Downloaded from SHAREOK. Persistent Handle URL: https://hdl.handle.net/11244/1725

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

STUDIES ON THE ETHOLOGY OF THE NORTHERN GRASSHOPPER MOUSE (ONYCHOMYS LEUCOGASTER)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

DAVID GRAY RUFFER

Norman, Oklahoma

1964

STUDIES ON THE ETHOLOGY OF THE NORTHERN GRASSHOPPER MOUSE (ONYCHOMYS LEUCOGASTER)

APPROVED BY

DISSERTATION COMMITTEE

ACKNOWLEDGEMENTS

I am deeply indebted to Dr. Charles C. Carpenter who suggested this problem and under whose direction it was conducted. His obvious enthusiasm for ethology and keen interest in animals gave me much encouragement during my graduate program. For his advice and counsel, for the use of space and equipment in the Animal Behavior Laboratory, and for the encouragement needed by any graduate student, I express my sincere thanks.

Drs. Howard P. Clemens, Arthur W. Ghent, William T. Penfound, and Carl D. Riggs have read the manuscript and offered valuable help and criticism.

Financial assistance from the Department of Zoology in the form of a Graduate Assistantship during the 1960-1961, 1961-1962 academic years and the first semester of the 1962-1963 academic year; and a Special Instructorship during the Spring Semester, 1962-1963 and the fall semester 1963-1964 has enabled me to pursue my graduate program. Assistance in the form of a National Science Foundation Grant-in-aid from the University of Oklahoma Biological Station made it possible for me to use the facilities at the station during the three summers of 1961, 1962 and 1963 (N. S. F. Grants G8289 and G23583).

I am also indebted to Dr. Carl D. Riggs for making available the facilities of the University of Oklahoma Biological Station. Drs. Paul Buck, Robert Burns, Robert Clarke, Robert Lynn, Howard McCarley, and Kirk Moseley, John Preston, and Robert Richardson have supplied me with animals at various times. Bob Richardson also accompanied me on several field trips and gave valuable assistance in the field.

Finally, I am especially grateful to my wife Marilyn for her encouragement and assistance during this study.

TABLE OF CONTENTS

Page

LIST OF TABLES vii

LIST OF FIGURES viii

CHAPTER

I. INTRODUCTION 1

Taxonomic Relationships 2
Distribution and Ecology 8
Methods and Materials 12

II. SHELTER-SEEKING BEHAVIOR 17

Burrow Types 17
Burrow Climate 22
Burrowing Behavior 22
Use of Other Burrows 27

III. AGONISTIC BEHAVIOR 28

General Aspects 28
Types of Agonistic Encounters 31
Territoriality 36

IV. SEXUAL BEHAVIOR 38

Courtship and Copulation 39
Gestation and Litters 43
Ontogeny of Behavior 44
Paternal Care of the Young 46
Play 47
Adult Molt 48

V. INVESTIGATIVE, ELIMINATIVE, AND GROOMING BEHAVIOR 50

TABLE OF CONTENTS (cont.)

Page

V. (cont.)

Ingestive Behavior 50
Eliminative Behavior 53
Grooming Behavior 54

VI. MISCELLANEOUS OBSERVATIONS 57

Communication 57
Investigative Behavior 59
Use of the Tail 61
Swimming 63

VII. DISCUSSION 65

Review of the Ethogram 65
Comparison of Onychomys and Peromyscus Behavior . 86
Comments on Behavioral Evolution within Onychomys . 89

SUMMARY 92

LITERATURE CITED 95

APPENDIX 103

LIST OF TABLES

Table | Page

1. Mammals found to be associated with Onychomys 14

2. Frequency of agonistic encounters during the first and third half hour of contact for O. leucogaster 34

3. Skin and skull measurements of 8 male and 12 female Onychomys leucogaster used in this study 104

LIST OF FIGURES

Figure		Page
1.	Phylogeny of Some Families of Rodents According to Wood, 1959	5
2.	Phylogeny of the genera and subgenera of Nearactic Cricetinae according to Hoffmeister, 1944	6
3.	Geographic Distribution of Onychomys leucogaster and Onychomys torridus	9
4.	Western division of the Upper and Lower Sonoran Life Zones	11
5.	Two Views of the Enclosure Used in This Study	16
6.	The Nest Burrow of Onychomys leucogaster The Retreat Burrow of Onychomys leucogaster	18
7.	A Typical Arrangement of Onychomys leucogaster Burrows within an Enclosure	21
8.	Temperatures at the Sand Surface and Within a Nest Burrow on 25 July, 1963	23
9.	Temperatures at the Surface and 1, 6 and 12 Inches Deep in the Sand Within an Enclosure on 9 July, 1963	24
10.	Temperatures at the Surface, One Inch Above the Surface and Within a Nest Burrow in an Enclosure	25
11.	Two Agonistic Postures of Onychomys leucogaster	30
12.	Three Postures of Onychomys leucogaster	33
13.	Some Sexual Postures of Onychomys leucogaster	40
14.	Patterns of Adult Molt in O. leucogaster	49
15.	Feeding Postures of O. leucogaster	52
16.	Mutual Grooming Posture of the O. leucogaster Being Groomed	56
17.	Onychomys leucogaster Investigative Postures	60
18.	Tail Positions in O. leucogaster Under Differing Degrees of Unfamiliarity With the Enclosure	62

STUDIES ON THE ETHOLOGY OF THE NORTHERN GRASSHOPPER MOUSE (ONYCHOMYS LEUCOGASTER)

CHAPTER I

INTRODUCTION

Prior to the early part of this century, the study of animal behavior was characterized by a lack of objectivity in observation, an anthropomorphic interpretation of data, and a lack of concern for systematics. From 1911 to the present time the field of ethology has grown and has introduced and developed the objective approach. The ethologist is not interested in behavior per se, but in its survival value to the species. Early work by Oskar Heinroth, Julian Huxley, and Konrad Lorenz; and later work by Karl von Frisch, Niko Tinbergen, and others have developed a body of thought and ideas peculiar to ethology and on which many zoologists are currently basing ethological studies of a wide variety of species. Interest in the field of ethology is rapidly increasing and such studies will contribute more and more to our knowledge of animal relationships.

The behavior of members of the rodent family Cricetidae has been studied by many workers (Dice, 1932; Burt, 1940; Petter, 1957;

McCarley, 1958; Kaye, 1961; Eisenberg, 1962, 1963), and the ethology of several species is quite well known, particularly members of the genus Peromyscus. These studies have also contributed much to our knowledge of mammalian speciation. Few studies, however, have been made on the behavior of grasshopper mice (Genus Onychomys). Bailey and Sperry (1929) recorded observations on the life history and habits of this genus from notes on a group of five individuals collected over a 35-year period. Scattered notes, mostly quoting Bailey and Sperry, appeared in various regional and local faunal lists and similar works but no detailed studies were conducted until 1960 when Egoscue made a laboratory study of some aspects of the behavior of O. leucogaster utahensis. Clark (1962a, b) studied aggressive behavior in the same subspecies and examined the effect of chlorpromazine on this behavior.

Eibel-Eibesfeldt and Kramer (1958) and Tinbergen (1951) emphasized the importance of the ethogram (complete inventory of the behavior patterns) of a species as a prerequisite to further studies on the ethology of that species. This idea has considerable merit when one considers that without a knowledge of the ethogram of a species, isolated postures observed in a study of only one aspect of the total behavior are difficult at best to analyze. Clark (1962a) has proposed the use of the grasshopper mouse (Onychomys leucogaster) for studies of aggression and as a general purpose laboratory animal.

The purpose of the present study was to determine the ethogram of O. leucogaster. It is not meant to be a definitive study, but will serve

as a basis for more detailed work on various problems associated with certain of the behavior patterns.

Taxonomic Relationships

Onychomys leucogaster fits into the taxonomic heirarchy as follows (after Simpson, 1945 and Hoffmeister, 1944):

Order Rodentia

Suborder Myomorpha

Superfamily Muroidea

Family Cricetidae

Subfamily Cricetinae

Tribe Hesperomyini

Grasshopper Mouse Group

Genus Miochomys (Extinct)

Genus Symmetrodontomys (Extinct)

Genus Onychomys

This also agrees with the revised rodent classification of Wood (1955). There are two extant species in the genus Onychomys, O. leucogaster and O. torridus. Hoffmeister (1944) listed five extinct species: O. martinii, O. bensoni, O. fossilis, O. gidleyi, and O. pedroensis, all from Pleistocene, and middle and upper Pliocene of North America.

Wood (1959) proposed that the family Cricetidae diverged from the Sciuravidae in middle Eocene and that the Muridae did not evolve until

Miocene. A portion of his proposed phylogeny of the Rodentia is given in Figure 1. According to Hoffmeister (1944), the grasshopper mice probably diverged from the genus Peromyscus during or prior to Upper Miocene as the genus Miochomys from which Symmetrodontomys and Onychomys evolved in middle Pliocene (Fig. 2).

Maximillian, Prince of Wied, collected the first grasshopper mouse in 1833 at the Mandan Indian villages near Fort Clark, North Dakota. He placed it with the present day genus Clethrionomys in Hypudaeus leucogaster (Bailey and Sperry, 1929). Baird (1858) proposed the genus Onychomys for these mice, and Hollister (1915) revised the genus and recognized two extant species, O. leucogaster and O. torridus.

Hollister (1915) pointed out that although in tooth structure Onychomys resembles the old world genus Cricetulus (Tribe Cricetini) much more than it does Peromyscus. Other characters separate it from Cricetulus by both Peromyscus and Baiomys. Hollister suggested that the subgenus Podomys of Peromyscus was intermediate between Onychomys and Peromyscus, but Hoffmeister (1944) discounted this.

Hall and Kelson (1959) diagnosed the genus Onychomys as follows:

> External measurements in millimeters: 119-190; 29-62; 17-25; 11-24. Stout mice with short, relatively thick tails; forefeet with 5 plantar tubercles, hind feet with 4; sole of hind foot densely furred from heel to tubercles. . . . Skull with distinctly wedge-shaped nasals, which extend beyond the premaxillary tongues; interorbital constriction narrow; zygomatic plate narrow, straight anteriorly; molars more hypsodont than in Peromyscus; M^3 reduced, coronoid process of mandible high.

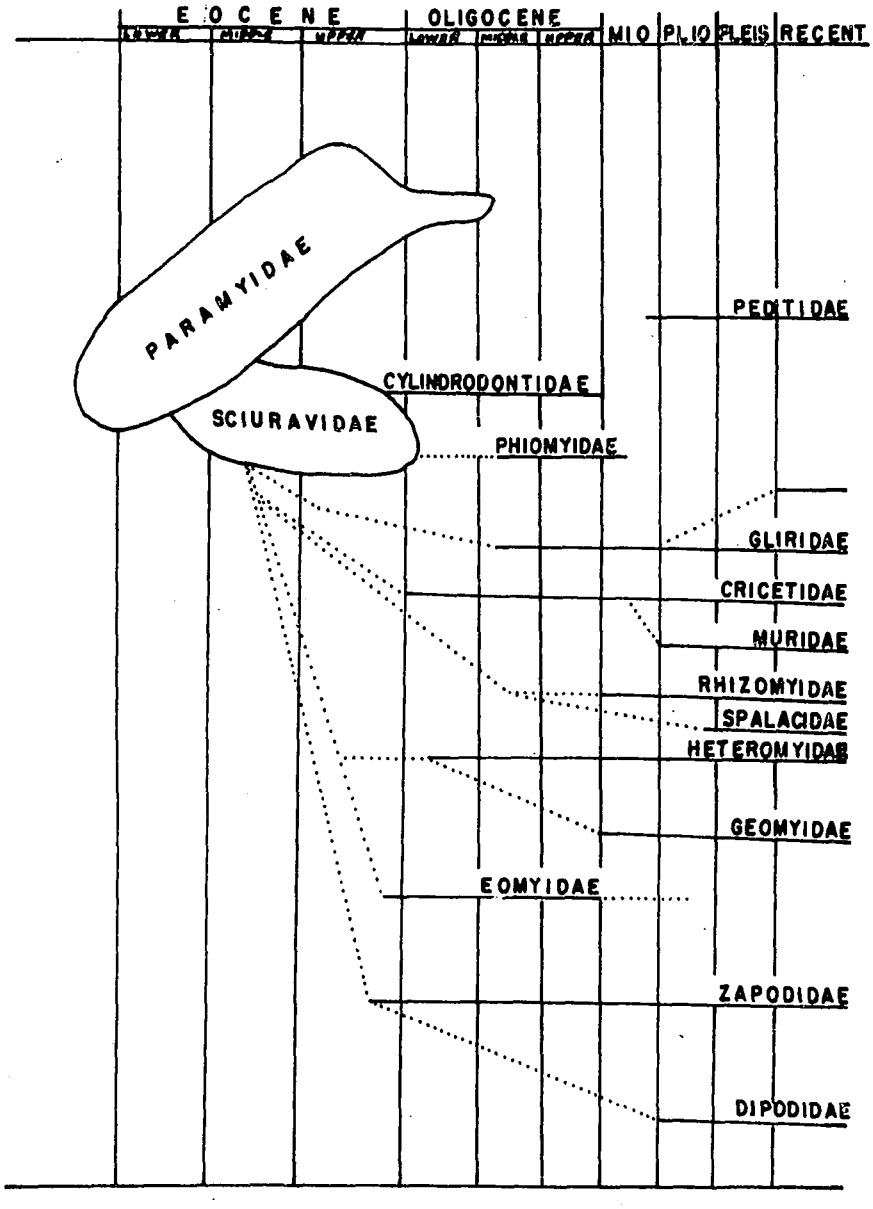


Fig. 1 -- Phylogeny of some families of rodents according to Wood (1959).

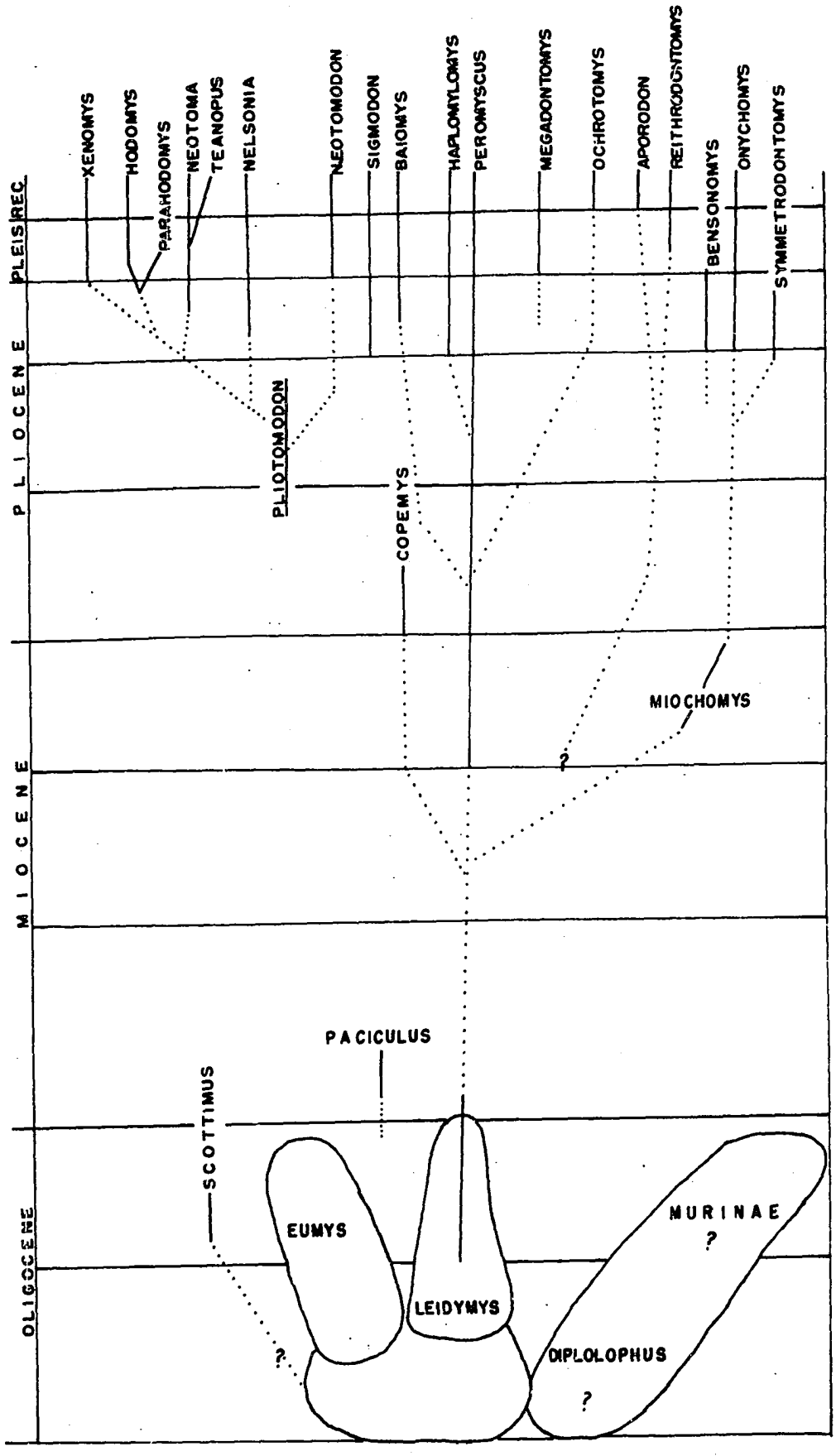


Fig. 2 -- Phylogeny of the genera and subgenera of Nearactic Cricetinae according to Hoffmeister (1944).

