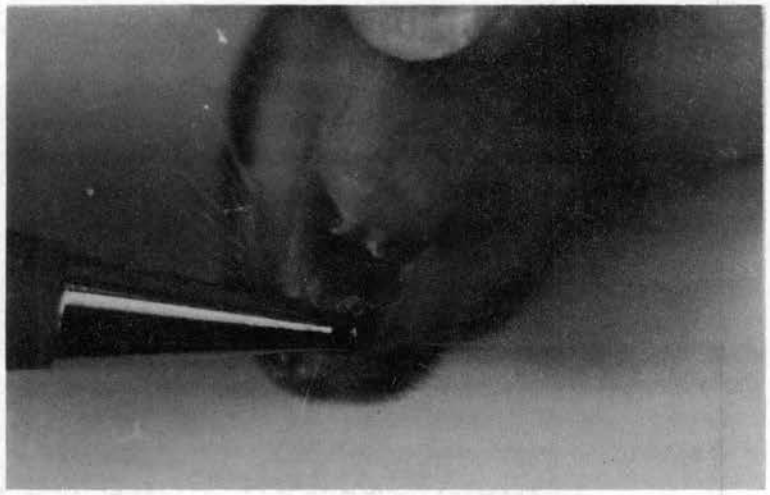

Figure 10. Head of a Cross E Young at One Day of Age Showing Recurved Incisors.

If the ears were folded at birth they were usually erect by the second day. They grew rapidly and approached adult size by the end of the first month.

The tail developed a sparse hair cover and lost the segmented appearance by the end of the second week. In contrast to the feet and ears, the tail appeared to increase markedly in length even after adulthood was reached.

Pelage increased from a sparse cover of long, grayish-white guard hairs and short, dark underhair on the dorsal and lateral surfaces at birth to a relatively complete but short juvenile hair cover by the third day. Pelage color becomes dark, blue-gray in the young of N. floridana and F_1 hybrids of crosses C and D. Color of N. micropus young is lighter gray and young of other hybrids are either more like N. floridana or more like N. micropus depending on the degree to which the two species are represented in the individual's lineage.

Young of N. floridana retain the juvenile pelage until about six weeks of age. The first indication of a change to subadult pelage is the appearance of brownish hair along the sides midway between front and rear legs. The area increases in size by extending forward, to the rear, and up toward the midline of the back. At the same time, gray hair on the venter is being replaced by white hair in the throat, pectoral, and pelvic regions and by white-tipped, gray hair in the abdominal area.

By age 54-56 days brownish hair has replaced the dorsal and lateral juvenile hair except for a mid-dorsal stripe of blue-gray hair. Subadult pelage is usually complete by the end of the second month and resembles adult pelage.

F_1 hybrids of crosses C and D undergo pelage changes similar to N. floridana and both subadult and adult pelages are more like N. floridana than N. micropus. Hybrids of crosses C and D differ from N. floridana by having a darker appearance which results from an increase in the ratio of black to brown hairs.

Pelage changes in N. micropus are more difficult to detect visually than changes in N. floridana and F_1 hybrids because of the color similarities of juvenile, subadult, and adult pelages. As in N. floridana, juvenile hair is of a finer texture than subadult and adult hair and the change in texture is only slightly more obvious than the subtle color changes from light gray overall to a darker gray on dorsal and lateral surfaces and white ventral surface. The change from juvenile to subadult pelage occurs at approximately the same age as in N. floridana and F_1 hybrids.

Except for offspring of cross G, all other hybrids exhibited adult

pelage colors most similar to the species (either N. floridana or N. micropus) that was represented to the greatest degree in their lineage. Litters of cross G, the offspring of two F_1 hybrids, contained offspring whose adult pelage varied from N. floridana-like to N. micropus-like to the intermediate F_1 pelage.

Representative museum skins and skulls of subadults and adults of both parent species and all hybrid crosses were prepared and are housed in the vertebrate museum mammal collections of Oklahoma State University and Kansas State Teachers College.

Ecological Relationships and Distribution

Observations made during this study and habitat descriptions by Finley (1958), Blair (1939), Cockrum (1952), Bailey (1931), and others, indicate that N. micropus is usually found in dry, wooded, rocky ravines; or in shortgrass-soapweed, (Yucca), associations. Fitch and Rainey (1956), Rainey (1956), Murphy (1952), Pearson (1952), and my own observations indicate that N. floridana is usually found in moist woodlands, along wooded rock outcrops, or in areas such as osage orange hedgerows. Because most subspecies of N. floridana (N. f. campestris excepted) occupy relatively mesic habitats and N. micropus inhabits more xeric areas, considerable interest was generated by the collection of N. micropus specimens in the bottomland forest of Woods and Woodward counties, Oklahoma, and the collection of N. floridana from a mesquite-prickly pear cactus association in the gypsum rock outcrops west of Okeene in Blaine County, Oklahoma.

Figure 11 shows a wood rat house in a bottomland forest located approximately seven miles west of Cleo Springs in Woods County,

Oklahoma, from which a female N. micropus was taken. The house was composed of large pieces of cottonwood bark, dried cow dung (not visible in Fig. 11), and other woody debris. The food cache within the house consisted of fruits of Carolina horsenettle, red bud, wild grape, and a variety of tree leaves, all produced the previous growing season. All of these items have also been taken from caches in N. floridana houses of similar construction.

Figure 11. A N. micropus House in Bottomland Forest of Woods County, Approximately Seven Miles West of Cleo Springs, Oklahoma.

Houses of N. floridana located in the gypsum rock, mesquite-prickly pear area west of Okeene, were composed of prickly pear stem sections, dried cow dung, and short branches of mesquite, red cedar, and skunk bush, Rhus aromatica. The food cache in one house consisted of green twigs of red cedar, and mesquite and skunk bush fruits. Stem sections of prickly pear scattered around the house entrance and

incorporated in the house material also apparently were used as sources of food and water. The houses were indistinguishable from houses occupied by N. micropus in other areas.

As previously indicated, both species and possible hybrids of the two species were collected on the north side of the North Canadian River between Chester and Seiling, Oklahoma, in an area extending approximately one-half mile east and one-quarter mile west of U. S. 281 highway. Only N. micropus were collected in an area five miles west of Chester, Woodward County, Oklahoma, and only N. floridana were collected in an area along the Dewey-Major County line six miles east of U. S. 281 highway. The exact extent of the area of sympatry has not been determined.

Within the area of sympatry, specimens of both species were taken from neighboring houses as were specimens tentatively identified as hybrids. On 18 December 1965 a female N. floridana, D.L.S.#215, was collected from a house which was in close proximity to two other houses from which N. micropus, D.L.S.#207 and #208, were collected. One other instance of an intimate association of the two species was noted.

A total of 18 specimens of the two species and possible hybrids was collected from the area of sympatry. The total included 12 females, one of which was a juvenile, and six males, one of which was a subadult. Identification of the specimens based on qualitative characters such as pelage, shape of the anterior projection and posterior border of the hard palate, size of sphenopalatine vacuities, and shape of the baculum, indicates that of the total, six were probably N. floridana, three were probably N. micropus, and nine exhibited a mixture of N. floridana and N. micropus characteristics and were probably hybrids or intergrades.

Four of the 12 females had placental scars and had probably reproduced in the area.

One possible hybrid female, D.L.S.#391, was captured alive and later crossed with a N. floridana male. One young male, D.L.S.#425, was produced and when sacrificed as a subadult exhibited a mixture of qualitative characters characteristic of some laboratory-produced hybrids.

Specimens of the two species were also collected along the north side of the Cimarron River east and west of Cleo Springs, in Woods and Major counties. However, no area of sympatry was identified. N. floridana was collected in the bottomland forest and stabilized dune area on the west side of Eagle Chief Creek one and one-half miles north and one-fourth mile west of Cleo Springs. N. micropus were collected in the stabilized dune habitat four miles west of Cleo Springs, on the Edsel Cornelson ranch. The collection sites of the two species were separated by a distance of less than three miles and the stabilized dune habitat is continuous between the two sites. It is believed that an area in which the two species are sympatric does exist in the stabilized dune habitat on the north side of the Cimarron River west of Cleo Springs. Further field work in the vicinity should delimit the area of sympatry.