Egoscue (1963) studied the two color phases of Onychomys and described a pale phase and a dark phase. The pale phase had the upper parts between Avellaneous and Vinaceous Buff (Ridgway, 1912) ears light brown with varying amounts of white, and the underparts white. In the dark phase the upper parts were dark blackish-brown heavily overlaid with black, upper surface of tail blackish almost to tip, and underparts white. The dark phase behaved as a simple autosomal recessive in the presence of the pale phase. Burt and Grossenheider (1952), Hall and Kelson (1959), and my own observations indicated that adults may be either a cinnamon phase similar to the pale phase described by Egoscue (op. cit.), a dark phase also like that of Egoscue, or a gray phase which Egoscue maintained was only a juvenile pelage. Hall and Kelson (1959) stated that as individuals grew old, they became gray; on five occasions I have had adult animals which were captured in the cinnamon phase and, while in the laboratory, changed to a gray phase.

The skulls of 20 specimens of O. leucogaster averaged 25 mm. or more in length, slightly larger than O. torridus; and had a comparatively narrow interorbital region. The teeth, as compared with O. torridus, were higher crowned; the unworn cusps of M^1 being higher than long; and the anterior cusps more coniform with less indication of incipient division of the summit into two or three cusplets. M^1 in O. leucogaster was less narrow and elongated, stouter and relatively short, being less than one half the length of the tooth row in O. leucogaster and more than one half

the length of the tooth row in O. torridus. M^3 was larger than in O. torridus, longer than wide, or subcircular with longitudinal and transverse diameters nearer equal. The tail of O. leucogaster was usually less than one half the length of the head and body while the tail length was more than one half the head and body length in O. torridus. Measurements from mice used in the present study are given in Appendix I.

Distribution and Ecology

The distribution of grasshopper mice is restricted to North America. O. torridus (Fig. 3) has been collected in the northern Mexico and southwestern United States and the distribution of O. leucogaster (Fig. 3) extends from extreme northern Mexico northward through the United States to southern Alberta, Saskatchewan, and Manitoba, Canada. As can be seen, the range of O. leucogaster is more extensive than that for O. torridus and covers much of the western half of the United States. Although the two species have a sympatric geographic distribution, many regional and local faunal lists indicate that they may be ecologically allopatric.

The common names for the species arise from their geographic range and feeding habits. The term grasshopper mouse comes from their habit of eating grasshoppers which, in some regions, constitute a major portion of the diet (Bailey and Sperry, 1929). O. torridus is the southern grasshopper mouse and O. leucogaster is the northern grasshopper mouse (Hall, 1957).

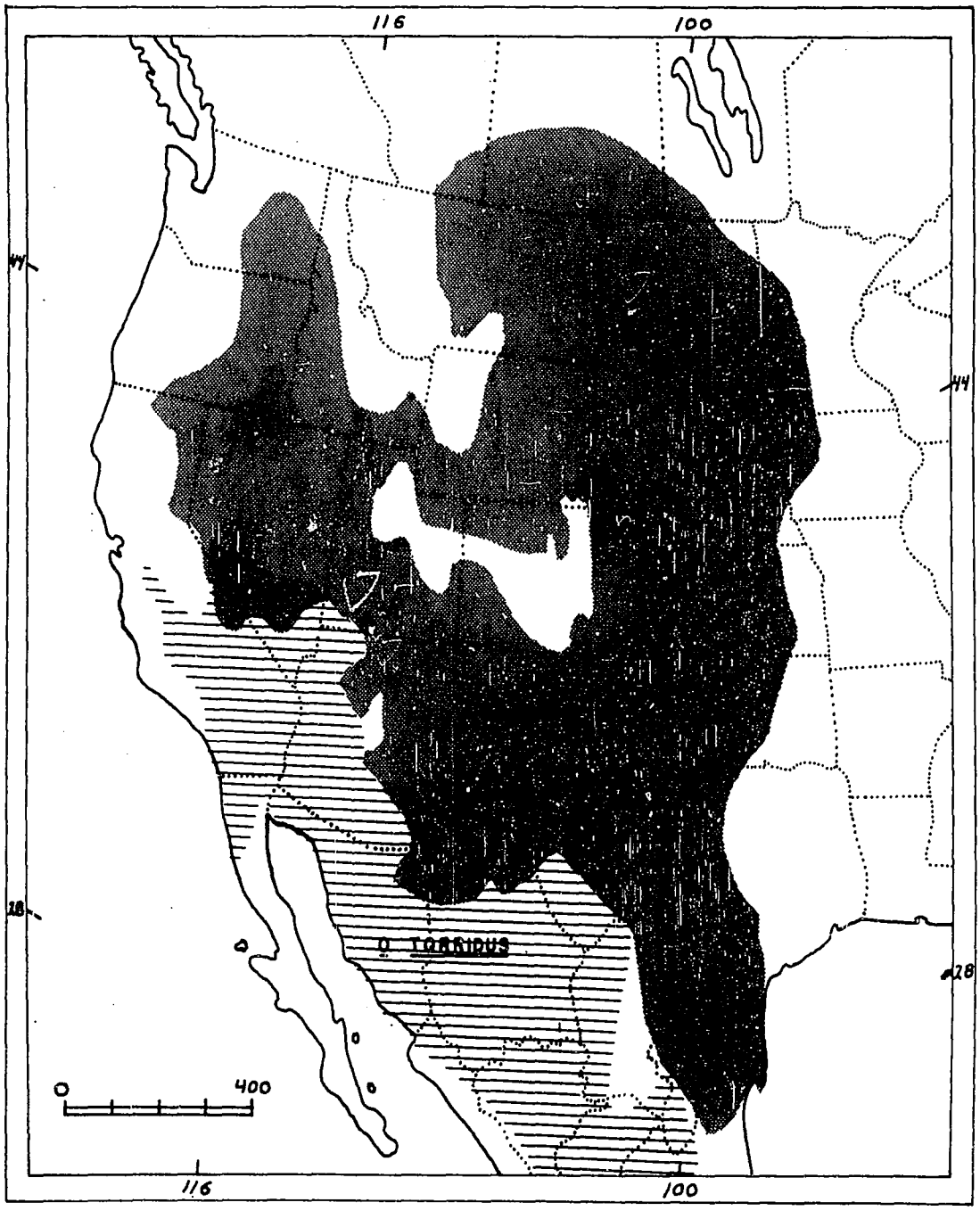


Fig. 3 -- Geographic distribution of Onychomys leucogaster and O. torridus.

Two subspecies are found in Oklahoma: O. l. breviauritus from the western half of the state, excluding the panhandle, and O. l. arcticeps from the panhandle. The easternmost record for the state is from a point halfway between Guthrie and Kingfisher on the north side of the Cimarron River in Logan County.

Cary (1911), Hollister (1915), Bailey and Sperry (1929), Bailey (1931, 1936), Hall (1946). Dalquest (1948), and Ivey (1957) found that O. leucogaster was restricted wholly or in part to, or was very common in, the Upper Sonoran Life Zone. On the other hand, Benson (1933) and Baker (1956) listed it as characteristic of the Lower Sonoran in the southwestern United States. Hollister (1915) and Bailey and Sperry (1929), however, described O. torridus as being characteristic of the Lower Sonoran. The extent of the western division of the Upper Sonoran and Lower Sonoran, as described by Merriam (1890 and 1892) and Allee, et. al., (1949), (Fig. 4) indicates that, the ranges of the two species (Fig. 3) correspond rather closely to these Life Zones. In the southern portion of its range, however, O. leucogaster is, in fact, found in the Lower Sonoran. Detailed ecological studies need to be conducted in order to elucidate the ecology of this species.

Cary (1911), Benson (1933), Dalquest (1948), Davis (1960), and Egoscue (1960) found grasshopper mice to be common in sandy areas. Jones, et. al., (1960) caught O. leucogaster at 8800 feet elevation in New Mexico in an area of Yellow Pine, Douglas Fir, Quaking Aspen, Gambel

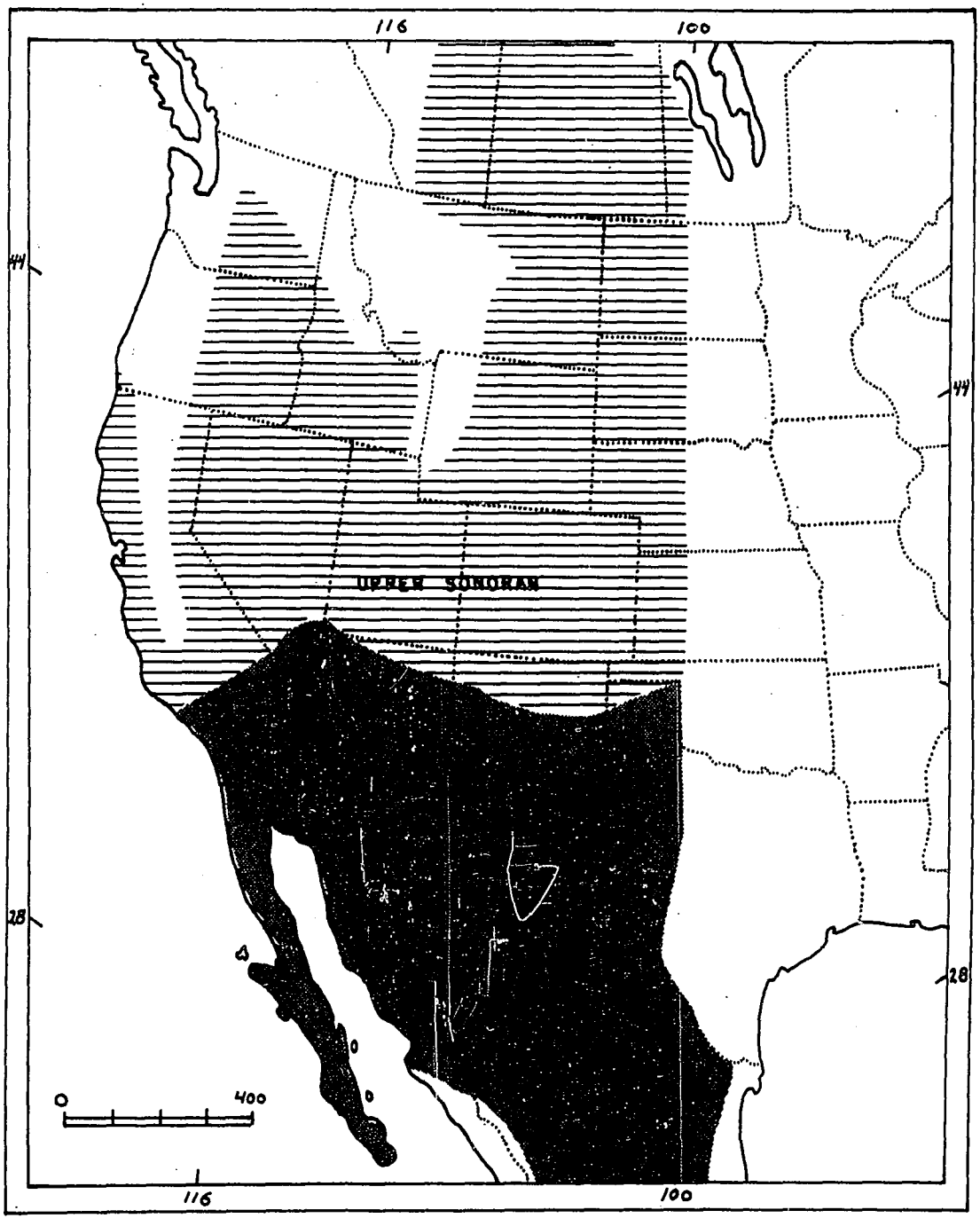


Fig. 4 -- Western division of the upper (lined area) and lower (stippled area) sonoran life zones. (After Merriam, 1890 and 1892 and Allee, et. al., 1949)

Oak, and Englemann Spruce. Blair (1939), Hibbard (1944), Hall (1946), and Baker (1956) found O. leucogaster common in short grass prairie areas. Blair (1939) found them in mixed grass prairie while Calhane (1947), Blair (1939), Bailey (1931, 1936), Burt and Grossenheider (1952), Cary (1911), and Warren (1942) listed O. leucogaster as a "prairie animal". Dalquest (1948) and Bailey (1931) found that they avoided heavy cover. Desert and Semidesert was given by Dice (1930), Blair (1943a), Calhane (1947), Hoffmeister and Goodpaster (1954), Baker (1956), and Davis (1960) as the habitat preference. Egoscue (1960) found that there was no clear-cut habitat preference and that the edaphic requirements which included conditions permitting frequent dust bathing may have restricted the ecological distribution more than any other physical factor of the environment.

In Oklahoma, grasshopper mice have been taken from semi-stabilized sand dune areas along the north side of rivers in the western part of the state and from Permian soils in the southwestern part of the state (Preston, 1963, and personal collections). Jackson and Warfel (1933) collected them in areas surrounding the Great Salt Plains in northern Oklahoma. In addition, I have collected grasshopper mice from short grass prairie areas with Buchloe dactyloides and Buteloua gracilis as dominant grasses (E. L. Rice and Wm. T. Penfound, personal communication) and from Mixed Grass Prairie areas with Andropogon scoparius, Bouteloua curtipendula, Buchloe dactyloides and Buteloua gracilis as dominant grasses. Others were captured from Sand Sage

grassland and Mesquite grasslands. Collecting points in the state were in northern Ellis County, central Woodward and Alfalfa counties, and southern Woods County, western Logan and Canadian counties, eastern Beckham County, and Harmon and Jackson counties.

Table 1 is a list of small mammals that have been found associated with Onychomys leucogaster. These data were obtained from: Merriam (1892), Benson (1933), Dalquest (1948), Kelson (1951), Justice (1957), Cutter (1958), Egoscue (1960), Jones, et. al., (1960), Preston (1963 and personal communication) and from my own records (those marked with an asterisk). Predators on Onychomys leucogaster included the following: Great Horned Owl (Finley, 1954, and Long and Kerfoot, 1963), Barn Owl (Glass, 1953), Coyote (Sperry, 1941), Kit Fox (Egoscue, 1962) and Swift Fox (Cutter, 1958).

Methods and Materials

Animals were housed individually in similar cages measuring not less than 6 by 6 by 12 inches. One inch of sand was placed in the bottom of each cage. The diet consisted of a mixture of equal portions of sunflower seeds, wheat and oats, and commercial rat pellets. This was supplied every five days and was supplemented at irregular intervals with various species of insects and other mice. Each cage was provided with a glass nozzled water bottle. The mice were never without food and appeared to thrive on this diet, several animals living in captivity for three years.

TABLE 1

MAMMALS FOUND TO BE ASSOCIATED WITH ONYCHOMYS

Order Insectivora

Family Soricidae

Notiosorex crawfordi

Order Lagomorpha

Family Leporidae

Lepus californicus* - Sylvilagus floridanus*

Order Carnivora

Family Canidae

Canis latrans*- Urocyon cinereoargenteus* - Vulpes macrotis - Vulpes velox

Family Mustelidae

Mephitis mephitis*

Order Rodentia

Suborder Sciuromorpha

Family Sciuridae

Sciurus aberti - Tamiasciurus hudsonicus - Citellus leucuras - C. tridecemlineatus* - C. spilosoma* Eutamias cinereicellis - E. quadrivittatus

Family Geomyidae

Geomys bursarius* - Thomomys bottae

Family Heteromyidae

Perognathus apache - P. flavus* - P. longimembris P. parvus - P. hispidus*-Microdipodops megacephalus Dipodomys ordii* - D. spectabilis

Suborder Myomorpha

Family Cricetidae

Reithrodontomys megalotus* - Peromyscus crinitus P. maniculatus* - P. truei - Baiomys taylori - Sigmodon hispidus* - Neotoma lepids - N. micropus* Microtus mexicanus

Observations of the mice were made by placing various numbers of individuals and combinations of sexes in a 15 by 15 by 3 foot sheet metal enclosure (Fig. 5) set into the ground about 10 inches. A sand substrate of sufficient depth to allow unrestricted burrowing was provided. The enclosure was placed out-of-doors in the summer and inside in the winter. A canvas blind at one corner allowed the observer to remain hidden from the mice while observations were being made. Richardson (1958) and Grubitz (1963) successfully used this type of enclosure for mammal studies. A few observations were made on mice placed in 50-gallon aquaria or in cages measuring 24 by 16 by 14 inches, each of which had enough sand to facilitate burrowing.

The enclosures and observation cages were lighted by 100 watt red bulbs which, preliminary observations had established, did not noticeably affect the behavior of the mice. Notes were taken on a tape recorder and later transcribed, and were supplemented by 35 mm. photographs. Animals were permanently marked by clipping various combinations of toes. A pattern of marks of blue Columbus Vaccine Company Chick Dye across the back was used to facilitate identification of individuals.

Observations began in November, 1960, and ended in August, 1963. During the summers of 1961, 1962, and 1963 the work was done at the University of Oklahoma Biological Station, Willis, Oklahoma; work during the academic year was carried on at the Animal Behavior Laboratory on the Norman (North) Campus of the University of Oklahoma.

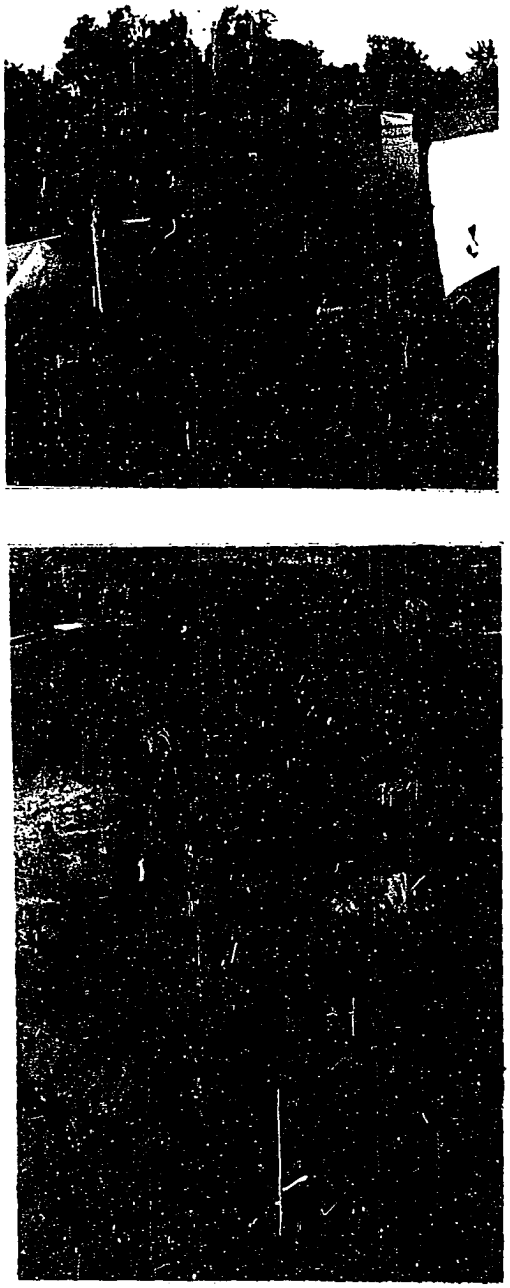


FIGURE 5

TWO VIEWS OF THE
ENCLOSURE USED IN THIS STUDY

CHAPTER II

SHELTER-SEEKING BEHAVIOR

Burrow Types

The mice were placed in enclosures which had a sand substrate of sufficient depth to allow unrestricted burrowing, and were allowed to burrow in the enclosure for a period of not less than three days, during which other observations were made. They were then removed with Sherman live traps and plaster of Paris casts were made of some burrows while measurements and sketches were carefully made of others that were dug up. The length, diameter (the mean of the greatest and least diameter) at 5 cm. intervals, depth below the surface and size of the entrance of each cast were recorded; and the use made of the burrow was noted.

From these data it became evident that four general types of burrows were constructed by Onychomys leucogaster: a nest burrow, a retreat burrow, a cache burrow, and miscellaneous burrows including those used for defecation and signposting.

The nest burrow (Fig. 6) was a shallow U-shaped burrow with a mean over-all length of 48 cm. and mean depth of 14 cm. at the deepest

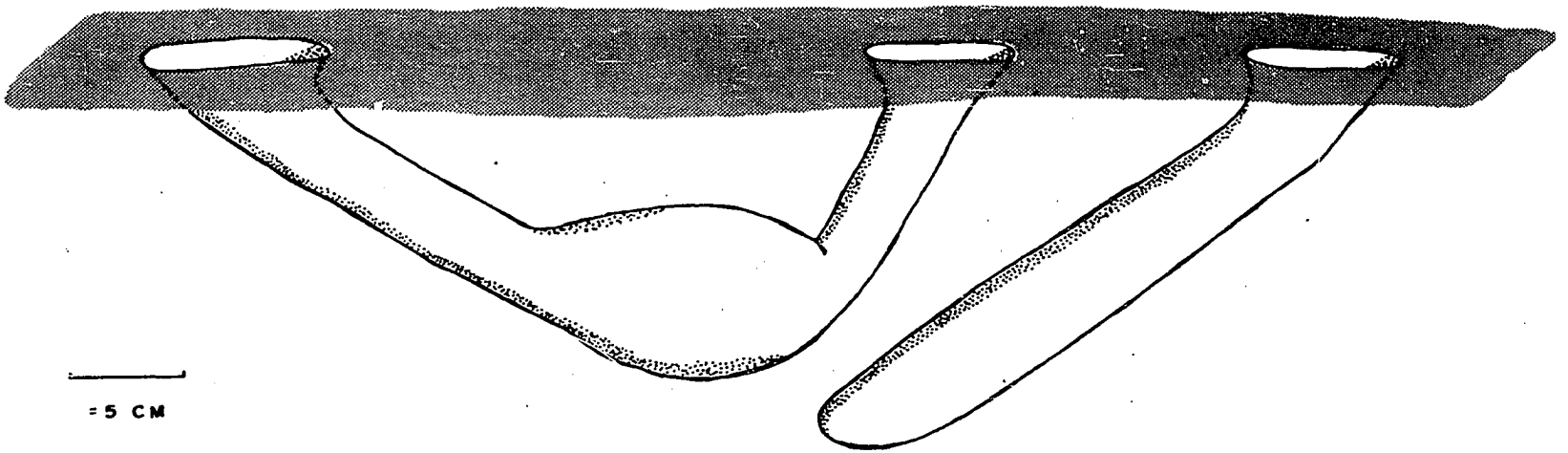


Fig. 6 -- The nest (left) and retreat (right) burrows of Onychomys leucogaster.

point below the surface. Near the center of the burrow was the nest portion which was a rough fusuoid averaging 12 cm. long, 9 cm. wide, and 7 cm. high; the remainder of the burrow, averaged about 4.5 cm. in diameter, and the two entrances to each nest burrow measured 6.7 cm. in length by 4.7 cm. in width. The twelve nest burrows measured were used for sleeping, retreat, rearing of young, and some feeding, and were the center of activity in the enclosure. Within the nest portion was a small oval platform of grass and a small cache of seeds. Usually, only one entrance was used, the other being plugged; often both were plugged during the day. Nest burrows were dug and utilized by pairs of mice while individual mice lived in a hollowed-out chamber under a rock or grass clump.

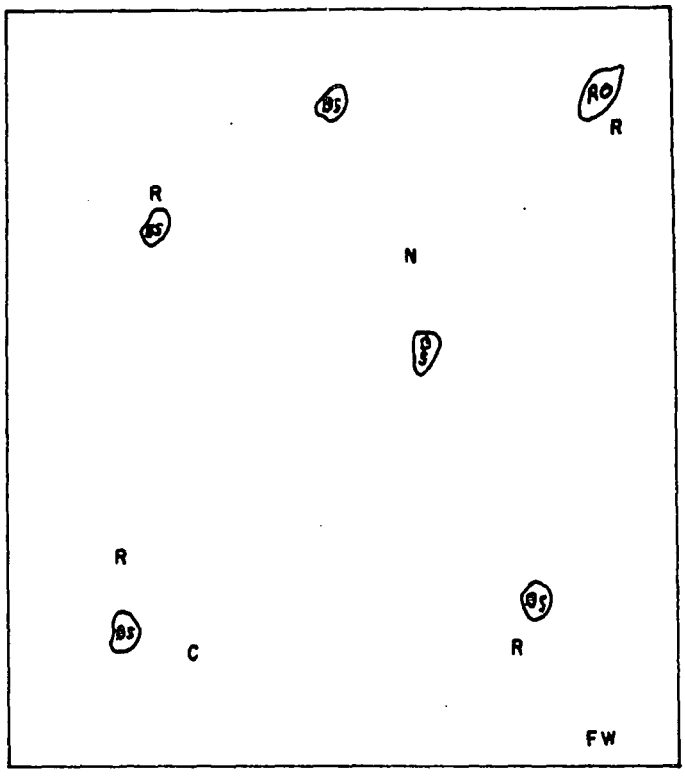
Eighteen retreat burrows had a mean over-all length of 23 cm. and a mean depth of about 20 cm. at the deepest point below the surface. The diameter of retreat burrows and the size of the single entrance were similar to those for the nest burrow. The retreat burrow (Fig. 6) was not used for nesting and had no enlarged chamber as had the nest burrow. If a mouse was frightened while moving about the enclosure it ran to the nearest burrow and then, if it had gone into a retreat burrow, came out after a few minutes (depending upon what caused the retreat) and moved over to the nest burrow.

The third burrow type, the cache burrow, was used to store seeds at various locations about the enclosure. Insects were never cached in

these burrows. They were never more than 10 cm. long, were dug in the sand at an angle of not more than 45 degrees from the horizontal, filled with seeds, and covered with a one-cm. layer of sand. They were not located near the food supply. Cache burrows were not used as a regular source of food if insects and other mice were available as food in the enclosure.

Several other burrows were observed in the enclosure. Some were used as places of defecation, these being about 5 cm. long and dug at an angle of almost 90 degrees from the horizontal. There were also many places where burrows had been started and abandoned. Certain other burrows, less than 3 cm. long, were used to mark a territory (see agonistic behavior).

An enclosure generally had one nest burrow, three or four retreat burrows located at least eight feet from the nest burrow, and one or two cache burrows. A typical arrangement of burrows within the enclosure is shown in Figure 7 (data obtained from over 100 recorded arrangements). The first burrow to be dug was a nest burrow. Although the time was quite variable, a male-female pair, when released into an enclosure, always completed a nest burrow within one hour of introduction, although the actual digging time was less than 5 minutes. After completion of the nest burrow, one retreat burrow was dug the first night. During the second night in the enclosure the mice dug two or three more retreat burrows and often one cache burrow. By the end of the second night, the burrow arrangement was similar to that in Figure 7. Nest burrow entrances were never closer than 1.5 feet to a clump of grass or other protection.



= 1.5 FT

BS = BLUESTEM CLUMP

C = CACHE BURROW

F = FOOD

N = NEST BURROW

R = RETREAT BURROW

RO = ROCK

W = WATER

Fig. 7 -- A typical arrangement of Onychomys leucogaster burrows within an enclosure.

Burrow Climate

A twelve channel Yellow Springs Instrument Company Tele-Thermometer was employed to record temperatures at various locations within the enclosure and in nest burrows. Hourly temperatures within a nest burrow fluctuated 12 degrees and on the sand surface fluctuated 49 degrees (Fig. 8). Temperatures taken at the surface and at depths of one, six, and twelve inches (Fig. 9) showed that the sand acted as an insulator and maintained the temperature within a range of 14 degrees at six inches and only 4 degrees at 12 inches compared to a 43-degree range at one inch deep and a 72-degree range on the surface. Temperatures taken one inch above the sand surface, at the sand surface, and within a burrow showed a similar reduced fluctuation within the nest burrow (Fig. 10).

It was apparent from these data that a burrow provided a mouse with an atmosphere that was not always cooler (see temperatures between 0100 and 0400 hours), but provided a place where the mouse could avoid the extreme fluctuations it would encounter on the surface (including the extreme diurnal surface temperature). Equipment was not available to measure relative humidity within Onychomys burrow.

Burrowing Behavior

Burrows were dug in the following manner. The mouse stood on its hind legs, held its forefeet together, and with simultaneous

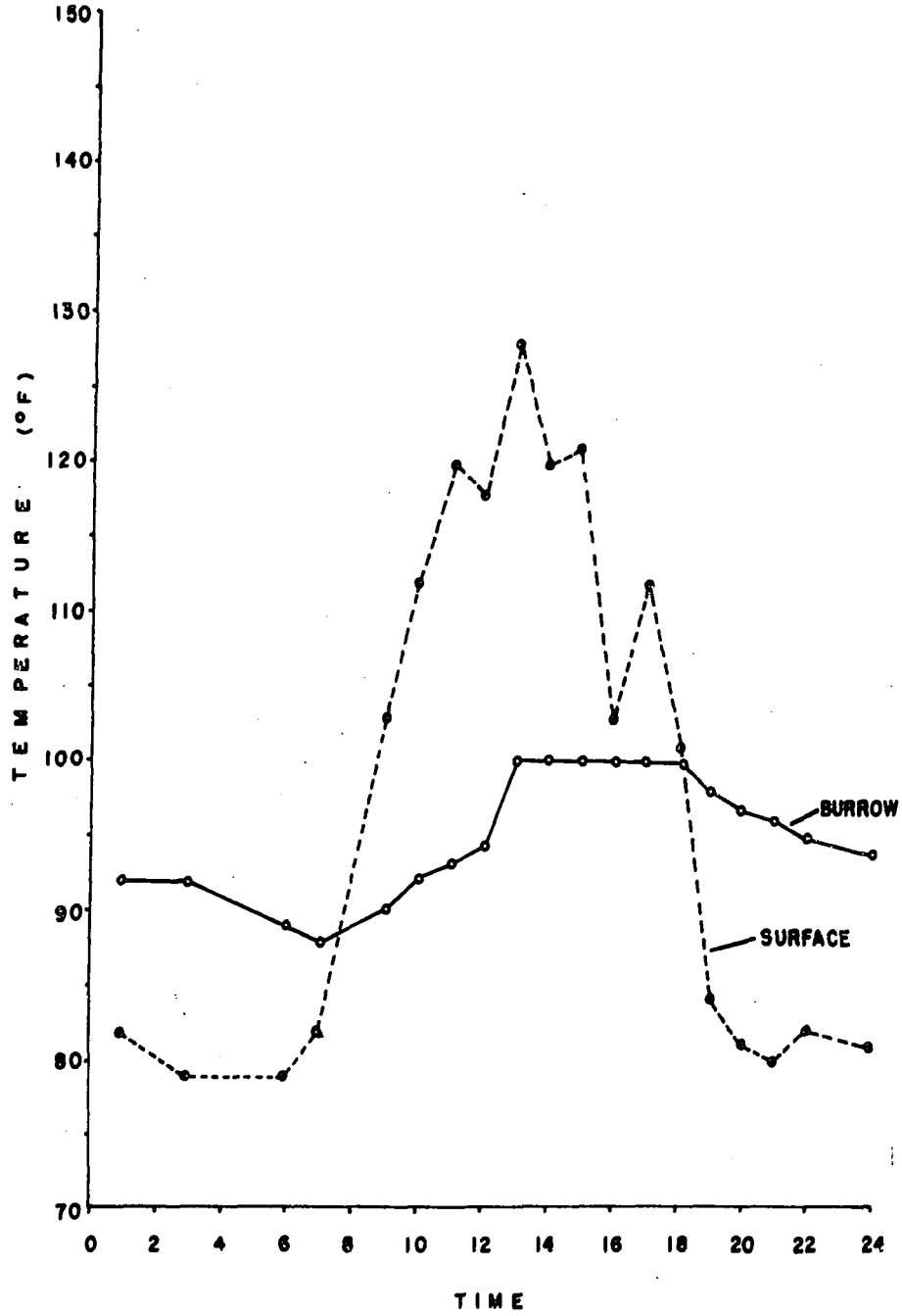


Fig. 8 -- Temperatures at the sand surface and within a nest burrow in an enclosure on 25 July, 1963.

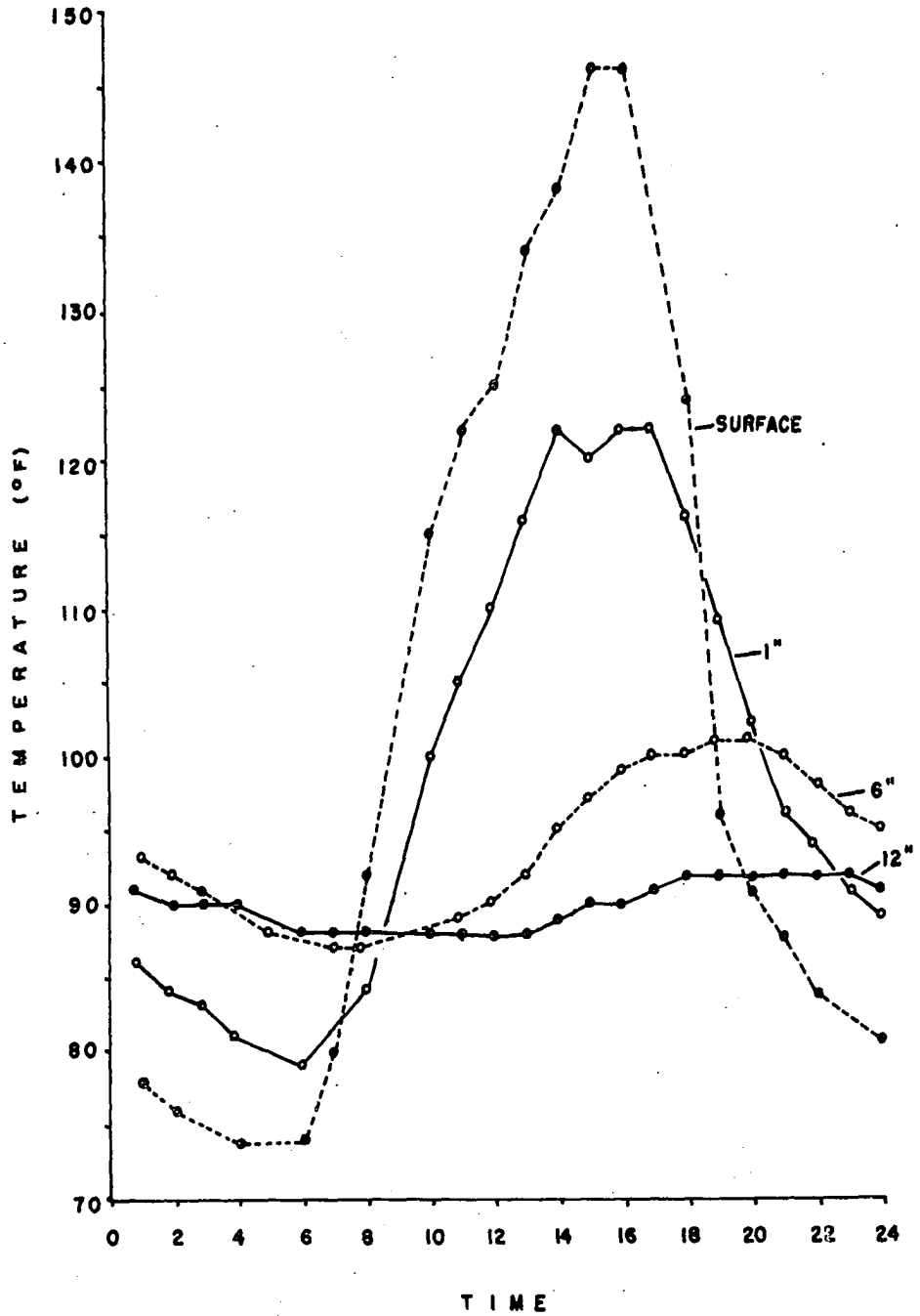


Fig. 9 -- Temperatures at the surface and 1, 6 and 12 inches deep in the sand within an enclosure on 9 July, 1963.