In view of the collections made during this study, information received from Dr. Knox Jones of the University of Kansas pertaining to Oklahoma specimens of Neotoma in the University mammal collection, information from Dr. Bryan Glass and specimens in the Oklahoma State University Museum of Zoology, and correspondence with Dr. Keever Greer of the University of Oklahoma and Mr. Lyle Stemmerman, former director

of the Great Salt Plains National Wildlife Refuge, the following map (Fig. 12) showing the distribution of N. floridana and N. micropus in Oklahoma represents, as accurately as present information will permit, the present distribution of the two species in the state.

Reproduction of Non-Laboratory Specimens

From 1963 through 1966 reproduction data were recorded from males and females of both species captured alive or trapped in the field. These data provided information about length of breeding seasons, number of embryos and living young, and litters per year.

Breeding Season

N. micropus females - N. micropus females, either pregnant or with young, were collected from areas in Oklahoma and Kansas during the months of February, March, April, May, June, October, and November.

Three N. m. canescens taken in Hamilton County, Kansas, on 27 February 1963 had litters of young judged to be three, seven, and nine days of age at the time of capture. Number of young in the litters were four, two, and four, respectively. One of the females had another litter while in captivity on 13 April 1963 and had not been with a male while in captivity. The second gestation period of 49 to 54 days probably resulted from copulation during a postpartum heat period.

Assuming the litters of the three females were their first of 1963 and a gestation period of 35-36 days for first litters, the females probably entered estrus around the middle of January 1963.

N. m. micropus females, either pregnant or with young in the nest, or both, were collected from Major, Woods, and Woodward counties,

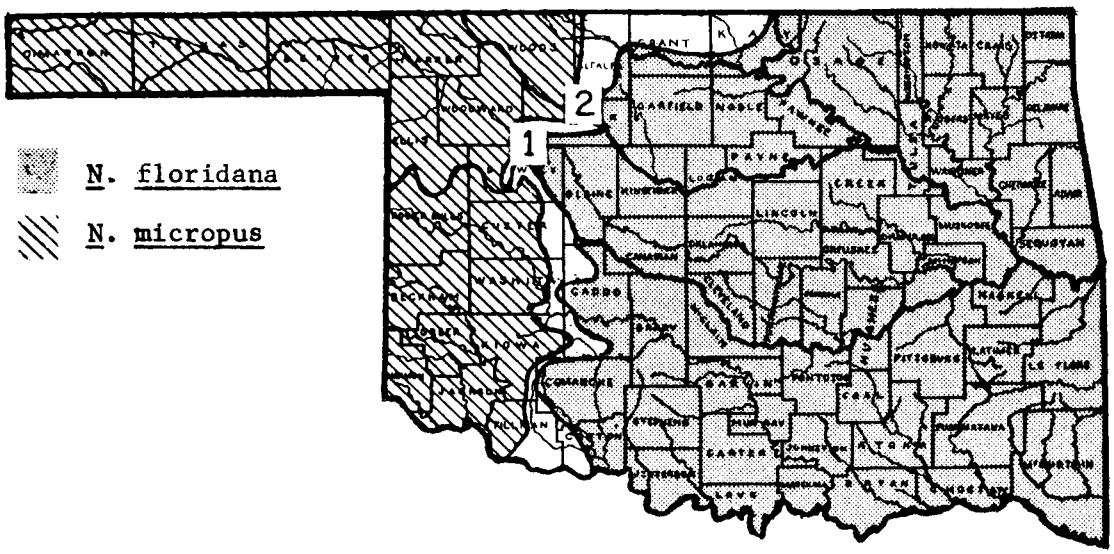

Figure 12. Distribution of N. floridana and N. micropus in Oklahoma. 1 = Area of Known Sympatry, 2 = Area of Probable Sympatry.

Oklahoma, in March, April, May, and June, 1965. Number of embryos ranged from two to four with a mean of three and number of young ranged from one to four with a mean of two.

One N. m. micropus female collected on 24 April 1965 had two young approximately 12 days of age and was also pregnant with three small embryos. Another female taken the same day had one young approximately 30 days of age and was pregnant with two embryos of 35 mm and 37 mm crown-rump length.

Attempts to collect pregnant N. micropus in July, August, and September 1965 were unsuccessful. Females were collected but they were neither pregnant nor with young.

One N. m. micropus female collected on 9 October 1965 in Major County was pregnant with three nearly full-term embryos and, of six adult females taken in Harmon County on 14 November 1964, four had from 2 to 4 young varying from approximately 15 to 30 days of age and one was pregnant with four small embryos. Parturition for the pregnant female would probably not have occurred until after 1 December.

One captive female, D.L.S.#353, had three litters of three, two, and three young each during the summer of 1965. They were born in April, June, and September, respectively.

N. micropus males - Testis and epididymis measurements, sperm smears, and behavior of males toward estrous females were relied on to provide information about the breeding seasons of males of both species. Of the three sources of information, behavior seemed the best indicator of ability to reproduce.

Measurements of adult testes were taken from fresh or frozen specimens collected during every month that females were collected. Testis

position during the period February to November was usually scrotal or inguinal and apparently abdominal during December and January.

Testis size varied somewhat but the average size for what appeared to be sexually active males was approximately 16 mm in length and 12 mm in width. This compares with an anverage of 9 mm x 5 mm for three sub-adult males at 180 days of age.

Sperm smears showed some sperm present in testis of all males sampled. However, sperm were much more numerous from February through May and in September. During these times the epididymis was prominent.

While pairing males and females in the laboratory, it was noted that males would not attempt copulation with estrous females in the late winter (January), soon after females entered estrus, and in late July and August. Sperm smears taken from males during these times yielding sperm, however.

Reproduction data for N. micropus in Kansas and Oklahoma suggest a breeding season beginning in late January and extending through May, followed by a quiescent period during June, July, and August; a resumption in September and October, and extending into November, at least in the southwestern part of Oklahoma. Males probably determine the limits of the breeding season to a greater degree than do females. Females probably have as many as three litters per year with an average of three per litter, and most probably have a postpartum heat period, at least following parturition of the first litter each year.

N. floridana females - N. floridana females, either pregnant or with young, were collected during the months of March, April, May, June, and September. The earliest date on which pregnant females were collected was 27 March 1965. Two females, each with two young, were

collected from the stabilized dune habitat in Dewey County, Oklahoma. Neither of two females collected in the same area two weeks earlier on 13 March 1965 had young but one contained three large embryos. Five females collected in Chase County, Kansas, on 6 February and 20 March 1965 were not pregnant but two of those collected on 20 March exhibited perforate vaginas, and a sixth female had five embryos. One female collected in Wabaunsee County, Kansas, on 21 March 1965 contained four small embryos whose mean crown-rump length was 5 mm.

Pregnant females and females with young were collected in April, May, and June 1965 in Chase and Lyon counties, Kansas, and Blaine and Dewey counties, Oklahoma. The average number of embryos for each of six females was three and the average number of young for each of seven females was three. Number of embryos ranged from one to four and for young, the range was two to four.

A pregnant female was collected alive on 28 March 1963 and retained in captivity. On 7 April the female gave birth to five young and successfully nursed all five young until they were 30 days of age, at which time they were sacrificed. This is noteworthy, for in Neotoma there are only four teats.

One female was collected on 25 September 1965 in Lyon County, Kansas, with three young that appeared to be approximately one week old and juvenile young were taken in late October 1964 in Dewey County, Oklahoma. The juveniles appeared to be approximately one month old.

One captive female N. floridana, D.L.S.#314, had three litters during 1965. They were born in April, June, and September and contained four, four, and three young, respectively.

N. floridana males - Data from testis measurements, sperm smears,

and behavior of males toward females for N. floridana males showed only slight variations from those for N. micropus males. Testis size during the breeding season was similar and averaged 17 mm x 11 mm as opposed to the 16 mm x 12 mm for micropus. Sperm smears yielded some sperm from all specimens and an increase in abundance of sperm in smears corresponded to an increase in epididymis size. Captive males also failed to respond to estrous females during late winter and mid-summer.