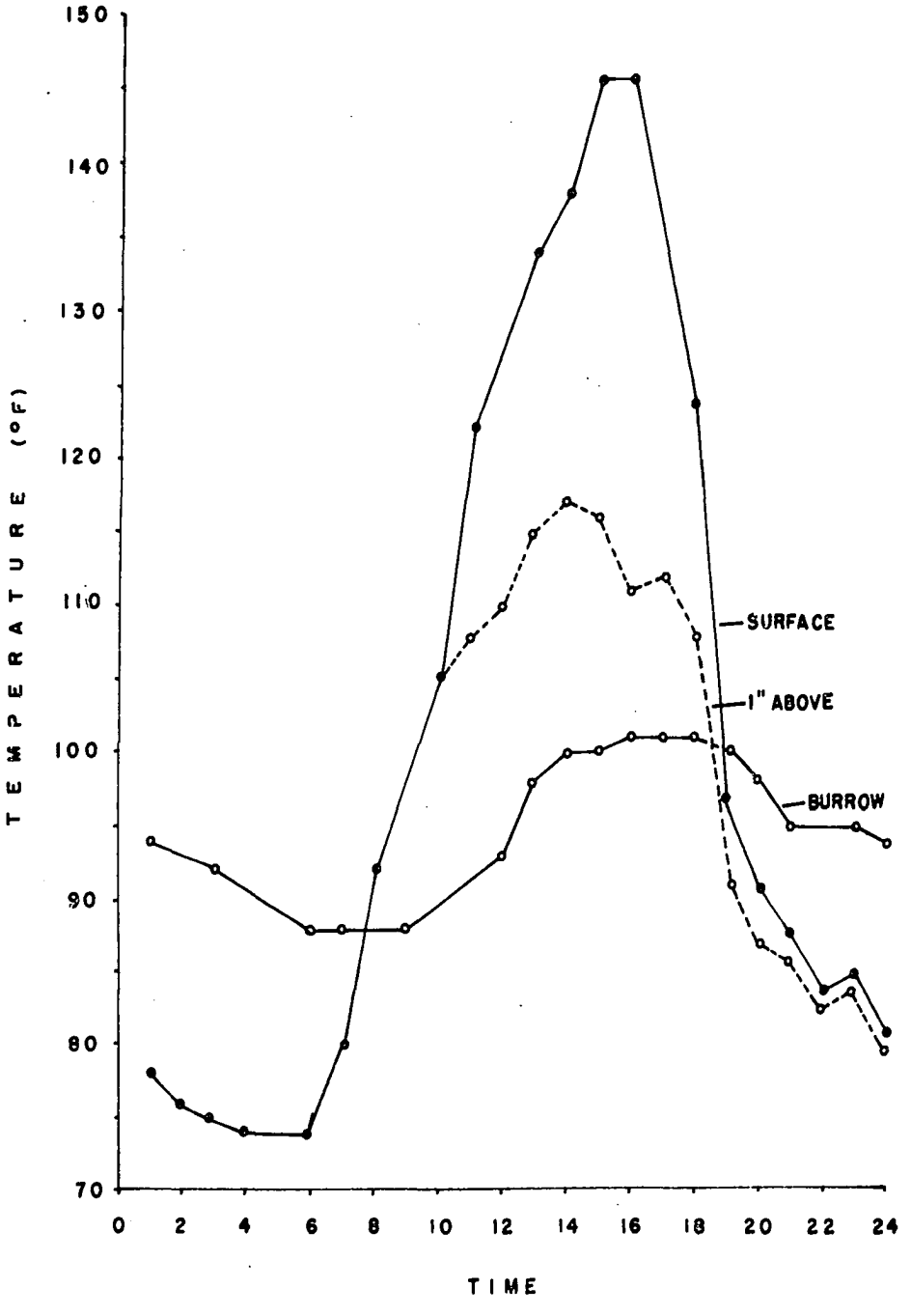


Fig. 10 -- Temperatures taken at the surface, one inch above the sand surface and within a nest burrow, within an enclosure.

movements of the forefeet, scooped sand under its belly. At intervals the mouse held itself up with the forefeet and with alternating kicks of the hind feet, moved the dirt as far as 18 inches behind. While digging, the tail was held straight out behind and appeared to be rather stiff. When a burrow was being dug, a pile of sand accumulated at the entrance, and this was then scattered over an area of 14 inches radius around the entrance by the same alternating kicks of the hind legs. The result of this was that the entrance was not noticeably raised above the surface. Burrows began as a vertical tunnel which, at a depth of about 10 cm. angled off. This vertical shaft was eliminated by enlargement of the entrance.

Nest burrows, like those in Figure 6, were only dug by a male with the help of a female. While digging within a burrow, the male was unable to kick sand out of the burrow unless he moved backward as he kicked. While digging a nest burrow, the male kicked sand behind him and the female followed behind him and moved it out of the burrow. A female followed the male into an uncompleted burrow and began moving sand out of it as soon as he entered, and even before he had begun to dig. Working together, a male and female could complete a nest burrow in five minutes.

Juvenile mice, both males and females, were frequently observed "helping" the mother dig a shallow burrow. They moved behind her and kicked the sand, although they did not move it very far.

Use of Other Burrows

In an attempt to determine whether Onychomys would live in burrows dug by other species, pairs of Dipodomys ordi and Perognathus hispidus were released into enclosures. After three day periods they were removed and pairs of O. leucogaster were released into the enclosures. Three trials with each species resulted in the same pattern of activity. During the first night grasshopper mice used the burrows of the other species as a place of retreat but dug their own nest burrow. By the second night the burrows of the other species were not used at all and by the third night they were mostly destroyed by wind erosion and movement of the Onychomys over them, and the Onychomys had dug retreat burrows of their own.

Grasshopper mice were later released into the enclosures from which kangaroo rats (Dipodomys ordi) had not been removed. The kangaroo rats were soon killed, but the burrows were not used. These data indicated that, under the conditions of this study, Onychomys leucogaster did not nest in burrows dug by other species. One factor of importance may be that the burrows of D. ordi and P. hispidus were not the same size and configuration as those of Onychomys (as determined from a cursory examination of casts and excavated burrows).

CHAPTER III

AGONISTIC BEHAVIOR

General Aspects

Verplanck (1957) defined agonistic behavior as a broad class of behavior types that includes attack, threat, appeasement, and flight. Similarly, Scott (1958b) regarded agonistic behavior as any sort of adaptation connected with a contest or conflict between two animals. Aggressive behavior is a part of agonistic behavior and is limited to fighting (Scott, 1958a). Thus, according to these definitions, territoriality would be included in the broad category of agonistic behavior since it reinforces dominance relationships and reduces sexual fighting (C. R. Carpenter, 1958) among other things.

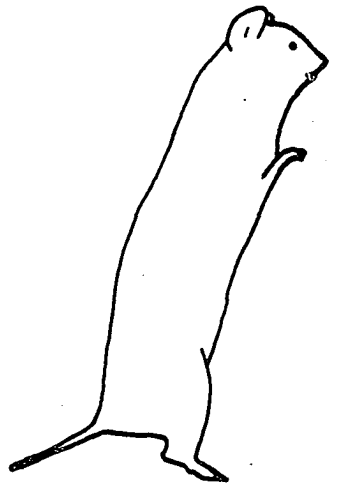
O. leucogaster, a predatory mammal, displayed a well developed pattern of aggression. This pattern, similar in intra- and interspecific encounters, consisted of the aggressor rapidly pursuing the victim with repeated pounces upon it, until he obtained a hold with the forefeet. Should the grasshopper mouse in the role of a victim assume a defensive posture in which he stood on his hind legs, tail stiff, ears perked up, back straight and forefeet raised against the thorax, paws down (Fig. 11a),

the aggressor nipped at his tail and legs until he was forced to expose his back to attack. Using his forefeet, the aggressor then seized the victim from the rear and bit through the posterior region of the skull (Fig. 11b), and the victim was killed within ten seconds after seizure. The claws were never observed to be used as weapons.

Occasionally, during the course of a chase, the victim stopped abruptly and the aggressor ran past the victim, apparently without seeing him stop. This would cause the aggressor to lose the victim until the latter moved again.

The first three intraspecific contacts established the dominant-subordinate relationship which lasted the duration of the encounter and ended in death of the subordinate within three days. The dominant-subordinate relationships, obtained from records of frequency of contacts between members of a group of mice released into the enclosure, indicated that there was one dominant and no hierarchical arrangement among the subordinates.

Twenty-three interspecific encounters were staged between O. leucogaster and the following species: Dipodomys ordi, Perognathus hispidus, Reithrodontomys megalotis, Peromyscus maniculatus, P. leucopus, Sigmodon hispidus, and Mus musculus and inevitably resulted in death of the subordinate within two hours of the first contact. All of the introduced species appeared to recognize O. leucogaster as a predator on first contact and O. leucogaster was never subordinate.



A



B

Fig. 11 -- Two agonistic postures of Onychomys leucogaster. A: upright defensive posture; B: aggressor biting and holding a victim.

This even applied to Sigmodon hispidus males who were three times as large by weight as the Onychomys. Although there was no observable difference in the reaction of an individual male or female grasshopper mouse to an aggressor, if a male-female pair encountered another animal of the same species or of another species, the male of the pair was the aggressor and the female remained in the nest burrow during most of the encounter.

An intraspecific encounter between O. leucogaster was initiated by and interspersed with circling. In 132 recorded like-sex encounters the diameter of the circle was not less than 36 cm., and in 174 recorded unlike-sex encounters it was of a 10-15 cm. diameter (about the body length of the individuals involved). Circling was immediate and in over 100 recorded observations never failed to be of the above mentioned type, indicating that sex recognition must be immediate.

Types of Agonistic Encounters

For purposes of quantitating agonistic behavior, intraspecific encounters were grouped into three general types: the fight, the chase, and the approach. In a chase, as described previously, the aggressor pursued the victim for distances of three feet to fifteen feet. Chases were frequently interspersed with fights. Any agonistic contact between two animals, except nips at the tail, was considered a fight. In a fight the two animals faced each other, raised up on their hind legs, backs straight, tails stiff, ears perked, with the forefeet raised against the

chin (Fig. 12a), and sparred with each other. They then met and assumed a "lock" position with their ventral surfaces together at right or near right angles (Fig. 12b). While in this posture they rolled around for superior position and attempted to bit the back of the others head. They then separated and resumed the chase.

During the third type of agonistic encounter, the approach, the subordinate animal moved away at the approach of the dominant. An approach by the dominant as distant as 12 feet could cause the subordinate to move away.

Since one role of a dominant-subordinate relationship is to reduce the amount of fighting between the individuals involved, a change in the frequency of these three types of agonistic encounters should be expected once the dominance has become established. It was observed that dominant-subordinate relationships were always established within 20 minutes of the first encounter. To measure the affect of this relationship on the frequency of agonistic encounters, situations were staged in which three animals of all combinations of males and females were placed together and the frequency of each type of encounter recorded during the first and third half hour after release. Of the three kinds of encounters, chasing and fighting were both markedly violent, while approaches were non-violent. Table 2a demonstrates that it is permissible to group fighting and chasing together under the single category "violent encounters," since the proportion of these two types of

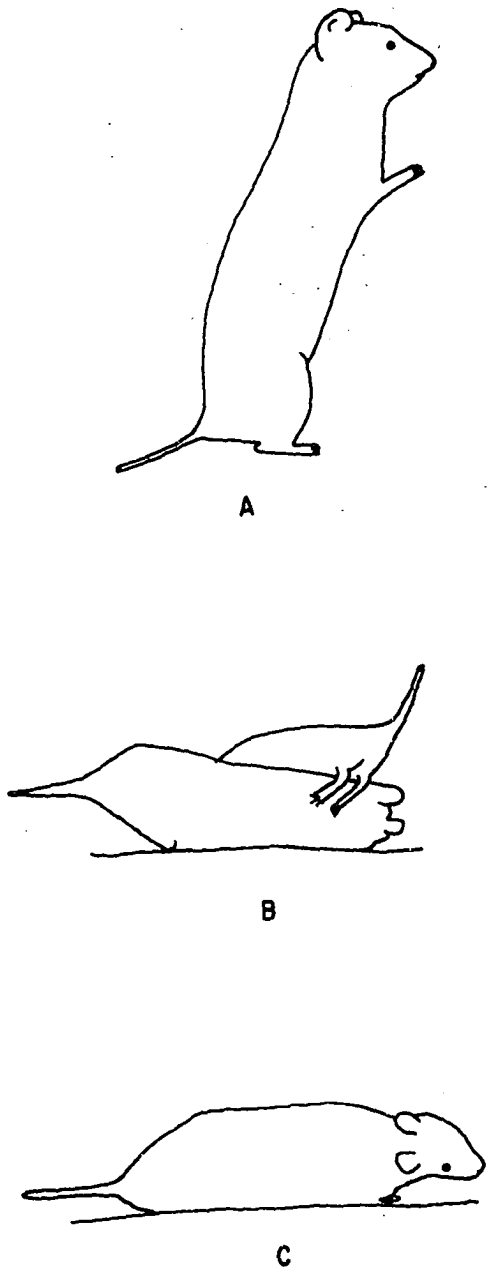


Fig. 12 -- Three postures of Onychomys leucogaster. A: upright defensive sparring posture; B: the "lock posture during a fight; C: the submissive posture.

TABLE 1

FREQUENCY OF AGONISTIC ENCOUNTERS DURING THE FIRST AND THIRD HALF HOUR OF CONTACT FOR O. LEUCOGASTER

a

	VIOLENT ENCOUNTERS		
	FIGHTS	CHASES	TOTAL
FIRST HALF-HOUR	obs = 28 ex. = 27.65	obs = 269 ex. = 269.35	297
THIRD HALF-HOUR	obs = 3 ex. = 3.35	obs = 33 ex. = 32.65	36
TOTAL	31	302	333

b

	ALL ENCOUNTERS		
	VIOLENT	NON-VIOLENT	TOTAL
FIRST HALF-HOUR	obs = 297 ex. = 251.9799	obs = 42 ex. = 87.0200	339
THIRD HALF-HOUR	obs = 36 ex. = 31.0200	obs = 73 ex. = 27.9799	109
TOTAL	333	115	448

encounters is nearly identical in the first and third half hours. It is obvious from Table 2a that the frequency of both kinds of encounters is much greater in the first half hour than in the third, but the relative frequencies of fighting and chasing are not changed. From inspection of Table 2a it is obvious that the observed values are almost in perfect agreement with expectation. Chi-square analysis of this table is untrustworthy because of the low expected frequency of fights in the third half hour, but the Fisher exact test indicates a probability of 0.5621 for the observed and all more extreme tables.

In Table 2b, "violent" encounters (fights and chases lumped) and "nonviolent" encounters are compared, again as a 2 x 2 contingency analysis. Deviations of observed from expected values is large ($\pm$ 45.02), and the resulting chi-square (125.94) indicates a probability of very much less than one in ten thousand. Thus the null hypothesis, that violent and nonviolent encounters occur in the same proportion during the first and third half hours, is rejected. The proportion of violent to nonviolent encounters changes drastically after the establishment of the dominance relation, there being a much larger proportion of nonviolent encounters during the third half-hour.

Under these conditions, although an animal was more likely to engage in a nonviolent agonistic encounter after the dominant-subordinate relationship was established, the relative proportions of violent and nonviolent encounters remained the same. Also, the total number of

encounters was significantly lowered during the third half hour. This was tested as a 1:1 ratio by chi-square analysis, indicating a probability of less than 0.0001.

Territoriality

Burt (1940) defined the territory as the defended portion of the home range when the latter was defined as, ". . . that area about its established home which is traversed by the animal in its normal activities of food-gathering, mating, and caring for young." Observations in the enclosures indicated that O. leucogaster had a strongly defended territory, larger than the enclosure, but of undetermined size. When more than one male-female pair or when more than one individual of the same sex was placed in an enclosure, the subordinate mouse (or mice) was forced, by the dominant, to limit its activity to one small corner of the enclosure. This corner did not contain burrows dug by the occupant of the territory. The dominant animal marked the edge of the enclosure except for a portion in one corner which reached about three feet down the two sides. In sign-posting the dominant animal dug a small hole about 3 cm. deep where he then took a sand bath in which he rubbed the side of his head, his back and his belly in the spot. These marks were noticeable to the other animals as evidenced by the fact that they did not cross this "line" when the dominant was out of his burrow and when they came to a mark they often took a one-roll sand bath in the spot. The dominant was not restricted by this line. To test the accuracy of these spots in indicating

a territorial boundary, on two occasions they were carefully dug up and moved to another location where they were respected as a territorial boundary the same way they had been in their previous location.