Vaginal smears taken from two N. micropus females immediately following copulation with N. floridana males on 8 and 9 March 1964 failed to yield sperm. It is possible the males were unable to ejaculate semen at that time.

Reproduction data for N. floridana in Kansas and Oklahoma indicate a shorter breeding season for the species than for N. micropus in the two states. The onset of breeding probably does not occur until mid-February and mating probably continues well into May. This species may also enter a quiescent period during June, July, and early August followed by a brief period of reproductive activity in late August and early September. Climatological factors no doubt influence breeding activity and a period of mild weather in January and early February or cool summer temperatures would probably extend the breeding season.

N. floridana females also have a postpartum heat period. Experience with captive females of both species and hybrids indicate the period of receptivity following parturition is approximately 24 hours.

Age of Sexual Maturity

Observations of captive specimens of both species and hybrids indicate the age of sexual maturity for both males and females to be

approximately 300 days. Attempts to bring about mating of young-of-the-year females with adult males and young-of-the-year males with adult females were unsuccessful. Even though some young-of-the-year females born in April had well-developed ovarian follicles in September, they failed to enter estrus before the following spring. Sub-adult males sacrificed in November had a few sperm but failed to respond sexually to estrous females in September.

Vaginal Plugs

Rainey (1956) referred to the presence of vaginal plugs in *N. floridana* females, but observations made during this study failed to provide evidence of their presence. Females of both species and hybrids were examined immediately following copulation and at various intervals up to 24 hours after copulation. Mucous vaginal plugs were not observed.

Ventral Abdominal Gland

Field-caught and laboratory-reared males of both species and hybrids exhibit a discolored, relatively hairless area along the midline of the abdomen which is most pronounced during the breeding season. The area is approximately 5 to 7 mm wide and 50 to 65 mm long in adult males and appears thickened, rough and scaly. The area is more obvious in *N. micropus* than in *N. floridana*.

Histological sections of the area reveal an abundance of sebaceous glands emptying into hair follicles. The sebaceous glands are larger and more numerous in adult males sacrificed in May and September than in adult males sacrificed in December. Females and sub-adult males

also possess sebaceous glands in the region but they are poorly developed when compared to adult males in breeding condition.

When captive adult males were released into the observation box prior to introduction of females they spent considerable time dragging their venters over rocks, sticks, water containers and other objects in the box. Examination of males whose venters were not already stained revealed an oily exudate on the hair and skin along the middle of the abdomen. The exudate was flourescent under ultra-violet light.

Males frequently continued with the venter-dragging behavior after females, both estrous and anestrous, were placed in the box with them.

The venter-dragging behavior is believed to be a "sign posting" activity and is probably involved with sex recognition and territory marking. Venter-dragging by N. floridana males has been observed soon after specimens were released from live-traps on the Ross Natural History Reservation, Chase County, Kansas.

Qualitative and Quantitative Morphological Characters

In order to determine the possible relationships between the eastern and the southern plains wood rats, specimens of the two species, known laboratory-produced hybrids, and specimens collected from the region of sympatry in Oklahoma were assigned group numbers I, II, III, and IV and data from each group were analyzed. Group I includes N. floridana specimens collected from regions in Kansas and Oklahoma where the species is known to be allopatric; Group II includes Kansas and Oklahoma specimens of N. micropus from allopatric areas; Group III includes all hybrids produced by laboratory crosses; and Group IV includes specimens collected in the stabilized dune habitat type on the north

side of the North Canadian River in Major County, Oklahoma, an area in which the two species are known to be sympatric.

Goldman (1910) in his systematic review of the wood rats of the genus Neotoma relied on certain qualitative and quantitative characters to divide the genus into species and subspecies. The characters were pelage, body and skull measurements, and qualitative skull characters such as relative size of sphenopalatine vacuities, development of anterointernal re-entrant angle of first molar, and presence or absence of posterior median projection of the palate. Others (Hall and Kelson, 1959, and Finley, 1958) have referred to similar characters when discussing species differences. Burt and Barkalow (1942) referred to baculum shape and size as distinguishing characters for N. floridana and N. micropus.

Because determination of the presence or absence of significant differences for these characteristics among the four groups would aid in drawing conclusions as to group relationships, the following qualitative data were gathered:

1. skull characters
    a. shape of the anterior projection of the hard palate
    b. shape of the posterior border of the hard palate
    c. relative size of sphenopalatine vacuities
2. pelage color
3. baculum shape

Quantitative characteristics for which data were recorded are:

1. skull measurements
    a. condylonasal length
    b. zygomatic breadth
    c. nasal length
    d. least interorbital constriction width
    e. left upper cheek tooth row length
2. body measurements
    a. total length
    b. tail length
    c. rear foot length
    d. length of ear from notch

3. baculum measurements
   a. length
   b. lateral width
   c. dorso-ventral width
   e. shaft diameter

Qualitative Characters

Anterior Projection of Hard Palate

Figure 13, a ventral view of N. floridana skull, shows a forked bony projection extending anteriorly from the anterior border of the hard palate. This characteristic has been designated by Goldman and others to be representative of the species.

Figure 14, a ventral view of a N. micropus skull, shows a straight anterior projection from the anterior border of the hard palate. The sources cited above have designated the straight anterior projection as characteristic of N. micropus.

Table III shows the number from each of the four groups that exhibit either forked or straight anterior projections. The hypothesis that classification by species is independent of classification by type of anterior projection was tested for Groups I and II by calculating chi square from a 2 x 2 contingency table. The chi square value of 73.20 is significant at the 0.005 level and rejects the hypothesis.

Posterior Border of Hard Palate

Figure 13 shows a median notch in the concave, posterior border of the hard palate which has been considered characteristic of N. floridana.

Figure 14 shows a median posterior projection of the concave posterior border of the hard palate which has been considered

characteristic of N. micropus.

TABLE III

THE NUMBER OF EACH OF FOUR GROUPS OF WOOD RATS EXHIBITING EITHER FORKED OR STRAIGHT ANTERIOR PROJECTION OF HARD PALATE

Groups	Anterior Projection of Hard Palate		
	Forked	Straight	Totals
I. N. floridana	83	13	96
II. N. micropus	21	67	88
III. Known Hybrids	21	30	51
IV. Possible Hybrids	7	10	17
TOTALS	132	120	252

Table IV shows the number of each of the four groups of wood rats having the posterior border either concave with a median notch, concave with a median, ventral projection, or concave and lacking either projection or notch. The hypothesis that classification by species is independent of classification by shape of the posterior border was tested for Group I and II by calculating chi square from a 2 x 2 contingency table. The chi square value of 264.51 is significant at the 0.005 level and rejects the hypothesis.

Sphenopalatine Vacuities

To the right and below the posterior border of the hard palate in

TABLE IV

THE NUMBER OF EACH OF FOUR GROUPS OF WOOD RATS HAVING POSTERIOR BORDER OF HARD PALATE AS EITHER CONCAVE TOWARD ANTERIOR, CONCAVE TOWARD ANTERIOR WITH MEDIAN NOTCH, OR CONCAVE TOWARD ANTERIOR WITH MEDIAN PROJECTION

Groups	Shape of Posterior Border of Hard Palate: Con.	Con. & Med. Notch	Con. & Med. Proj.	Totals
I. *N. floridana*	13	61	2	76
II. *N. micropus*	28	6	55	89
III. Known Hybrids	20	12	19	51
IV. Possible Hybrids	8	7	2	17
TOTALS	69	86	78	283

TABLE V

THE NUMBER OF EACH GROUP OF WOOD RATS HAVING EITHER NARROW, INTERMEDIATE, OR WIDE SPHENOPALATINE VACUITIES

Groups	Size of Sphenopalatine Vacuities: Narrow	Intermediate	Wide	Totals
I. *N. floridana*	91	2	1	94
II. *N. micropus*	7	59	20	86
III. Known Hybrids	31	18	1	50
IV. Possible Hybrids	8	7	2	17
TOTALS	137	86	24	247

Figs. 13 and 14 can be seen the sphenopalatine vacuities. Narrow vacuities as in Fig. 13 have been designated characteristic of N. floridana and the wider vacuities as in Fig. 14 have been designated characteristic of N. micropus. Table V shows the number of each group of wood rats having either narrow, intermediate, or wide vacuities. Because of the small number of N. floridana exhibiting intermediate and wide vacuities, chi square was not calculated for Groups I and II due to low frequencies within the groups.

Pelage Types

From published descriptions of the pelages of the two species, examination of identified museum specimens, and several years of personal experience working with the species, pelages of specimens from the four groups were classified as being one of six types. The pelages were: Type 1 for specimens within the color range of summer and winter N. floridana; Type 2 for specimens within the color range of summer and winter N. micropus; Type 3 for intermediate pelage characteristic of F_1 hybrids; Type 4 for pelage intermediate between Types 1 and 3; Type 5 for pelage intermediate between Types 2 and 3; and Type 6 for pelage unlike Types 1 through 5.

Table VI shows the number from each group of wood rats exhibiting each pelage type.

Baculum Shape

Burt and Barkalow (1942) indicated obvious differences in the shapes and sizes of the bacula of N. floridana and N. micropus. Observations of the bone in this study of the two species revealed rather

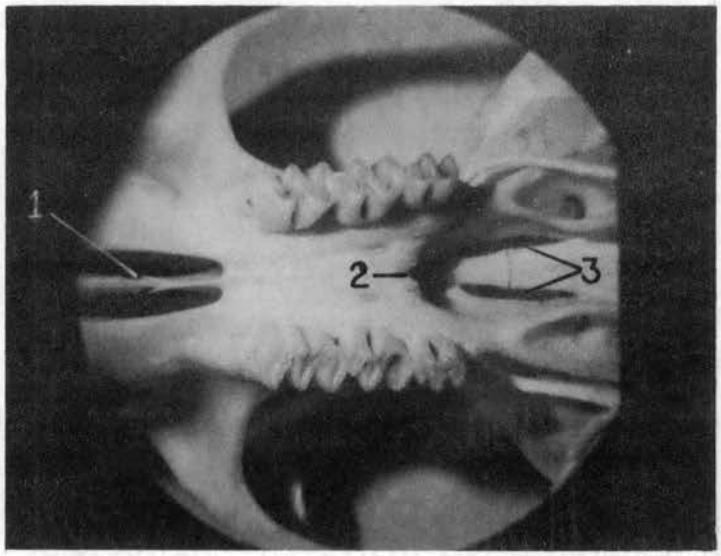

Figure 13. Ventral View of N. floridana Skull.

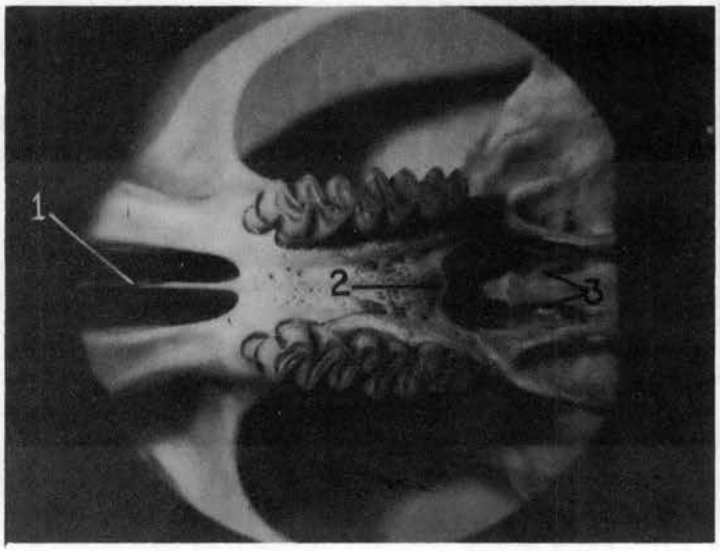

Figure 14. Ventral View of N. micropus Skull.

pronounced specific differences. Figure 15 shows bacula of the two species and hybrids.

TABLE VI

THE NUMBER OF EACH GROUP OF WOOD RATS EXHIBITING EACH PELAGE TYPE

Groups	Pelage Color						
	1	2	3	4	5	6	Totals
I. *N. floridana*	62	0	0	0	0	0	62
II. *N. micropus*	0	61	0	0	0	0	61
III. Known Hybrids	2	11	12	2	17	1	45
IV. Possible Hybrids	5	4	3	3	3	0	18
TOTALS	69	76	15	4	20	1	186

1 = like *N. floridana*; 2 = like *N. micropus*; 3 = like F_1 (intermediate between 1 and 2); 4 = between 1 and 3; 5 = between 2 and 3; 6 = unlike 1 through 5.

Table VII shows the number from each group of wood rats having the expanded proximal end of the baculum either like *N. floridana*, like *N. micropus*, or intermediate between the shapes characteristic of the two species.

Quantitative Characters

Ranges, means, and standard deviations of quantitative characters were determined for varying numbers of specimens in each of the four groups.

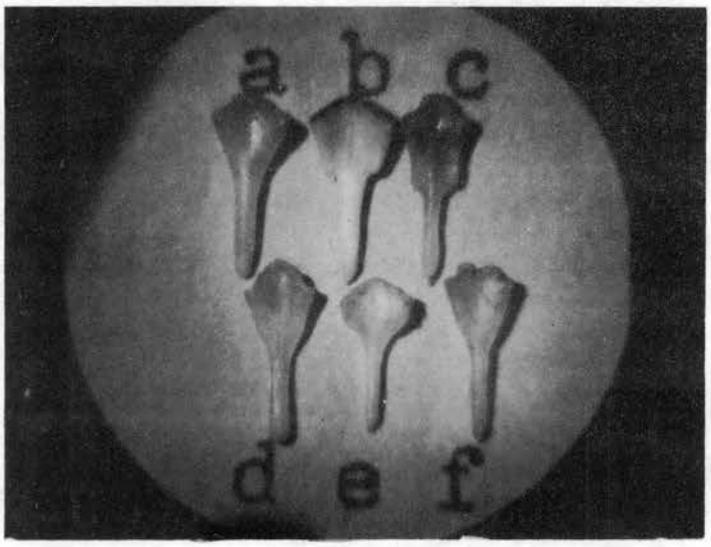

Figure 15. Bacula of Two Species of Wood Rats and Hybrids of the Two Species. (a) N. micropus, (b) N. floridana osagensis, (c) N. floridana campestris, (d) cross G, (e) cross G, (f) cross D.

TABLE VII

THE NUMBER OF EACH GROUP OF WOOD RATS HAVING THE EXPANDED PROXIMAL END OF THE BACULUM EITHER N. FLORIDANA-LIKE, N. MICROPUS-LIKE, OR INTERMEDIATE

Groups	Baculum Shape			
	N.f.-like	N.m.-like	Inter.	Totals
I. N. floridana	11	0	0	11
II. N. micropus	0	11	1	12
III. Known Hybrids	3	7	7	17
IV. Possible Hybrids	1	0	3	4
TOTALS	15	18	11	44

Skull Measurements

Means and standard deviations of five skull measurements were determined for 96 specimens in Group I, 83 in Group II, 27 in Group III, and 15 in Group IV and are presented in Table VIII.

TABLE VIII

MEANS AND STANDARD DEVIATIONS IN MM OF FIVE SKULL MEASUREMENTS FOR FOUR GROUPS OF WOOD RATS

		Condylonasal Length		Zygomatic Breadth		Nasal Length		LIC Width		LUTR Length	
Group	N	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
I	96	49.03	2.10	26.35	1.44	19.34	3.54	6.57	0.31	9.46	0.35
II	83	48.32	1.91	26.18	1.12	19.00	1.10	6.23	0.37	10.22	0.41
III	27	50.01	2.18	26.63	1.28	19.61	0.97	6.23	0.41	9.73	0.34
IV	15	47.89	1.24	25.51	0.90	18.71	0.44	6.44	0.43	9.53	0.48

LIC = Least interorbital constriction
LUTR = Left upper cheek tooth row

Body Measurements

Means and standard deviations of four body measurements were determined for 33 specimens in Group I, 39 in Group II, 24 in Group III, and 14 in Group IV and are presented in Table IX.