Subordinates entered the territory of the dominant when he was in a burrow, but ran to the corner when he came out. Territories were not defended by fights, but chases or, in most cases, approaches were sufficient to cause the subordinate to leave. Females did not establish a territory, nor did they help defend it, although, if two or more females and no males were placed in an enclosure, the dominant female eventually killed the others. Mice in addition to one male and one female could not remain in an enclosure more than two nights without being killed.

A mouse which was defeated in a fight was not killed during the first few fights if it assumed a submissive posture lying on its side with the forefeet against the thorax, tail stiff, ears back, and eyes closed (Fig. 12c). When this posture was assumed, the aggressor ceased the attack for a period of time from 4 to 12 minutes. After this period of time, the subordinate animal would again be attacked. This subsequent attack could take place even though the subordinate still maintained the submissive posture.

CHAPTER IV

SEXUAL BEHAVIOR

Scott (1958b) included in the category of sexual behavior, ". . . courtship, coition, and any related behavior." Tinbergen (1953) proposed that insemination, synchronization of activities, persuasion, orientation, and reproductive isolation were the functions of mating (sexual) behavior. These aspects as well as reproductive data and behavior of the young will be discussed in this chapter.

As described previously, sex recognition took place immediately upon meeting, and only male-female pairs could be kept together in an enclosure. Smell appeared to be the most important factor in sex recognition, since there is no striking morphological or behavioral sexual dimorphism. This conjecture was supported by a series of tests in which five male and five female mice were presented, individually, either with balls of clean cotton, or with balls of cotton in which a male or a female had nested. All animals each ignored the clean cotton, and showed only slight interest in the cotton in which their own sex had nested. In contrast, test animals showed marked interest in the balls from nesting-cotton that had been used by the opposite sex, and even performed

portions of their premating behavior with such cotton balls. These tests need further elaboration before the full role of smell in sexual recognition can be fully defined. Smell may also have been important in location of members of the same species. This was suggested by the behavior of 4 animals that escaped from the enclosure and traveled 150 feet to the location of the colony cages. To reach these, it was necessary for them to travel towards an area of human activity, and much of the way through an area of building construction. In the absence of some attractive stimulus, it seems reasonable to suppose that such areas would be avoided.

Courtship and Copulation

Courtship behavior followed a variable pattern which was stopped and resumed at various points. The general pattern was as follows (based on 34 observations through at least stage four):

1. The male and female met and moved in a tight circle (agonistic Behavior) for a variable number of revolutions followed by the female following the male with her nose touching his anal region or the base of his tail. This following response covered a distance of 10 feet to 60 or 70 feet.

2. They stopped and circled again, then raised up and touched noses in a naso-nasal posture (Fig. 13a).

3. The female then sniffed the male's genital region and the two rose up in the naso-nasal posture. At this point the courtship could

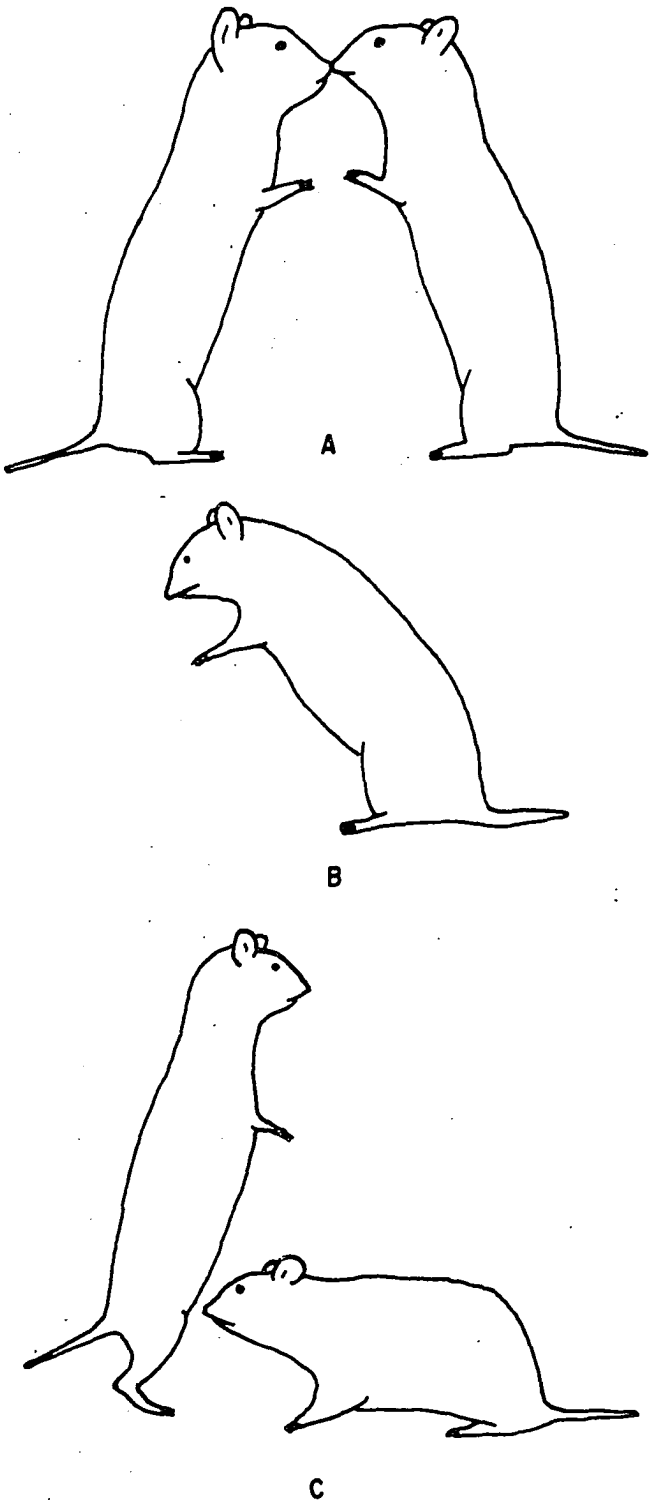


Fig. 13 -- Some sexual postures of Onychomys leucogaster. A: the male-female naso-nasal posture; B: the posture of a female while a male rubbed his back on her belly; C: a female standing on her hind legs with a male smelling her genital region.

break off, either for several hours or for a few minutes, and be resumed at the next step or discontinued.

4. The male then followed the female and stayed about 1 cm. from the base of her tail. They occasionally stopped and assumed the naso-nasal posture.

5. The male then sniffed the female's genitalia and walked back and forth in front of her two to six times while she sat on her haunches.

6. The female then raised up on her haunches (Fig. 13b) and the male moved under her, rubbing his dorsal side across her ventral side.

7. The female then raised up on her hind legs (Fig. 13c) and the male nosed her genetalia and groomed her face with his mouth. At this point the courtship again might be interrupted for varying periods of time, not exceeding 30 minutes, at which time the sequence could again be continued. At this point, the procedure could also be stopped.

8. The male and female circled and they placed their ventral sides together, held each other with the forefeet, and the female performed a very quick backward somersault while, at the same time, the male performed a forward somersault. This stage was observed only three times.

9. The female then assumed a position on her side and the male sniffed and nibbled her neck and side.

10. The female then stood on all four feet, tail to one side, back only slightly arched, and ears back. The male approached her from behind and mounted.

This ten phase pattern was interrupted at the points indicated, but if interrupted, the male often attempted to mount, but was never successful. Steps 1, 2, 4, 5, 7, 9, and 10 were necessary for successful copulation, and as long as three hours were required for completion of the entire sequence. Steps 1 through 3 took from 5 to 20 minutes (mean 10.5 minutes), steps 4 through 7 from 3 to 10 minutes (mean of 6.0 minutes), and the final phase took from 2 to 4 minutes (mean 2.5 minutes).

Copulation followed an unusual pattern for the Cricetidae. The male approached from behind and placed his forefeet on the anteriodorsal region of the female. He then inserted his penis for 1.5 seconds with a single thrust. Upon insertion, the female raised and stretched her head forward and her tail stiffened to one side. Then, while in-copula, they rolled on their sides and remained in this position for two seconds after which the female got up and groomed and the male got up, but remained hunched up for two seconds, then groomed his genital region and moved about. This pattern of copulation was observed on eight occasions with six different pairs of mice. On one occasion the female got up before the penis was withdrawn and dragged the male about six inches before his penis was released.

The male stopped the following response of the female when he assumed a posture in which he sat on his haunches and placed his nose at the base of his tail. This not only caused an immediate cessation of the following response of the female, but also caused a permanent interruption of that particular courtship sequence. Homosexual behavior was never observed.

Gestation and Litters

Six litters were born in captivity and these supplied some information on gestation and litter size. The earliest record of parturition I have was for a litter of four young born on 11 March 1963. Allowing for a 32 day minimum gestation period, this required breeding to have occurred on 8 February. The latest record of birth I have was a litter born on 9 October, 1961, which required mating on or before 7 September, 1961. Litters for which I have records were born in March, May, June, August, and October.

Thus, these records indicated breeding occurred in Oklahoma from February through September and examination of females indicated that they were polyestrous during that time. The gestation period for two litters was definitely known. Litter A was born on 11 May, 1961 after a gestation period of 34 days and Litter E was born 10 August, 1963 after 32 days gestation.

Of the nine litters for which I have records, litters of 3, 4, and 5 individuals were observed 4, 3, and 2 times respectively, and indicate

an average litter size of about 3.8. Sex ratios were obtained for 6 of these 9 litters, and taken together with 65 field captures, yield an observed sex ratio of 45 females to 43 males. This suggests a 1:1 sex ratio, or some very close approximation to equality.

Successful copulations were observed for two females on the night following parturition. This has also been observed by J.R. Preston (personal communication) among O. leucogaster kept at the Fort Worth Children's Museum.

Ontogeny of Behavior

Evidence from six litters of O. leucogaster observed every day from birth to 90 days of age, produced the following data. A behavior pattern was not recorded until it appeared in half of the young observed. Prior to that date, it was either not observed, or observed in only a few mice.

Day 1. The mice were born naked and helpless and there was considerable squeaking from the nest.

Day 2. The mice could move about the nest but were very shaky and uncoordinated. The body was covered by a dorsal gray fuzz with white fuzz on the ventral side.

Day 3. The young began to gain equilibrium, moving more easily about the nest. The ears unfolded.

Day 4. They now remained right-side-up most of the time.

Day 5. They moved out of the nest for the first time.

Day 9. The incisors appeared.

Day 10. The eyes opened, the mice still moved about with rather jerky movements and were easily frightened. They began to eat sunflower seeds and the abdomens of insects which the mother had not eaten. While eating, they put their food on the ground more often than did adults.

Day 14. The mice dug in the sand for the first time. They now spent as much time grooming as did the adults. They still moved with quick hurried movements but were less jerky. Some fighting between litter males was observed on this day.

Day 16. The mice ate insects in the adult manner, did not frighten so easily, were very curious, burrowed readily, and, although they now ate all types of food, occasionally nursed.

Day 21. The young abandoned the litter nest and dug their own burrow which was a hollow under a rock or bluestem clump.

Day 24. The mice were weaned and nursing was not observed after this day.

Day 32. This was the first day that attempted mountings were observed. These were always heterosexual.

Day 43. For the first time, the mice killed several of a group of insects prior to eating any (see ingestive behavior for an elaboration).

Day 60. The adult molt was observed for the first time.

Paternal Care of the Young

Paternal care in Onychomys leucogaster was observed in six litters, four of which were raised by a female alone, one raised from 24 days of age (time of weaning) by a male alone, and one by a male and female. The adults were solicitus of the young and huddled over them when the nest was inspected. However, if the adults and litter were removed from the nest can, the parents immediately ran away and did not attempt to protect the young. When the inspection was completed, both parents carried the young back into the nest. The parents held the young in their mouth by the nape of the neck and on two occasions young were picked up by one leg. There was no observable difference in the way males and females carried the young. Frightened females often ran out of the next with one or more young still attached to their nipples, but usually the young were detached from the nipples before she left the nest.

Until the young were 14 days old, at which time they began to groom themselves, the female parent spent considerable time grooming them. Her efforts were concentrated on the young's head and back. Males did not assist in grooming the young.

Adults ate all but the wings and abdominal exoskeleton of insects they captured and later ate the abdomen. However, when the young were between the age of ten days and 16 days, the parents appeared to leave some of the abdomens for the young.

At about 16 days of age, the parents stayed away from the young for longer periods of time, and by 24 days, the parents ceased to care for the young. At this time, fight caused mortality among litter mates increased and the litter had to be separated at 30 days of age if both the male and female parents were present. However, if only a female parent was present, and if they were in a small cage, they could be kept together for up to 60 days before they had to be separated.

Play

Beach (1945) listed as play activities general bodily activity (running etc.), youthful practice of adult activities, and exploration. He mentioned that play carried with it the emotional element of pleasure, was characteristic of immature individuals and was non-utilitarian. Young O. leucogaster frequently engaged in activities described as play. They did not differ from those described by Beach and included general running about, digging in the sand, and, after 14 days of age, included fighting. Practice of sexual activities was observed infrequently and no homosexual activity was observed. Young mice kept in a cage with hardware cloth sides and top spent considerable time running up one end of the cage, upside down across the top and down the other end. They ofen did this for 30 minutes without stopping.

Play began at the age of five days and increased in amount until the age of 21 days when they abandoned the nest. From day 21 it decreased until at 60 days of age there was almost no activity that could be classified as play.

Adult Molt

The adult molt (change to adult pelage) began 60 days after birth. Figure 14 shows the progress of the molt from the juvenile gray pelage to the adult cinnamon phase pelage, shaded areas indicating the new pelage. The adult molts of 15 mice were observed and sketched from onset to completion to arrive at this composite pattern. Molting began with a thin cinnamon bar which appeared just behind the forelegs and progressed posteriorly, faster on the ventral end of the bar than on the dorsal. By ten days the cinnamon color had about covered the animal between the forelegs and hindlegs. At twelve days one small spot appeared on the rump, and the sides were cinnamon between the forelegs and hindlegs. At day 15 of the molt (75 days after birth) the anterior and posterior spots had spread a little and a spot of cinnamon appeared on the neck, just behind the ears. By day 18 these spots had spread until almost the whole rump was covered, the spot behind the ear had progressed down to meet the anterior shoulder spot and a spot appeared on the top of the head. These spots progressed anteriorly and posteriorly to complete the cinnamon phase by the twentieth day (80 days after birth). It can probably be assumed that the dark adult color phase described previously was molted in a similar fashion although this was not observed. Molting from one adult pelage to another was also not recorded.

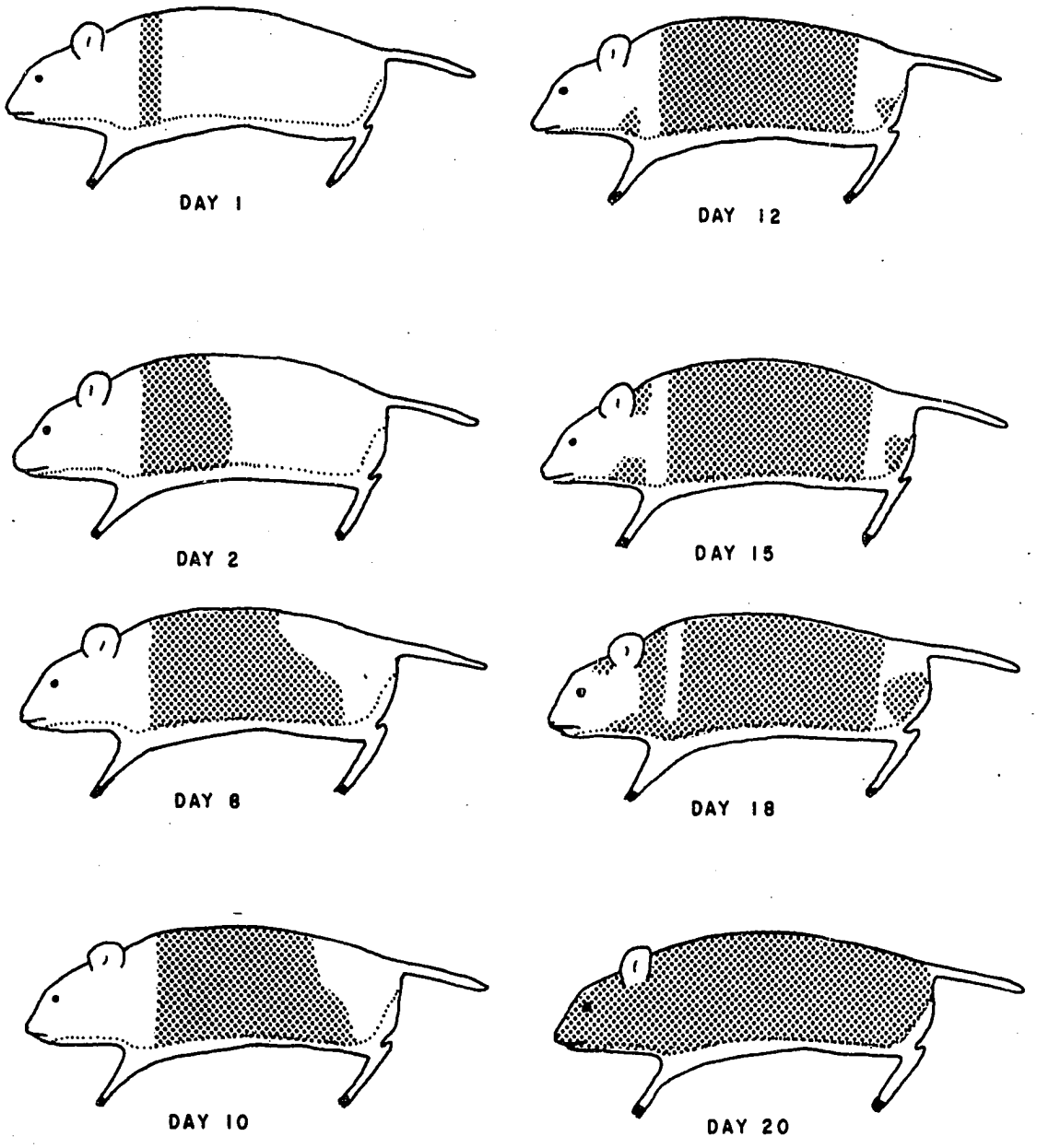


Fig. 14 -- Pattern of the adult molt in Onychomys leucogaster (Stippled areas indicate new pelage).

CHAPTER V

INGESTIVE, ELIMINATIVE, AND GROOMING BEHAVIOR

Ingestive Behavior

Kinds of Food

During the present study, grasshopper mice killed and ate the following species of small mammals: Perognathus hispidus, Dipodomys ordi, Reithrodontomys megalotis, Peromyscus leucopus, P. maniculatus, Sigmodon hispidus, and Mus musculus. Ants were the only species of local insects not eaten, and although a study of the species eaten was not conducted, no others were refused. Onychomys seemed to prefer the larger insects, particularly grasshoppers, june bugs, and moths. They also ate chunks of sand (observed in one 40 day old animal), a leopard frog (Rana pipiens), a six-lined racerunner (Cnemidophorus sexlineatus), and a dead English Sparrow (Passer domesticus). The mice could not be induced to eat eggs. Although grasshopper mice that were killed in intraspecific fights had their brain pierced and often had a slit in the dorsal abdominal wall through which a loop of the small intestine had been pulled, no cases of cannibalism were observed.

Hoarding Behavior

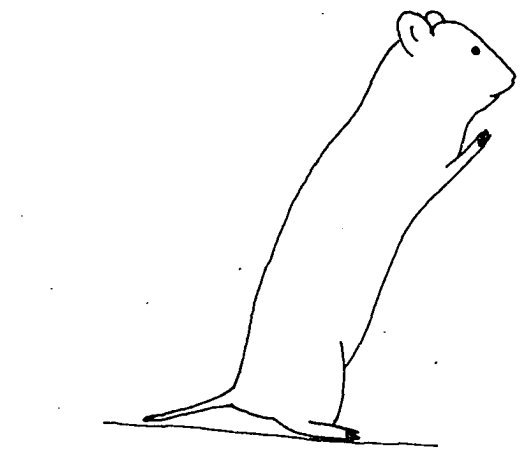
Onychomys dug cache burrows in which seeds were stored, a small cache of seeds was found in the nest chamber and the nests in colony cages usually contained a supply of seeds (Chapter II). If insects or other animal food was available, the stores of food were not used.

Method of Eating Food

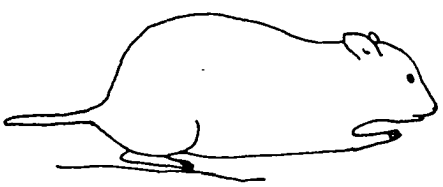
Seeds were held in the forepaws, the seed coat was removed in strips with the teeth, and the cotyledons removed and eaten. Insects were grasped with the teeth, held in the forepaws, the head chewed off, and all but the wings and distal portion of the abdomen was eaten. When a mouse was given several insects at one time, he bit the heads off of most of them before eating any one of them.

Figure 15 shows two postures assumed while insects and seeds were eaten. These are only representative and indicate the two extremes of this variable posture. Figure 15b was characteristic of younger animals but was also observed in adults. Another mouse, after being killed, was held down with the forefeet and the flesh torn away with the teeth and all but the skin was eaten.

The young nursed while the mother stood on all four feet with her hind legs spread. The young either laid on their back with their head under the mother, or they laid on their belly with their head stretched forward and grasped a nipple to nurse. While lying on their back to nurse, the young either held onto the mother with their forefeet or held



A



B

Fig. 15 -- Feeding postures of Onychomys leucogaster. A: the upright feeding posture; B: the prone feeding posture.

their forefeet against their abdomen. The grip on the nipple was sufficient to allow the young to be dragged about the enclosure when the mother was frightened while they were nursing.

Water was lapped from a dish and the paws were not used in drinking. Food was either eaten on the surface, as was the case with seeds and insects, or dragged into the burrow. The male member of a pair killed the small mammals and ate a little of them outside the burrow before dragging the carcass into the burrow where, presumably, the female ate some of it. The skin was then dragged out of the burrow and left on the surface.

Coprophagy

On four occasions young grasshopper mice sat on their dorsal pelvic region or laid on their side, placed their mouth over the anus and ate the first fecal pellet expelled. These were the only four instances, in either close or casual observation, in which coprophagy was observed. On these four occasions, there was no "sampling" of pellets as I have observed in Geomys bursaius, which seemed to discriminate between fecal and the favored caecal pellets.

Eliminative Behavior

In the present study, mice used one corner of the cage, away from the food and water, for urination and defecation and few fecal pellets were scattered about the floor of the cage. Nest cans or nest burrows never contained fecal pellets and urine deposits.

Four burrows were found which contained a deposit of fecal pellets. Although they were never observed in use, they were described as defecation burrows. During several sundown to sunup observation periods, eliminative behavior was never observed.

Grooming Behavior

Individual Grooming

Individual grooming followed a definite pattern which began with several short wipes of the paws over the nose and mouth and under the mouth. Next the paws were moved in unison over the face and ears. Subsequent strokes began further back until the whole head was included. This was followed by the paws being washed and rubbed over the sides and abdomen, accompanied by nibbling the fur. Next the forearm was held stiff and the fur cleaned with the mouth. The mouse then sat on the dorsal pelvic region, held the stiff hind leg in the forepaws, and cleaned the fur with the teeth, starting at the knee and proceeding toward the proximal and distal end. Finally the tail was pulled through the forepaws and cleaned.

Of six half-hour observation periods, 11 per cent of the time was spent grooming. Grooming of the face and paws was always observed after a chase and when a mouse finished eating.

When taking a sand bath the animal stood on all four legs, placed the side of its head on the sand, lifted the forefeet and, while pushing forward with the hind legs, quickly turned on the back of the neck, then the back and got up. The mouse moved forward about 8 cm. and turned completely over. Occasionally, only the base of the chin and belly were

rubbed in the sand. Young animals began to take sand baths at the age of 12 days. In these early baths the animal merely laid on the side and wiggled a bit. At the age of 14 days they followed the adult pattern in sand baths. On three occasions mice sat on their dorsal pelvic region and scratched their head with their hind leg, but such scratching was not found to be a regular part of grooming.

Mutual Grooming

The back of the head and shoulder region of Onychomys leucogaster were groomed by another grasshopper mouse using its teeth. Mutual grooming occurred in all litters from 14 days of age in which females groomed males, males groomed females, and young groomed their mother. Male-male and female-female grooming was not observed. A posture as in Figure 16 was assumed by the animal being groomed and the animal doing the grooming stood near him, the groomer's postures being quite variable.

Frequency of Grooming Types

During six two-hour observation periods of male-female pairs, the frequency of head and facial grooming, whole body grooming, and mutual grooming was recorded. Of 232 observations, 142 (61 per cent) were of head and facial grooming, 46 (20 per cent) of whole body grooming, and 44 (19 per cent) of mutual grooming. This averaged 23.67 head and face, 7.67 whole body and 7.33 mutual grooming records per pair per two-hour period. Chi-square calculations confirmed the significance of the obvious departure of these data from a 1:1:1 ratio.



Fig. 16 -- Mutual grooming posture of the O. leucogaster being groomed.

CHAPTER VI

MISCELLANEOUS OBSERVATIONS

Communication

Olfactory Communication

Autopsies made during this study revealed that O. leucogaster did not possess lateral or mid-ventral dermal sebaceous glands but did have a concentration of glandular material at the anal region which produced the musky, mustelid-like odor characteristic of this species. Some indication has already been given as to the role which smell played in the behavior of grasshopper mice. It was probably involved in sex recognition, almost certainly involved in species recognition, and was used in marking territories.

Auditory Communication

Several authors have noted the calls of grasshopper mice and anyone who has kept them in the laboratory is aware of the noise a group of these mice can make. Four types of calls were recognized in this study: (1) Young animals, until about four days of age; and adults during some fights, gave a squeak call; (2) a high-pitched chirping call -- ech, ech, ech, ech -- was an alarm note given by individuals during an

intense fight and when they were being removed from the cage; (3) a high-pitched, piercing call which lasted an average of 0.8 seconds; (4) this type was similar to the third but was broken so that it sounded like two shortened type three calls, one immediately following the other, and lasted an average of 0.9 seconds. The type three call was, as here recognized, a means of intraspecific localization. This call was given by individuals who were alone in an enclosure or who were otherwise separated from other grasshopper mice. The type four call was given when a mouse had located another but was unable to make contact with it or to otherwise specifically locate it. To my knowledge, the type four call has not been recorded previously. Although it was possible to hear most of the calls, at times apparently calls were given (as indicated by postures) that were inaudible.

The posture assumed while a type three or four call was given varied considerably. Both sexes held the body in various positions from a prone one on all four feet (similar to Fig. 16) to an upright posture standing on the hind legs. Occasionally the head was held back, the ears back, and the eyes partially closed while these calls were given. However, the usual posture was with the head stretched forward, only slightly raised, with the eyes partially closed, the ears lying back, and the mouth slightly opened to expose the teeth. No definite posture was associated with the other two types of calls.

Investigative Behavior

As reported by Egoscue (1960) the initial reaction of grasshopper mice to unfamiliar situations denoted curiosity or, at most, cautious deliberation rather than apprehension. This departed from the behavior of most other Cricetine rodents under similar circumstances. During this study, the mice gave no indication of being diurnal.

Investigative behavior included tactile and olfactory testing of objects within an enclosure and general movement about the enclosure. In an unfamiliar area, exploration or investigative behavior in grasshopper mice was not directed toward one object but included the entire enclosure, beginning with the edges and progressing toward the center so that within ten minutes of introduction, they had moved over the entire area. In this way a mouse quickly became acquainted with the enclosure and was, presumably, better able to defend his territory and was better able to escape from predators in the wild.

Figure 17 shows four postures assumed by grasshopper mice while looking about an enclosure. Figure 17a was assumed by animals when they were not under cover or near a burrow. The ears were forward, the paws against the chest, and they looked in one direction. While they ran about, the animals often stopped and stared ahead, standing with three legs on the ground and one foreleg raised, the ears were forward and the tail stiff (Fig. 17b). Figure 17c presents a posture assumed when a mouse paused while digging a burrow, or while running

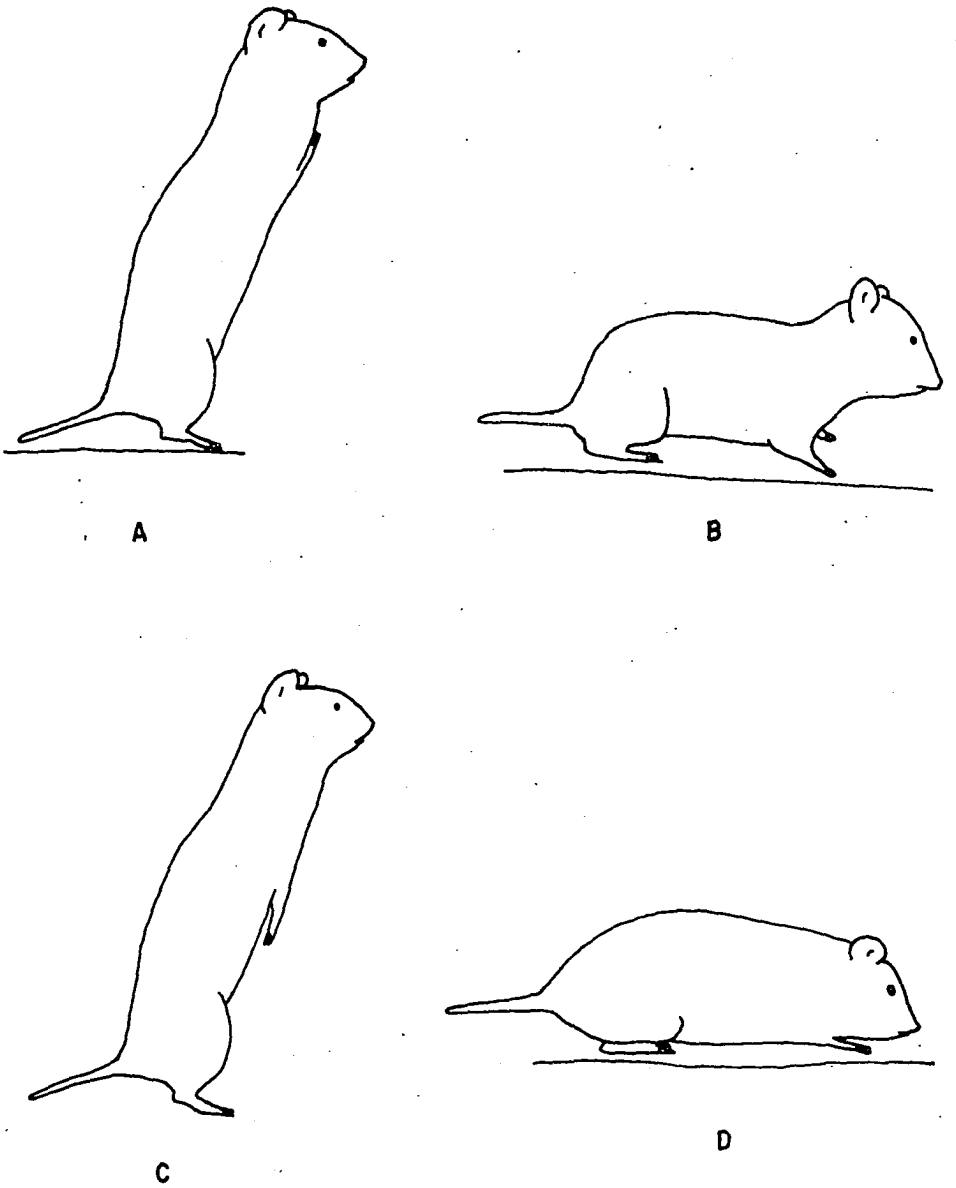


Fig. 17 -- Onychomys leucogaster investigative postures. A: the posture assumed while looking about when the mouse was not under cover; B: the posture assumed while running about when the mouse stopped to look about; C: the posture assumed while a mouse was digging and stopped to look about; D: the posture assumed when a loud disturbance was heard.

about the enclosure. The ears were forward, the forelegs were held, paws together, palms down, against the abdomen. Lastly, Figure 17d was the posture assumed when there was a loud disturbance or when a mouse was confronted with an entirely new addition to a familiar enclosure.

One feature common to all these postures was that the mouse stared in one direction and did not move its head while looking in one direction. On some occasions it was possible to note that the eyes were not moved either. No pattern was detected in the length of time these various postures were held.

Although no quantitative data were kept, it seemed as though there was as much as a 50 per cent reduction in the amount of investigative behavior when O. leucogaster became oriented in a new situation.

Use of the Tail

Grasshopper mice use the tail as a prop or "third leg" while sitting on his haunches or standing (Fig. 17). The short tails of this species (less than one-half the body length), were not observed to be used for any other apparent purpose.

The tail of grasshopper mice showed a degree of expressiveness. Figure 18 shows the position of the tail with varying degrees of unfamiliarity between the mouse and the enclosure or the differing amounts of supposed "tension". When first introduced into the enclosure or during a chase, the tail was carried very stiff and straight out behind or slightly curved up (Fig. 18a, b). After most of the enclosure was explored, the

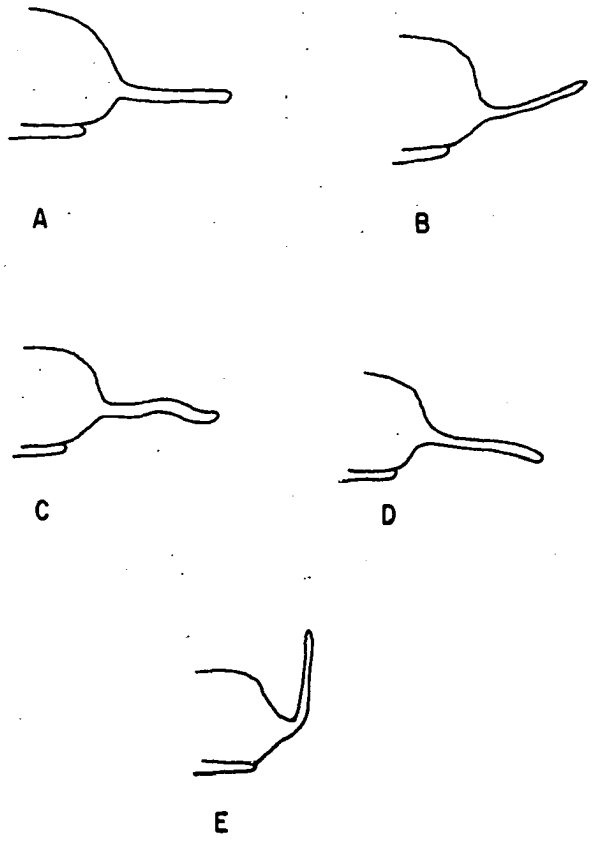


Fig. 18 -- Tail positions in O. leucogaster under differing degrees of unfamiliarity with the enclosure. (See text for explanation of the various positions)

tail was obviously more relaxed and curved down or was rather loosely held (Fig. 18c, d). Occasionally, when a mouse encountered a mouse it had not previously seen, when a subordinate met the dominant, when a male was followed by a female; or when a mouse confronted a new or unusual artifact placed in the enclosure by the observer, the tail became stiff and was held vertically (Fig. 18e). The rigidity with which the tail was carried was positively correllated with the degree of unfamiliarity between a mouse and some other aspect of environment.