TABLE IX

MEANS AND STANDARD DEVIATIONS IN MM OF FOUR BODY MEASUREMENTS FOR FOUR GROUPS OF WOOD RATS

Group	N	Total Length Mean	Total Length S.D.	Tail Length Mean	Tail Length S.D.	Rear Foot Length Mean	Rear Foot Length S.D.	Ear Length Mean	Ear Length S.D.
I	33	369.55	30.13	152.58	9.40	38.64	1.77	26.60	2.07
II	39	352.55	23.32	143.52	11.92	37.77	1.68	26.70	1.96
III	24	363.04	20.47	152.40	13.77	38.60	1.58	28.16	2.57
IV	14	352.13	15.61	147.53	9.73	37.73	1.62	26.37	0.96

TABLE X

MEANS AND STANDARD DEVIATIONS IN MM OF FOUR BACULUM MEASUREMENTS FOR FOUR GROUPS OF WOOD RATS

Group	N	Length Mean	Length S.D.	Lateral Width Mean	Lateral Width S.D.	Dorsal-ventral Width Mean	Dorsal-ventral Width S.D.	Shaft Diameter Mean	Shaft Diameter S.D.
I	10	7.29	0.86	3.02	0.46	1.44	0.31	0.66	0.12
II	10	7.00	0.73	2.89	0.34	1.50	0.28	0.80	0.09
III	9	7.63	0.59	2.93	0.23	1.58	0.25	0.77	0.10
IV	5	7.48	0.55	2.56	0.53	1.52	0.29	0.72	0.08

Baculum Measurements

Means and standard deviations of four baculum measurements were determined for 10 specimens in Group I, 10 specimens in Group II,

nine specimens in Group III, and five specimens in Group IV and are presented in Table X.

Quantitative Measurements Within Groups

In order to determine possible relationships between each skull character and all other skull characters, between each body measurement and all other body measurements, and between each baculum measurement and all other baculum measurements, simple linear correlations were determined within each group. Correlation coefficients were calculated and the levels of significance of the coefficients were determined for each comparison.

Table XI shows correlation coefficients and levels of significance of coefficients determined by comparing each skull measurement of each group with each of the other skull measurements of the group. It can be seen that in all groups zygomatic breadth and nasal length vary with condylonasal length, whereas, least interorbital constriction width varies with condylonasal nasal length only in Groups I and III. No significant correlation exists in any of the four groups between length of the upper cheek tooth row and skull length. All groups show correlation between zygomatic breadth and nasal length and except for Group IV, there is correlation between zygomatic breadth and interorbital constriction width. Except for correlation between nasal length and cheek tooth row length of Group IV, nasal length and cheek tooth row length, and interorbital constriction width and cheek tooth row length are not significantly correlated.

Table XII shows correlation coefficients and levels of significance of coefficients resulting from comparing each body measurement of each

TABLE XI

CORRELATION COEFFICIENTS AND LEVELS OF SIGNIFICANCE OF CORRELATION COEFFICIENTS DETERMINED BY COMPARING EACH SKULL MEASUREMENT OF EACH GROUP WITH EACH OF THE OTHER SKULL MEASUREMENTS OF THE GROUP

	Group I (N=96)				Group II (N=83)				Group III (N=27)				Group IV (N=15)			
Characters	Correl. Coeff.	Sig. Level .05	.01	.001	Correl. Coeff.	Sig. Level .05	.01	.001	Correl. Coeff.	Sig. Level .05	.01	.001	Correl. Coeff.	Sig. Level .05	.01	.001
1 vs 2	+0.8416	+	+	+	+0.8084	+	+	+	+0.7755	+	+	+	+0.8114	+	+	+
1 vs 3	+0.3910	+	+	+	+0.7679	+	+	+	+0.7393	+	+	+	+0.8251	+	+	+
1 vs 4	+0.3692	+	+	+	+0.1475	0	0	0	+0.3844	+	0	0	+0.0663	0	0	0
1 vs 5	+0.0603	0	0	0	+0.1221	0	0	0	+0.0538	0	0	0	+0.5914	0	0	0
2 vs 3	+0.3713	+	+	+	+0.5754	+	+	+	+0.5123	+	+	+	+0.6116	+	+	0
2 vs 4	+0.2153	+	0	0	+0.3023	+	+	0	+0.6259	+	+	+	+0.3977	0	0	0
2 vs 5	-0.0463	0	0	0	-0.0509	0	0	0	+0.0418	0	0	0	+0.4492	0	0	0
3 vs 4	-0.0420	0	0	0	+0.0834	0	0	0	+0.3727	0	0	0	+0.0321	0	0	0
3 vs 5	+0.0136	0	0	0	+0.1245	0	0	0	-0.1060	0	0	0	+0.7584	+	+	0
4 vs 5	+0.1481	0	0	0	-0.0052	0	0	0	+0.1500	0	0	0	+0.0891	0	0	0

Char. 1 = condylonasal length
Char. 2 = zygomatic breadth
Char. 3 = nasal length
Char. 4 = least interorbital constriction width
Char. 5 = left upper cheek tooth row length

TABLE XII

CORRELATION COEFFICIENTS AND LEVELS OF SIGNIFICANCE OF CORRELATION COEFFICIENTS DETERMINED BY COMPARING EACH BODY MEASUREMENT OF EACH GROUP WITH EACH OF THE OTHER BODY MEASUREMENTS OF THE GROUP

	Group I (N=33)				Group II (N=39)				Group III (N=24)				Group IV (N=14)			
Characters	Correl. Coeff.	Sig. Level .05	.01	.001	Correl. Coeff.	Sig. Level .05	.01	.001	Correl. Coeff.	Sig. Level .05	.01	.001	Correl. Coeff.	Sig. Level .05	.01	.001
1 vs 2	+0.6474	+	+	+	+0.7900	+	+	+	+0.8415	+	+	+	+0.8922	+	+	+
1 vs 3	+0.4560	+	+	0	+0.2639	0	0	0	+0.7832	+	+	+	+0.2724	0	0	0
1 vs 4	+0.5197	+	+	+	+0.4784	+	+	0	+0.4707	+	+	0	+0.7449	+	+	+
2 vs 3	+0.3654	+	0	0	+0.2164	0	0	0	+0.7233	+	+	+	+0.3764	0	0	0
2 vs 4	+0.4775	+	+	0	+0.2160	0	0	0	+0.4044	+	0	0	+0.8012	+	+	+
3 vs 4	+0.3610	+	0	0	+0.0721	0	0	0	+0.5789	+	+	0	+0.2807	0	0	0

Char. 1 = total length
Char. 2 = tail length
Char. 3 = rear foot length
Char. 4 = ear length

group with each of the other body measurements of the group. Groups I and III show significant correlations between all body measurement comparisons. Total length and tail length, and total length and ear length are significantly correlated in Groups II and III. In addition, Group IV shows a significant correlation between tail length and ear length.

Table XIII shows correlation coefficients and levels of significance of coefficients determined by comparing each baculum measurement of each group with each of the other baculum measurements for the group. All four baculum measurements for Group I are significantly correlated. Groups II and III exhibit a significant correlation between baculum length and lateral width. Lateral width and dorso-ventral width are significantly correlated in Group II, and baculum length and dorso-ventral width are significantly correlated in Group III. In Group IV lateral and dorso-ventral width, lateral width and shaft diameter, and dorso-ventral width and shaft diameter are significantly correlated.

Quantitative Measurements Among Groups

Comparisons of the means of skull, body, and baculum measurements for each group were made with the respective mean measurements of all other groups. Results from an analysis of variance (AOV) and Duncan's new multiple range test applied to skull and body measurement means are shown in Tables XIV and XV. The analyses showed no significant differences among mean baculum measurements of the four groups.