Swimming

A study of the role of swimming in the behavior of O. leucogaster was conducted in a half cylinder tank which measured 20 feet 6 inches long and 4 feet wide, with 13 1/2 inches of water, maximum depth. A 22 inch wide stationary platform with the floor at water level was constructed across the center of the tank about 2 feet from the top of the tank. Four males and one female were, at different times, placed on the platform and held for five minutes in a bottomless cage. The cage was then slowly lifted off the platform and the animals were observed for a 15 minute period. At that time, I attempted to catch the mice by hand. Two of the males were readily caught, but the other mice, apparently frightened, jumped into the water. They swarm to one end of the tank and then back to the platform, climbed onto the platform and did not go back into the water. They swam by "dog paddling" with their forefeet and kicking the hind feet in unison with each other. Distances

swum were: 16 feet, 20 feet, and 35 feet. These studies indicated that swimming while not a usual feature of investigative behavior, could nonetheless be used as a means of escape when no other was available.

Miscellaneous Observations

Walking or running involved a diagonal sequence of limb motion as follows: right foreleg, left hind leg, left foreleg, right hind leg. The mice showed no hesitation to climb and readily ascended and descended the wire sides of cages and during one portion of the study climbed verticle logs. Although in their natural environment they may never climb, or never encounter a tree or other object to climb, they were not reluctant to do so.

The vibrissae of one male were cut off and he was observed for a three day period. During this entire time he moved about with very jerky motions and was very easily frightened by things such as finger snaps or jumping insects which did not frighten normal animals. The movements of this male were very much like the movements of animals less than 10 days old.

No indication of hibernation was observed and mice were captured during October, November, January, February, and March as well as warmer months.

CHAPTER VII

DISCUSSION

Review of the Ethogram

The purpose of this study was to describe the ethogram for the Northern Grasshopper Mouse (Onychomys leucogaster). Eibel-Eibesfeldt and Kramer (1958) and Tinbergen (1951) stressed the importance of the ethogram or complete inventory of the innate behavior patterns of a species as a preliminary to further ethological studies of the species. Hinde and Tinbergen (1958) discussed the importance of the comparative approach to ethology in arriving at a tentative description of the course of evolution within a group. Thus, a description of the behavioral evolution of a group of animals should ideally include ethograms of all or most of the species involved. Many genera are so large that such a project would be impractical for an individual investigator. However, the genus Onychomys, which includes two species, is ideally suited to such an approach both from the standpoint of the small number of species and the behavioral divergence of the group from closely related genera.

Whitman (1899) proposed that "Instincts, like corporeal structures, may be said to have a phylogeny . . . the main reliance in getting at the

phyletic history must be comparative study." Mayr (1958) pointed out that behavior characters have taxononomic relationships. Also, Simpson (1958) showed that behavior was the actual means of interaction between physical organization and the environment -- the visible expression of adaptation. Thus, it is my intention to present here the ethogram for Onychomys leucogaster as a basis for further studies on isolated aspects of the behavior, and to later, if possible, work out the ethogram for O. torridus. The two species could then be compared in an attempt to describe the apparent course of evolution within the genus.

Shelter-seeking Behavior

Bailey and Sperry (1929) made the following statement concerning the nesting habits of O. leucogaster. "The strong claws of grasshopper mice resemble good digging tools, but there seems little evidence of extensive burrowing. They can dig rapidly in soft earth, and to some extent dig out and capture their prey in this manner. It is questionable whether they habitually dig their own burrows or generally use abandoned burrows or those of their victims." Later on in the same work the mice were described as being wanderers rarely captured at burrows that could be called their own or in places where they would be likely to have permanent homes. However, the statement was made that perhaps they did dig burrows during the breeding season.

Later, Bailey (1931) stated that grasshopper mice evidently occupied any burrow found abandoned or from which they could evict the

owner, although it was considered probable that they dug burrows themselves. Later, Bailey (1936) suggested that the long front claws of Onychomys were used as weapons rather than as tools and that O. leucogaster had no homes of their own.

These statements have been interpreted by many authors of regional and local faunae to mean that O. leucogaster did not burrow but rather lived in abandoned burrows of other animals or in those of their victims (Jackson and Warfel, 1933; Warren, 1942; Olin and Cannon, 1954; Hall and Kelson, 1959; Davis, 1960).

Since O. leucogaster is primarily an arid land mammal, it seemed evident that it would be of considerable adaptive advantage to the survival of the species to have evolved a pattern of burrowing. Bodenheimer (1957) proposed that about 70 per cent of arid land species were burrowing forms as compared to 6 per cent in wooded areas, and gave evidence that a burrow protected the occupant from extreme fluctuations of temperature to which he would be subjected on the surface. Petter (1953), in a study of the burrows of Meriones libycus, and Holdenried (1957) in a study of Dipodomys spectabilis found much this same thing. The burrows of Onychomys had a similar function as evidenced by the temperature data collected during this study. The burrow provided the animal a cooler atmosphere during the day and greatly reduced the temperature fluctuation to which it was subjected. Petter (op. cit.) and Holdenried (op. cit.) have also shown that relative humidity was

higher in a burrow than at the surface. Bodenheimer (1957) reported that the relative humidity inside a Dipodomys burrow ranged from 30 to 50 per cent, while that outside the burrow ranged from 1 to 15 per cent during the day and from 15 to 40 per cent at night. Although relative humidity within Onychomys burrows was not measured, it should not be expected to differ from those reported above.

Thus, to an arid land mammal, the burrow, or some similar means of protection from diurnal heat, is a necessity. It provides it with an atmosphere of greatly reduced temperature and humidity fluctuation and results in a reduced water loss from its body. This, accompanied with a nocturnal habit, keeps it out of the diurnal surface temperatures which may exceed 150 degrees F. Again, this indicated that a burrowing pattern would have survival value for Onychomys.

Herrick (1892) stated that O. leucogaster burrowed in sandy prairies. Seton (1909) stated that ". . . powerful forefeet and claws certainly proclaim it a digger." Bailey (1926) mentioned some fresh burrows that he said could have been dug by O. leucogaster, but, he stated, probably were not. Later, Bailey (1931) stated that Onychomys "doubtless have definite homes," but perhaps did not dig their own burrows. His intended meaning here seems to be simply that Onychomys may or may not burrow. Warren (1942) reported that O. leucogaster possibly dug holes of their own and Cockrum (1952) and Davis (1960) both stated that grasshopper mice may dig shallow burrows. Barnes

(1927) also said they lived in burrows, and Hoffmeister and Goodpaster (1954) briefly described a burrow dug by Onychomys.

Four burrow types were recognized in this study: nest, retreat, cache, and miscellaneous (including defecation and sign-post burrows). Burt (1940) commented that with several places of retreat, animals would be near one at any point in their home range where they happened to be disturbed. This was obviously the case in Onychomys which, as will be discussed later, had a rather large home range. The nest burrow and retreat burrow corresponded to the First and Second Category homes respectively of Hediger's (1950) classification. Bourliere (1954) for the red fox, Ruffer (1961) for Peromyscus leucopus, and Armitage (1962) for Marmota flaviventris have described nest types similar to those found for Onychomys.

The pattern of burrow digging was very consistent and nest burrows were only dug by a male with the help of the female. Quite in contrast to Sigmodon hispidus and Peromyscus spp., in which the nest entrance was in a protected area, the nest entrance of Onychomys was in the open and not in the shelter of a grass clump or rock. Dipodomys ordi, a species associated with Onychomys in the wild, also had an unprotected entrance.

The study of the relationship between O. leucogaster and the burrows dug by other species indicated that other burrows were not used by Onychomys. The reasons for this were not explored, but probably were related to the different configuration and size of the Dipodomys

and Perognathus burrows tested. This lack of use of the burrows of other species placed greater importance on the evolution of a burrowing pattern in Onychomys. Thus, it was revealed that under the conditions of this study, Onychomys leucogaster did have a definite pattern of burrowing and would not use the burrows of other species.

Grasshopper mice had a well-developed pattern of interspecific aggression which consisted of: pursuit by the aggressor, pounces on the victim, seizure of the victim from the rear, and piercing of the rear of the skull. The defensive posture of a grasshopper mouse in the role of victim (Fig. 12a) failed to stop the attack, rather the aggressor attempted to bite the tail of the victim to get it to turn around. This pattern was also observed by Clark (1962b), although he did not comment on defensive postures. In intraspecific encounters, the attack of the aggressor was stopped if the subordinate assumed a posture on his side on the sand (Fig. 12c). This posture was different from the submissive posture described by Eisenberg (1962) for Peromyscus maniculatus, in which the animal sat with its eyes closed, and P. californicus in which this posture was accompanied by the victim turning away from the aggressor. Eisenberg (1962) described a lock posture in P. maniculatus and P. californicus that was identical to that described in Onychomys (Fig. 12b).

Grasshopper mice are generally considered not to be very abundant except in very localized instances and my trapping records

revealed a similar situation in Oklahoma. Both Burt (1940) and Hediger (1950) stated that predatory animals must have a larger home range than herbivorous animals. Burt (1940) studied several herbivorous species and found the home range of Peromyscus leucopus to be less than 0.5 acres in breeding females and 1.5 acres for old males, 0.2 acres for Synaptomys cooperi, 0.2 acres for Microtus pennsylvanicus, and 0.25 acres for Pitymys pinetorum. Ruffer (1961) found that both male and female Peromyscus leucopus had a home range of approximately 0.2 acres. Williams (1955) found mature male P. maniculatus to range over 0.81 acres while mature females ranged over 0.63 acres.

Blair (1953) found the mean home range of four male Onychomys torridus was 7.8 acres while five females ranged over 5.9 acres. Four male O. leucogaster had an average range of 5.8 acres. These few data, coupled with my trapping experience, seemed to indicate that O. leucogaster, being a predatory mammal, had a larger home range and territory than did closely related, non-predatory genera.

Agonistic Behavior

Territory is related to home range in being the defended portion of the home range. Although home ranges may overlap, territories seldom do (Burt, 1940; Ruffer, 1960), and the territory size and home range size are not necessarily directly related. Noble (1939) found that territories offered a clear advantage to subordinate animals in that a subordinate animal in his own territory could win a fight with a dominant

animal. As discussed previously, my data indicated that a subordinate was reluctant to fight in a dominant's territory. C.R. Carpenter (1958) included the following functions of territoriality (from a list of 32 functions): it disperses a population, ensures adequate space, prevents overpopulation, reinforces dominance, and reduces sexual fighting and killing. All of these are clearly advantageous to any mammal, and a predatory mammal would need a larger territory since its food supply would be much more dispersed than would that of an herbivorous species. This is augmented in grasshopper mice by the development of an elaborate system of burrow types which are arranged throughout the territory to provide places of retreat.

My data indicated that grasshopper mice had a large well defined territory which was respected by other mice and defended by non-violent encounters. This is opposed to Clark's (1962a, b) observations. He found that laboratory-reared grasshopper mice could be kept indefinitely in groups of five or more. This would indicate that either the mice were not territorial, or that the territoriality was broken down. Certain of my observations and those of Mr. John Preston (personal communication) indicated that if a pair of grasshopper mice were kept in a small cage, no larger than a five gallon aquarium, the territoriality appeared to break down and several generations could live together, provided there was adequate food and water available. However, I have found that if these same animals were ever released into a larger cage or into the

enclosure, the territoriality was reinforced and the litters had to be separated. This seemed to indicate that Dr. Clark's observations were affected by the small size of the cages he used.

Smell played an important roll in establishing and maintaining a territory. Richmond and Roslund (1952) described a mid-ventral dermal sebaceous gland in Peromyscus polionotus and five subspecies of P. maniculatus. Autopsies made during the present study revealed no such skin glands in Onychomys leucogaster. Quay (1953) described the activity of the dorsal skin gland of the kangaroo rat but similar glands were not found in Onychomys. The scent for marking apparently came from a concentration of sebaceous-like glands in the anal region. The sand bath which accompanied the sign-posting activity included rubbing the anal region in the sand.

Sexual Behavior

Smell played an important role in sex recognition which was immediate and completely accurate as indicated by the circling types which varied with inter and intra-sex encounters. There were no observable behavioral differences upon first meeting and no morphological sexual dimorphism was observed. Smell seemed to be the important factor.

The courtship pattern of O. leucogaster was similar to that described for Peromyscus truei by Tamsitt (1961) but copulation, which involved lying on the side while in-copulo, was similar to that described in Mephitis mephitis by Wight (1931) although it did not take as long as

for the skunk. To my knowledge, this phase of lying on the side has not been observed in any other cricetid rodent and I am unable to speculate on the adaptive value of such behavior. Perhaps some undiscovered factor accompanyed the predatory habit which necessitated or made possible this pattern of copulation. Further study is needed to clarify this matter. The naso-nasal posture observed during courtship was similar to that described in ground squirrels by Balph and Stokes (1963) and Grubitz (1963) but differed from that described in P. maniculatus by Eisenberg (1962) in which the mice were on all four feet while assuming the naso-nasal posture.

An unusual feature of sexual behavior in Onychomys leucogaster was the lack of homosexual behavior of any type. This could have been related to the strong aggressive behavior which may not have allowed like-sex encounters to become sexual.

Egoscue (1960) reported that, from trapping records, he believed that grasshopper mice associated in pairs. From my trapping records and observations of nest building behavior, it was evident that Onychomys leucogaster associated in pairs and that these pairs were permanent, at least throughout the breeding season (February through October) and probably throughout the year.

The breeding season varied from one locality to another. Egoscue (1960) found that Utah mice were polyestrous from January to July and 69 per cent of the litters born in captivity were born between February

and August. Davis (1960) reported that Texas forms had a May to October breeding season. Capture records from the present study indicated breeding in Oklahoma from February to October.

Litter size averaged 3.78 individuals (6 litters) in the present study which differed slightly from Egoscue's (1960) mean litter size of 3.59 individuals (181 litters) for which he does not give the variance. Egoscue also reported a sex ratio of 106 females to 94 males and the sex ratio observed in the present study was 45 females to 43 males (102.28 females to 97.72 males on the conventional basis of 200 per cent). Egoscue (1960) reported that grasshopper mice were the only rodents among nine species bred in his laboratory which showed a secondary and tertiary sex ratio in favor of females (sex ratios are described as primary, at conception; secondary, at birth; or tertiary, at puberty ((Asdel, 1946))).

The two gestation periods for non-lactating females recorded in the present study were 32 and 34 days. Hall (1955) and Svihla (1936) reported that gestation in O. leucogaster was 33 to 47 days for lactating females and less than 32 days for non-lactating females. Egoscue (1960) reported a gestation of 32 to 38 days for lactating females and 29 to 32 days for non-lactating females. It was the intent of this author to use laboratory born animals in this study only for litter observations and thus much reproductive data was not available.

Data on the ontogeny of behavior in O. leucogaster differed

slightly from observations made by other authors. I observed that the ears unfolded on the third day after birth as did Davis (1960) and Svihla (1936). Taylor (1962) observed unfolding of the ears on day 2 in O. torridus. Incisors appeared on day nine while Bailey and Sperry (1929) reported their eruption on day 11. In the present study the mice were covered with gray fur on the second day which differed from Svihla's (1936) report of gray fur at day 12. Calhane (1947) reported that the eyes opened on day 14; Taylor (1962), Hall (1955), and Bailey and Sperry (1929) stated they opened at day 12, and Davis (1960) and Svihla (1936) found they opened on day 19. These were much later than in the present study in which the eyes opened on day 10. Bailey and Sperry (1929) reported that grasshopper mice ate seeds and greens for the first time on day 17; seven days later than mice which I studied. In this study, mice were weaned at day 24. Taylor (1962) reported weaning on day 18 in O. torridus, and Bailey and Sperry (1929) and Calhane (1947) reported weaning on day 24. Davis (1960) reported that the mice were probably evicted from the nest on the day of weaning. My data showed that the mice abandoned the nest at day 21 but some nursing was observed until day 24. Taylor reported fertility at 90 days of age in O. torridus.

The cause of this variation may be due to the method of recording the data. In my study days given for the appearance of a behavior type were the day when 50 per cent of the individuals exhibited the behavior while the other works cited were of single litters and refer to the first

time an observation was made. There was very little variation within a litter with regards to appearance of a behavior type. In almost all cases, the whole litter began to exhibit a particular behavior type on the same day.

Paternal care in Onychomys leucogaster was similar to that described in Peromyscus by Horner (1947). Both male and female grasshopper mice cared for the young but litter protection was broken down when the adults were frightened as when they were removed from the nest. At about 16 days of age the litter was left alone more frequently until day 24 when the parents no longer cared for the young.