A summary of significant differences between mean skull measurements of the four groups (Table XIV) shows: Groups I and II differ in one character (least interorbital constriction); Groups I and III

TABLE XIII

CORRELATION COEFFICIENTS AND LEVELS OF SIGNIFICANCE OF CORRELATION COEFFICIENTS DETERMINED BY COMPARING EACH BACULUM MEASUREMENT OF EACH GROUP WITH EACH OF THE OTHER BACULUM MEASUREMENTS OF THE GROUP

	Group I (N=10)				Group II (N=10)				Group III (N=9)				Group IV (N=5)			
	Correl.	Sig. Level			Correl.	Sig. Level			Correl.	Sig. Level			Correl.	Sig. Level		
Characters	Coeff.	.05	.01	.001	Coeff.	.05	.01	.001	Coeff.	.05	.01	.001	Coeff.	.05	.01	.001
1 vs 2	+0.6712	+	0	0	+0.8338	+	+	+	+0.8353	+	+	+	+0.1966	0	0	0
1 vs 3	+0.9023	+	+	+	+0.3879	0	0	0	+0.7073	+	0	0	-0.2059	0	0	0
1 vs 4	+0.8020	+	+	0	+0.1306	0	0	0	+0.4691	0	0	0	-0.0516	0	0	0
2 vs 3	+0.8931	+	+	+	+0.6340	+	0	0	+0.5936	0	0	0	+0.9210	+	+	0
2 vs 4	+0.5920	+	0	0	+0.0723	0	0	0	+0.3225	0	0	0	+0.9391	+	+	0
3 vs 4	+0.7747	+	+	0	+0.3371	0	0	0	+0.5214	0	0	0	+0.9346	+	+	0

Char. 1 = length
Char. 2 = lateral width
Char. 3 = dorso-ventral width
Char. 4 = diameter of shaft

TABLE XIV

ANALYSIS OF VARIANCE (AOV) AND DUNCAN'S NEW MULTIPLE RANGE TEST OF SKULL MEASUREMENT RELATIONSHIPS AMONG FOUR GROUPS OF WOOD RATS. ALL MEASUREMENTS ARE IN MM. MEANS DESIGNATED BY THE SAME LOWER CASE SUPERSCRIPT ARE NOT SIGNIFICANTLY DIFFERENT AT THE 0.05 LEVEL

	Condylonasal Length		Zygomatic Breadth		LIC		Nasal Length		LUTR	
	AOV		AOV		AOV		AOV		AOV	
Source	d.f.	m.s.	d.f.	m.s.	d.f.	m.s.	d.f.	m.s.	d.f.	m.s.
e.b.t.	3	26.21	3	4.84	3	2.05	3	4.35	3	9.37
e.w.g.	221	4.06	220	1.74	226	0.13	219	5.94	226	29.41
s	2.01		1.32		0.36		2.44		5.42	
Groups	N	Means	N	Means	N	Means	N	Means	N	Means
I	96	49.03^{a}	95	26.35^{ab}	97	6.57^{a}	96	19.34^{a}	97	9.46^{a}
II	83	48.32^{a}	84	26.18^{b}	86	6.23^{b}	84	19.00^{a}	86	10.22^{a}
III	27	50.01^{b}	27	26.63^{a}	28	6.23^{b}	27	19.61^{a}	28	9.73^{a}
IV	15	47.89^{a}	14	25.51^{c}	15	6.44^{ab}	12	18.71^{a}	15	9.53^{a}

LIC = least interorbital constriction
LUTR = left upper cheek tooth row
e.b.t. = error between treatments
e.w.g. = error within groups

differ in two characters (skull length and least interorbital constriction); Groups I and IV differ in one character (zygomatic breadth); Groups II and III differ in two characters (skull length and zygomatic breadth); Groups II and IV differ in one character (zygomatic breadth); and Groups III and IV differ in two characters (skull length and zygomatic breadth).

A summary of the significant differences between mean body measurements of the four groups (Table XV) shows: Groups I and II differ in two characters (total and tail length); Groups I and III differ in one character (ear length); Groups I and IV differ in one character (total length); Groups II and III differ in two characters (tail length and ear length); Groups II and IV exhibit no significant differences; and Groups III and IV differ in one character (ear length).

The results of summarizing significant and non-significant differences among the nine skull and body measurements are presented in Table XVI.

Data in Table XVI show Groups II (N. micropus) and IV (possible hybrids) to be most similar and Groups II (N. micropus) and III (known hybrids) to be least similar. Groups I and II, I and III, I and IV, and III and IV show an intermediate degree of similarity.

TABLE XV

ANALYSIS OF VARIANCE (AOV) AND DUNCAN'S NEW MULTIPLE RANGE TEST OF BODY MEASUREMENT RELATIONSHIPS AMONG FOUR GROUPS OF WOOD RATS. ALL MEASUREMENTS ARE IN MM. MEANS DESIGNATED BY THE SAME LOWER CASE SUPERSCRIPT ARE NOT SIGNIFICANTLY DIFFERENT AT THE 0.05 LEVEL

	Total Length		Tail Length		Rear Foot Length		Ear Length	
	AOV		AOV		AOV		AOV	
Source	d.f.	m.s.	d.f.	m.s.	d.f.	m.s.	d.f.	m.s.
e.b.t.	3	2161.35	3	660.53	3	7.49	3	18.07
e.w.g.	110	587.63	110	129.26	118	2.71	120	4.05
s	24.16		11.37		1.66		2.01	
Groups	N	Means	N	Means	N	Means	N	Means
I	33	369.55^{a}	33	152.58^{a}	34	38.64^{a}	34	26.60^{a}
II	39	352.55^{b}	39	143.52^{b}	42	37.77^{a}	43	26.70^{a}
III	24	363.04^{ab}	24	152.40^{a}	28	38.60^{a}	28	28.16^{b}
IV	14	352.13^{b}	14	147.53^{ab}	14	37.73^{a}	15	26.37^{a}

e.b.t. = error between treatments
e.w.g. = error within groups

TABLE XVI

A SUMMARY OF SIGNIFICANT (+) AND NON-SIGNIFICANT (0) DIFFERENCES AT THE 0.05 LEVEL FOR NINE MEAN SKULL AND BODY MEASUREMENTS AMONG FOUR GROUPS OF WOOD RATS. SKULL MEASUREMENTS ARE CONDYLONASAL LENGTH (CNL), ZYGOMATIC BREADTH (ZB), LEAST INTERORBITAL CONSTRUCTION (LIC), NASAL LENGTH (NL), AND LEFT UPPER TOOTH ROW (LUTR). BODY MEASUREMENTS ARE TOTAL LENGTH (TL), TAIL LENGTH (TAL), REAR FOOT LENGTH (RFL), AND EAR LENGTH (EL)

Groups	CNL	ZB	LIC	NL	LUTR	TL	TAL	RFL	EL	Totals +	Totals 0
I vs II	0	0	+	0	0	+	+	0	0	3	6
I vs III	+	0	+	0	0	0	0	0	+	3	6
I vs IV	0	+	0	0	0	+	0	0	0	2	7
II vs III	+	+	0	0	0	0	+	0	+	4	5
II vs IV	0	+	0	0	0	0	0	0	0	1	8
III vs IV	+	+	0	0	0	0	0	0	+	3	6

CHAPTER V

DISCUSSIONS AND CONCLUSIONS

Mayr (1963:19) defined species as follows, "Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." This definition is now widely accepted by biologists and represents the biological species concept. However, most early work in animal taxonomy occurred prior to the wide acceptance of this concept, and classification of species was based, for the most part, on morphological and anatomical characteristics of specimens from type localities. Only recently have the ecological and ethological implications inherent in the phrases "interbreeding natural populations" and "reproductive isolation" been considered as species criteria.

Goldman and others (Hall and Kelson, 1959; Finley, 1958; Blair, et al., 1957; and Cockrum, 1952) have shown that the two species with which this study was concerned are morphologically distinct where allopatric. Data collected during this study are in general agreement with these investigators.

Colors for the two species, except for seasonal variations, are essentially the same as described by Hall and Kelson. Mean body measurements for the two species (Table IX) fall within their ranges. Skulls of the two are described by Hall and Kelson as being similar and only one significant difference in skull measurements was detected in

this study (Table XIV). A significant difference exists between the two species for least interorbital constriction width. N. floridana averaged 6.57 mm for least interorbital constriction whereas, the same measurement for N. micropus was 6.23 mm. This slight but significant difference would hardly be noticeable if only visual observations were relied on to detect variation.

Presence of a posterior median spine on the hard palate of N. micropus and absence of the spine in N. floridana are significant characters for specimens of the two species included in this study, as are intermediate-to-wide sphenopalatine vacuities and a straight anterior palatal spine for N. micropus and narrow vacuities and a forked anterior palatal spine for N. floridana (Tables III and V).

Attempts to determine whether the anterointernal re-entrant angle of the first molar was shallow or moderately well-developed were unsuccessful because of variations in tooth wear among individuals of the same and different species. Finley (1958) also concluded depth of the re-entrant angle was a character of questionable value for distinguishing between the species.

Shape of the baculum was significantly different between the species (Table VII), but none of the four quantitative measurements taken of each baculum were significantly different between the species.

Burt and Barkalow (1942) listed the following baculum measurements in mm for two N. m. micropus males: length, 6.25-6.99; dorso-ventral diameter of base, 1.61-1.70; lateral diameter of base, 3.21; diameter of shaft, 0.70-0.89. These compare with means of 7.00, 1.50, 2.89, and 0.80 mm for 10 N. micropus males of this study (Table X).

Their measurements, in the same order as above, for five

N. f. baileyi were 7.28, 1.52, 3.03, and 0.75 mm. These compare with 7.29, 1.44, 3.02, and 0.66 mm for nine N. f. osagensis and one N. f. osagensis and one N. f. campestris of this study (Table X).

Line drawings of the bacula of the two species by Burt and Barkalow show a N. micropus baculum to be essentially like the baculum for N. micropus (Fig. 15), when viewed from above and from the proximal end. However, their sketch of the N. f. floridana baculum does not show the pronounced shoulders proximal to the shaft and at the distal end of the expanded base that were so characteristic of the N. f. osagensis and N. f. campestris of this study.

After comparing the various characters of the two species used in this study with descriptions provided by competent mammalian taxonomists, and after studying the ranges of the two species in North America, it seems safe to conclude that each species is morphologically distinct to some degree. However, the question remains, are the groups composing one species reproductively isolated from the groups of the other?

This study has shown conclusively that successful crosses can be made between captive specimens of the eastern wood rat and the southern plains wood rat. Fertile hybrids resulted from F_1, F_2, and back crosses (fertility of F_3 young was not tested because all were sacrificed before sexual maturity).

Mayr (1963:112) had the following to say about artificial hybrids:

> It is well known that many species can be crossed in captivity, but do not produce hybrids where their ranges overlap in nature. For instance, many sympatric species of Drosophila can be hybridized in the laboratory (Patterson and Stone, 1952). The same is true of birds and many species of fishes (for instance, in the genus Xiphophorus). The production of such hybrids has been cited as the basis of two kinds of wrong conclusions: first, that the hybridization is frequent in the animal kingdon;

> and second, that the possibility of such hybridization indicates conspecificity, particularily when the hybrids produced are fertile.

When laboratory hybridization of the two species was attempted in order to determine the presence or absence of possible isolating mechanisms between the species and so that morphological and anatomical characters of laboratory hybrids could be compared with possible hybrid specimens taken from areas of sympatry of the parent species, some rather definitive results were obtained. Captive specimens of the two species are not reproductively isolated as indicated by the fact that 10 of 15 different crosses attempted between hybrids yielded a total of 91 hybrid offspring. Furthermore, there was no visible behavioral isolating mechanism that prevented mating in any of the 15 attempted crosses. Gestation periods, litter sizes, birth weights, stage of development at birth, and development following birth were essentially the same for hybrids and both species, and age of sexual maturity, breeding seasons, and mating behavior were similar for hybrids and both species.

It has already been shown that the two species are sympatric in a small area in westcentral Oklahoma. They are not ecologically isolated in the area of sympatry and it has been shown that in certain areas where the species are allopatric each species can survive successfully in the habitat type characteristic of the other species.

Evaluation of the relationships between the two forms hinges, therefore, on the existence and nature of populations in the zone of sympatry. Population density and morphological characteristics of intermediate forms in the zone must be determined before status of the parental types can be evaluated.

Nine specimens collected in the region of sympatry appeared to be hybrids of the two species. Others collected in the area were identified as probably being either N. floridana or N. micropus. Because of the high probability that hybrid specimens were present, and the possibility that some introgression had occurred in the population, all specimens from the area of sympatry were designated as Group IV wood rats and referred to as possible hybrids.

Comparisons of qualitative and quantitative data for N. floridana, N. micropus, known hybrids, and possible hybrids - Groups I, II, III, and IV respectively - will reveal possible relationships among groups.

Table III shows approximately 40% of known hybrids and 40% of possible hybrids have a forked anterior palatal spine. The remaining 60% of both groups have straight anterior palatal spines, a feature characteristic of N. micropus.

Table IV shows 37% of known hybrids and 12% of possible hybrids have a median posterior palatal spine characteristic of N. micropus. The remaining 63% and 88% for the two groups lack a posterior spine, a characteristic of N. floridana.

Table V shows 38% of known hybrids and 53% of possible hybrids have intermediate and wide sphenopalatine vacuities characteristic of N. micropus. Sixty-two percent of known hybrids and 47% of possible hybrids have narrow vacuities characteristic of N. floridana.

Table VI shows six pelage colors for known hybrids and five for possible hybrids. All N. micropus and N. floridana exhibited their respective species pelage color.

Table VII shows 41% of known hybrids had bacula of the characteristic N. micropus-shape, 16% had bacula like N. floridana, and 41% had

bacula of a shape intermediate between the two species. Of the four bacula from possible hybrids, one was shaped like a N. floridana baculum and the other three were intermediate between N. floridana and N. micropus.

A summary of the comparisons of qualitative and quantitative data for the four groups shows the possible hybrid group to be no more like known hybrids than either of the parent species. Of the five qualitative characters relied on in this study, a majority of both known and possible hybrids exhibited only one characteristic considered typical for N. micropus. Each of the two groups had the majority of specimens exhibiting two characteristics considered typical of N. floridana, although the two were different characters. Both groups displayed a much greater range of pelage colors than either parent species, and baculum shape varied more for known and possible hybrids than for either parent species.

The greatest variations appeared in comparisons of quantitative characters. Comparisons of quantitative skull measurements within each group (Table XI) show possible hybrids to be similar to N. floridana in seven measurement comparisons, to N. micropus in eight comparisons, and to known hybrids in seven comparisons. Body measurement comparisons (Table XII) show similarities of three, five and three between possible hybrids and N. floridana, N. micropus, and known hybrids, respectively. Comparisons of baculum measurements (Table XIII) show three similarities between possible hybrids and N. floridana, three between possible hybrids and N. micropus, and one between possible hybrids and known hybrids.

Comparisons of significant differences between mean skull and body

measurements among the four groups (Table XVI) show one less significant difference between mean skull and body measurements of possible hybrids and N. micropus than between possible hybrids and N. floridana, but there was one more significant difference between possible hybrids and known hybrids than between possible hybrids and N. floridana and two more than between possible hybrids and N. micropus. One out of five skull measurements of possible hybrids and N. floridana was significantly different, one out of five of possible hybrids and N. micropus and two out of five of possible hybrids and known hybrids. One out of four body measurements of possible hybrids and N. floridana was significantly different, one out of four of possible hybrids and known hybrids, and zero out of four of possible hybrids and N. micropus. There were no significant differences between baculum measurements of any of the four groups.

Specimens from the area of sympatry exhibit some characteristics of each of the parent species but are not sufficiently similar to either species to be considered identical. The specimens probably compose a mixed population consisting of some hybrids, others that represent various degrees of introgression, and some individuals of both parent species. The latter are probably added to the population as a result of dispersal of N. floridana from the more mesic areas to the east and of N. micropus from the more xeric areas to the west. Assuming gene flow into the population from neighboring areas in which the parental species are allopatric, and the existence of many generations of hybrids containing various recombinations of parental traits, it seems logical that the natural hybrid population would be more variable than the laboratory hybrid population in which hybridization and

introgression had occurred for only three generations. Also, the region of sympatry appears to provide a "hybrid habitat" (Anderson, 1948:7), to which natural hybrids may be as well adapted as either parent species. The close proximity and interspersion of bottomland forest and savannah - sage - grassland in the area of sympatry forms this "hybrid habitat."

If the two forms hybridize they are not reproductively isolated. It appears that because of the absence of reproductive isolation the two forms should not be considered as separate species but as subspecies. However, Mayr (1963:134) had the following to say about breakdown of isolating mechanisms between species:

> Occasional breakdown of isolating mechanisms has been found to occur in most taxonomically well-known groups of animals. Relatively most frequent among the various forms of hybridism is the occurrence of occasional sterile, or at least nonreproducing, species hybrids. Evidence of backcrossing with one or both of the parental species is found much more rarely, and rarer still is the complete breakdown of the barrier between species resulting in hybrid swarms.

Analysis of the Group III (possible hybrid) population indicates that hybridization and introgression has occurred. Too few data are available at this time to allow speculation on the presence or absence of a hybrid swarm in the area of hybridization. In fact, recognition of a hybrid swarm, if one exists, is dependent on recognition of N. floridana and N. micropus as separate species.

Bigelow (1965:457) recognized the interpretation of hybridization as a problem in sematics and questions Mayr's (1963:111) claim that the definition of hybridization as the crossing of individuals belonging to two different species "results in circular argument because the decision whether or not to include two populations in the same or in two different species may depend on the occurrence of hybridization."

Bigelow said, "If the term hybridization is so defined it cannot be used, by definition, until the presence of two different species can be assumed."

Much more field work needs to be carried out along the North Canadian and Cimarron rivers in Oklahoma in the vicinities of the known area of sympatry along the North Canadian and the area of probable sympatry along the Cimarron in order to establish limits of the hybrid zones, if they exist. A comprehensive analysis of wood rat karotypes and morphological characters of populations within and surrounding the hybrid zone(s) will be helpful in determining the extent of gene flow between populations of the parent species. LeFever and Spencer (personal communication) have preliminary data on chromosome numbers and karyotypes of the two species.

Available data indicate the hybrid zone in the stabilized dunes along the north side of the North Canadian River is at least one-half mile long. It could be as much as eleven miles, which is the distance separating the two points where homogeneous populations of the two species were collected. However, the investigator does not believe the area exceeds one mile in length.

Nothing in the literature describes recent mammalian distribution within the study area, and one can only speculate about the possible distribution of the parent species in the past. The family Cricetidae has a geological range from the Oligocene to the Recent in North America (Walker, 1964), and Scott (1962:188) said: "No doubt all our Recent genera of North American rodents were in existence in the Pleistocene." If one assumes that wood rats were present during the Pleistocene and their ecological requirements were at least somewhat

similar to present requirements, it is not inconceivable that advancing ice sheets separated the then-existing species of Neotoma into at least two groups. One group could have been the forerunner of, or was, the present mesic-adapted N. floridana that was confined to the eastern or southern parts of the present United States and, the other group of southwest North America or Central America, could have been the source of present day xeric-adapted species, of which N. micropus is a representative. Through adaptation, and as a result of a warming trend accompanying the receding Pleistocene ice sheets, it is possible that eastern-southeastern wood rats moved north and west and southwestern wood rats extended their range north and east until a zone of secondary contact was established in what is now the area of sympatry.

Mayr (1963:502) said: "When a geographical isolate reestablishes contact with the parental species (owing to the breakdown of the isolating barriers) before the isolating mechanisms have been perfected, a hybrid zone will develop in the contact zone." He further stated that most hybrid zones in the temperate region are the result of fusion of populations expanding into the area vacated by retreating ice, and described the interbreeding of the two previously-isolated populations in the zone of contact as secondary integradation in cases where the interbreeding populations have not yet reached the species level.

Blair (1951:22) had the following to say about the influence of changes on secondary intergradation:

> The shifting of populations, both the spatial isolation of parts of previously interbreeding populations and the reestablishment of contact by previously isolated populations, apparently results from major, regional changes in environment. Present day distribution of species, of speciating allopatric populations, and of zones of secondary integradation between previously separate populations must be interpreted in relation to Pleistocene climatic shifts.

He also contended, based on the assumption that rates of evolution and of spread are different in different species, that the population pairs formed by Pelistocene isolation in Florida and Mexido should vary in their stage of speciation and five stages can be recognized. Two of the stages are represented by: 1. populations that are now sympatric due to post-glacial spread after effective isolating mechanisms were developed and, 2. populations that underwent a post-glacial spread and established contact before they had developed effective isolating mechanisms.

Blair (1951:24) cited several examples of previously-isolated populations that have spread until their ranges meet or overlap. Among the cited species were N. floridana and N. micropus whose ranges meet but do not overlap in central Texas and interbreeding does not occur. If this is true, the absence of sympatry and interbreeding in central Texas and the presence of sympatry and interbreeding in central Oklahoma can probably be attributed to the lack of "hybrid habitat" in the zone of contact in central Texas.

The two wood rats with which this study was concerned appear to be sufficiently dissimilar morphologically to warrant designation as separate species. However, in view of the high probability that they are not reproductively isolated and that they interbreed in the area of sympatry, their species status is questionable if one recognizes the biological species concept as valid. Their present distribution and the fact that they are sympatric, at least in one area in west-central Oklahoma, seems to indicate that the area of sympatry is a zone of secondary integradation of two previously-isolated populations which have not yet reached the species level.

CHAPTER VI

SUMMARY

1. A study of two species of wood rats, Neotoma floridana (Ord) and Neotoma micropus Baird, that occur in Kansas and Oklahoma was conducted from January, 1964, to December, 1966. The two species were known to be allopatric throughout most of their ranges. The possibility existed that they may be sympatric in certain areas of westcentral Oklahoma. Because of the probability of sympatry and the possibility of hybridization in the area of sympatry, a study of the species status of the two wood rats was undertaken based on the criteria of the biological species concept.

2. Specimens of the two species from Kansas and Oklahoma were collected for morphological comparisons. Distribution and ecology data were accumulated for Oklahoma specimens, and reproduction data were collected from specimens in both states.

3. Laboratory populations of the two species were maintained for hybridization studies, as were populations in an outside enclosure.

4. One area of sympatry and a second area of probable sympatry were located in Major County, Oklahoma.

5. Specimens of the two species, laboratory hybrids, and possible hybrids from the area of sympatry were assigned to separate groups for analysis and comparisons of qualitative and quantitative morphological characters. Mating behaviors, reproduction data, and postnatal

development of the parent species and laboratory hybrids were compared.

6. Three generations of laboratory hybrids and intergrades were produced. F_1, F_2, and intergrade offspring were fertile. Fertility for the F_3 generation was not established.

7. Mating behavior, reproductive seasons, litter sizes and post-natal development of laboratory hybrids and the parent species were similar. Isolating mechanisms that prevent interspecific crosses or that reduce the success of such crosses were not in evidence in the laboratory hybridization study.

8. Field collections of the parent species showed the mesic adapted eastern wood rat, N. floridana, living in woodlands and along rock outcrops with woody cover. The southern plains wood rat, N. micropus, ranges throughout the more xeric short grass-prickly pear and mesquite-prickly pear-grasslands. However, each species was collected from habitat usually considered typical for the other species.

9. Specimens from the area of sympatry in Major County, Oklahoma, when compared with each of the parent species and laboratory hybrids, appeared to represent a mixed population consisting of specimens of both parent species, some hybrids, and others of varying degrees of introgression.

10. Analysis of qualitative and quantitative data for the four groups showed the parent species to be morphologically distinct from each other, the laboratory hybrids to be distinct from each parent species, and specimens from the area of sympatry to be unlike either parent species or laboratory hybrids.

11. Because the parent populations are not reproductively isolated as shown by successful laboratory hybridization and the high

probability of natural hybridization in the area of sympatry, the area of sympatry is probably a zone of secondary integration of the two previously isolated parent populations which have not yet attained the species level.

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