The pattern of adult molt observed in Onychomys differed considerably from that described for Peromyscus leucopus (Gotteschang, 1956) or that described as characteristic of the Cricetinae by Hoffmeister (1944). In Onychomys the main sequence of appearance of new pelage on the sides was anterio-posterior while in Peromyscus and other Cricetines it was a ventro-dorsal movement. The molt on the face and rump was similar to the Cricetinae pattern.

Armitage (1962) found play to be frequent in young Marmota flaviventris and it is probably characteristic of most young animals. Play in grasshopper mice was frequent and increased in frequency to 21 days of age after which it began to decrease until at 60 days of age when there was almost no activity that could be defined as play.

Ingestive Behavior

Bailey and Sperry (1929) found that 90 per cent of the material in the stomachs of 96 O. leucogaster was animal, 80 per cent of which was insects including: 56 per cent crickets, caterpillars, and moths; and 20 per cent beetles. Fautin (1946) examined the stomachs of six individuals and found that 66 per cent of the contents was crickets, 17 per cent grasshoppers, 6 per cent beetles, and 2 per cent was a lizard (Uta sp.). Warren (1942) reported that grasshopper mice ate insects and seeds, and Bailey (1926, 1931) reported that grasshoppers, crickets, scorpions, mole crickets, beetles, caterpillars, cutworms, insect eggs, lizards, salamandars, and many small mammals were included in the diet. Egoscue (1960) reported that O. leucogaster ate these things as well as darkling beetles (Tenebrionidae) and stink beetles and all species of local cricetids and heteromyids. Johnson (1944) reported that captive O. leucogaster ate snails (Helicina arbiculata). Olin and Cannon (1954) described Onychomys as insectivorous and Bailey (1926) described them as omnivorous. Martin, Zim and Nelson (1951) reported that, from a small sample, the percentage of animal material in the stomach contents of grasshopper mice was 50 per cent in the winter, no record for the spring, 81 per cent in the summer and 99 per cent in the fall. In comparison, they reported the following amounts of animal material in the stomachs of Peromyscus maniculatus: 6 per cent (winter), 76 per cent (spring), 32 per cent (summer), and 70 per cent (fall).

My data was similar to the list given by Bailey and Sperry (1929: 13-18). The mice had a preference for animal food and did not eat seeds when animal food was available. Although they did not eat ants, grasshopper mice failed to demonstrate the frantic behavior toward them described by Bailey and Sperry (1929). Bailey (1926) reported a case of cannibalism but this was not observed in this study.

Viek and Miller (1944) found that food deprivation was fundamental to hoarding behavior. Bailey (1926) stated that O. leucogaster stored food but later (1931) stated it did not. My data indicated that hoarding behavior may be a characteristic of natural populations. Seeds were stored in cache burrows and in the nest. These were not used if other food was available. Martin, Zim and Nelson (1951) indicated that the plant content of stomachs from O. leucogaster increased in the winter. Since the supply of animal food decreased in the winter due to reduction in numbers or inactivity, caches would provide an emergency food supply to supplement the winter diet.

Feeding postures did not differ from those of other small mammals. Bailey and Sperry (1929) described the nursing posture in which the young stood on all four feet but did not observe nursing when the young laid on their back.

Coprophagy or reingestion of fecal pellets has been reported in Sorex araneus (Crowcroft, 1952), Crocidura cassiteridum (Booth, 1956), many rabbits (summarized by Lechleitner, 1957), Aplodontia rufa

(Ingles, 1961), laboratory mice and rats (Geyer, 1947) and in Geomys bursarius (unpublished observations by Ruffer and Grubitz). The function of coprophagy is not known. Geyer (1947) reported that laboratory rats, when prevented from eating feces, grew significantly more slowly than the controls. He also found that if the animals which were prevented from eating feces were fed liver, there was no longer a significant difference in the growth rate. Barnes (1959) found that fatty acid deficiency was hastened when laboratory rats were prevented from eating feces. Meyers (1959) stated that coprophagy was a normal feature in the biology of the rabbit Oryctolagus cuniculus in Australia and was important in nutrition and vitamin economy. Bourliere (1954) stated that it may function to provide the animal with vitamin B. Coprophagy was observed four times in juvenile O. leucogaster but its role in nutrition was not studied.

Excretory Behavior

In the present study, grasshopper mice used one corner of the cage for defecation and urination and fecal pellets were not found in nests or scattered around the cage as described by Bailey and Sperry (1929). Certain burrows contained fecal pellets and, although they were not observed in use, were termed defecation burrows. Ruffer (1961) found that Peromyscus leucopus used some nest boxes as defecation places and many mammals defecate in one corner of a cage. Whether O. leucogaster regularly used a defecation burrow was not known but

perhaps unlikely since not all mice dug defecation burrows. Any habitat differences that may have existed in those places where such burrows were dug were not observed. It was particularly interesting that excretory behavior was never directly observed. Bailey and Sperry (1929) postulated that perhaps the musky odor of grasshopper mice came from the feces. This may have been a contributing factor but did not account for the burrows which marked a territory and which contained neither urine nor feces.

Grooming Behavior

Cloudsley-Thompson (1960) reported that mice may spend 50 per cent of their time grooming. In the present study, of six half-hour observation periods, grasshopper mice spent 11 per cent of their time grooming. The grooming followed a definite pattern similar to that described for Peromyscus maniculatus and P. californicus by Eisenberg (1962).

Mutual grooming, where one animal groomed another, was reported in Peromyscus (Eisenberg, 1962) and occurs in many other animals as well. Cloudsley-Thompson (1960) stated that mutual grooming was an important factor in maintaining the association of social species and that valuable salts may be obtained when animals lick each others fur. Mutual grooming in grasshopper mice played a role in courtship and helped to enhance and maintain the pair bond as well as serving the practical function of cleaning the back of the animal.

The data of this study also show that head and facial grooming is much more frequent than whole body or mutual grooming. This can probably be explained by the fact that the face is cleaned after every food item was eaten and head and face grooming is also employed as a displacement behavior expressed during fights and chases. In contrast, neither whole-body nor mutual grooming follow regularly as concomitants of any other frequent activity, nor are they resorted to as displacement activities.

Communication

Olfactory communication played an important role in maintaining a territory and in sex recognition. This supported the view of Hediger (1950) and Bourliere (1954) who stated that glandular secretions played a role in the integration of social behavior in most mammals.

Considerable confusion had arisen with regard to the calls of grasshopper mice. Bailey and Sperry (1929) described the call as a long, fine, shrill whistle given in a high key -- a wolf howl in miniature. Also, Bailey (1931) described it as similar to the hunting call of a timber wolf. Many authors have repeated these descriptions and Seton (1909) described it as like a calling hare, only higher pitched.

Hildebrand (1961) reported that the oscillograph curve for the call showed 10, 000 vibrations per second and stated that it could easily be distinguished from the wolf call. Young and Goldman (1944) described four calls of the wolf and none of these is like the calls of Onychomys.

Four types of calls were described in the present study. Types one, two and three were also described by Bailey and Sperry (1929) and Egoscue (1960), but to my knowledge the type four call has not been previously described. The type three and four calls were used for locating other grasshopper mice as proposed by Olin and Cannon (1954) and not as a hunting or mating call (Bailey and Sperry, 1929). Calls were never recorded when grasshopper mice were stalking another mouse unless the two had been introduced into an enclosure simultaneously and then a call was given only during a break in the stalking. The prey species gave no observable response to the call, again indicating it was probably not a hunting call.

The posture assumed while a type three or four call was being given has been variously described. Bailey (1931), Svihla (1936), Hill (1944), and Olin and Cannon (1954) each reported that the mouse giving the call threw his head back, pointed his nose up and opened his mouth very wide. Hill (1944) even compared it to the posture of an opera singer. Although this was observed, it was by no means the most usual posture observed in the present study. The posture during the call varied from a nearly prone position to an erect one.

Investigative Behavior

Herrick (1892) proposed that, because they ate diurnal insects, grasshopper mice must be diurnal. This was not supported by the present study and has never been seriously considered. Investigative

behavior was the means by which an animal became acquainted with its surroundings and all the artefacts within the home range. As reported for Microtus agrestis by Schillito (1963), the investigative behavior pattern of O. leucogaster was not oriented toward one object, rather included the entire enclosure. This shortened the time required for the grasshopper mice to become oriented in the new surroundings.

Orr (1959) reported that when Peromyscus leucopus became oriented in a new habitat, investigative behavior fell off. This same thing was obvious from observations of O. leucogaster. Although a quantitative study was not made, there appeared to be as much as a 50 per cent decrease in investigative behavior.

Use of the Tail

Horner (1954) found that Peromyscus used their tail as a prop, for balance, as a tactile organ and as a prehensile organ. The shortness of the tail of grasshopper mice (less than one-half the body length) probably accounted for the lack of its use as a balance or prehensile organ and may have reduced the adaptive value of its use as a tactile organ. It was readily used as a prop.

Schenkel (1947) described the expression shown by a wolf's tail and Eisenberg (1962) found that Peromyscus carried its tail stiff when first placed in an enclosure. The tail of O. leucogaster demonstrated a variety of expressions, all seemingly directly related to the degree of unfamiliarity with the enclosure. None of these appeared to serve a signal function.

Bailey and Sperry (1929) reported that the tail wagged when a grasshopper mouse came to close quarters and said that it twitched during prey pursuit. My data do not support these observations.

Swimming

Russel and Findley (1954) reported seeing a grasshopper mouse swim 12 feet across a stream. This brought up the question of the role of swimming in O. leucogaster behavior. Observations during the present study indicated that grasshopper mice would swim if frightened, but that swimming was not a part of general investigative activity when the mice were confined to a small area. Thus, swimming can serve as a means of escape but probably would not be very effective since the mice swam rather slowly and any predator could probably easily catch them in the water.

Miscellaneous Observations

Locomotion in O. leucogaster was the same as that described for Peromyscus (Eisenberg, 1962). The mice were very adept at dodging while running and this probably served to increase their chance of escape from an aggressor or a predator.

Bailey (1931) and Bailey and Sperry (1929) reported that O. leucogaster rarely climbed above the ground. During the present study, the mice showed no reluctance to climbing cage walls and verticle logs although it was my impression that climbing was not a regular part of the behavior and the mice did not climb grass clumps. A prey species could escape the pursuit of O. leucogaster if it climbed up in a grass clump.

Bailey (1926) reported that grasshopper mice in North Dakota probably hibernated. However, Bailey (1931), Dalquest (1948), and Hall (1955) reported that they did not hibernate. During the present study, the mice showed no indication of hibernation and captures were made during most of the cold months of the year.

The vibrissae were removed from one adult male and he demonstrated behavior similar to grasshopper mice less than ten days old. He was not able to become accustomed to the enclosure, moved about with very jerky movements, and was very easily frightened. This suggests that the young must learn to use the sensory capabilities of the vibrissae, or that the vibrissae, which are well developed at birth, did not gain a sensory function until the animals were eight or nine days old. This latter postulate seems the less likely of the two and it was my opinion that O. leucogaster young had to learn to use the vibrissae as sense organs. Harris (1952) found that Peromyscus maniculatus was not affected by lack of vibrissae in selecting artificial-grass or tree-trunk habitats.

Comparison of Onychomys and Peromyscus Behavior

Some aspects of the behavior of Onychomys, a carnivorous, predatory rodent differed from the closely related primarily herbivorous genus Peromyscus. The behavior of O. leucogaster was compared to that of six species of Peromyscus for which behavior information could be found to show these relationships and differences

in behavior. The species of Peromyscus used and sources of information for each were: P. californicus (Eisenberg, 1962; McCabe and Blanchard, 1950), P. maniculatus gambelii (Eisenberg, 1962), P. m. bairdii (Dice, 1932; Howard, 1948), P. crinitus (Eisenberg, 1962), P. e. eremicus (Eisenberg, 1962, 1963), P. leucopus (Burt, 1940), and P. (Ochrotomys) nuttalli (McCarley, 1958, 1959).

O. leucogaster had a definite pattern of burrowing which included four types of burrows. P. m. bairdii nested in a hollow under a log and californicus built a nest under a log or other shelter from as much as a bushel of sticks, coarse grass, and weeds and constructed rest stations as well as the nest. The other species built small, temporary nests in cracks or crevices or other protected areas. The nest entrance of leucogaster was always unprotected. P. polionotus also burrowed but the entrance was surrounded by a mound of dirt (Hall and Kelson, 1959).

Most agonistic postures were similar in form and function in Onychomys and Peromyscus; however, other aspects of the behavior differed. O. leucogaster had a set pattern of aggression, a strong dominant-subordinate relationship and a well marked and defended territory. For both P. californicus and P. m. gambelii, females invading a territory were never attacked by males unless the male was in a pugnacious state, while in O. leucogaster the male of a male-female pair attacked both males and females whenever they entered his territory. Territories were not present for P. nuttalli and were

present only during the breeding season in P. leucopus. P. californicus marked the territory with the preputial glands and gambelii probably marked the territory with urine. O. leucogaster marked the territory with anal-gland secretions. Submissive postures in californicus and gambelii involved the animal on all four feet with his nose forward, eyes closed and ears back. This differed from leucogaster in which the submissive animal laid on its side with the forefeet against the thorax, tail stiff, ears back, and eyes closed. P. leucopus may live in groups during the winter but O. leucogaster apparently does not.

Strong pair bonds were established in P. californicus and O. leucogaster, and temporary pair bonds in P. m. bairdii, and P. crinitus, eremicus, and nuttalli. A weak pair association was observed in P. m. gambelii. P. m. bairdii, P. eremicus and nuttalli were described as fairly social mammals in which the male, female and litter may live together and the others had a dispersed social relationship similar to O. leucogaster and P. californicus. In copulation, Peromyscus approached from behind, mounted, and gave several thrusts of the penis before withdrawing it. O. leucogaster has a single thrust copulatory pattern which was mustelid-like in nature.

Ingestive behavior differed in that O. leucogaster ate animal and plant food at the place of capture, took dead mice into the burrow and had a pattern of aggressive behavior which was associated with the predatory habit. Ingestive postures were similar in both Peromyscus and

Onychomys. Eliminative behavior was described in P. californicus and P. m. gambelii and was similar to that in O. leucogaster as to location of the feces. Feces were deposited in one corner of a cage and there was none in the nest. Grooming, also described in P. californicus and P. m. gambelii was similar to that in O. leucogaster.

O. leucogaster had a four call repertory of vocalizations. The type one and two calls were also recorded for P. californicus, P. m. gambelii, and P. nuttalli and P. californicus also gave whines or "mews" at times. Pattering of the forefeet was used as a communication method in P. eremicus and only slightly used in P. californicus and P. m. gambelii. O. leucogaster was the only one of these species in which calls described here as type three and four were given.

When placed in a new situation, O. leucogaster exhibited curiosity or at most mild apprehension while the other species considered here were very nervous and frightened easily in a new situation. O. leucogaster readily inspected unfamiliar objects. P. gambelii was described as being "nervous".

Comments on Behavioral Evolution within Onychomys

Hoffmeister (1944) described morphological evolution in the grasshopper mouse group which includes the Upper Miocene genus Miochomys, the Upper Pliocene genus Symmetrodontomys and the living genus Onychomys which has also been found in Upper Pliocene

and Pleistocene deposits. According to Hoffmeister, the grasshopper mouse group diverged from the Peromyscus stock sometime during middle Miocene and probably quickly developed the burrowing, predatory, carnivorous habit. An important morphological character of the teeth associated with the carnivorous habit and best developed in Onychomys, but also developed to a lesser extent in Symmetrodontomys and Miochomys, was loss of the mesoloph and reduction of other lophs so that the molar cusps appear as more or less separate points rather than being continuous ridges as in Peromyscus. These tooth modifications were accompanied by an increased size of the claws on the forefeet for use as digging tools. It was interesting that the burrow types were quite simple as compared to other arid-land burrowing mammals, probably because of the short period of time since separation from the non-burrowing Peromyscus.

Territorial behavior was probably accompanied by evolution of the type three and type four calls which, used as a means of species location, served to effectively reduce the agonistic encounters involved in territorial defense. I believe an intruder would not attempt to invade the territory held by another mouse whom he could find through the use of the calls. This would reinforce territorial behavior and contribute toward the evolution of a rigid territory. The survival value of a strongly defended territory is obvious. It reduces the competition for food and provides the mouse with a greater food supply.

Behavioral and morphological differences between Peromyscus and Onychomys were related to the adoption of the arid-land, predatory habit by Onychomys. This involved the development of burrowing, territoriality and predation. Differences in agonistic postures and sexual behavior are difficult to account for as is the difference between Onychomys and Peromyscus in juvenile-adult molt pattern. Perhaps further studies will serve to elucidate these problems.

SUMMARY

The ethogram for the northern grasshopper mouse (Onychomys leucogaster breviauritus) was compiled through observations of mice held in 15 by 15 foot enclosures. Large cages were used to a very limited extent.

Nest, retreat, cache, defecation, and sign-posting burrows were observed and studies of temperature relationships revealed that a nest burrow protected these nocturnal rodents from extreme fluctuations of surface temperature and, probably, humidity. Nest burrows were dug by a male with the help of a female. Grasshopper mice did not use abandoned burrows of Perognathus hispidus and Dipodomys ordi nor did they use the burrows of these species when they were victims of the Onychomys aggression.

Agonistic behavior included a well-developed pattern of intra- and interspecific aggression in which prey species never defeated Onychomys in an aggressive encounter. Agonistic postures were observed and these differed in some respects from Peromyscus postures. A well marked territory was observed which was defended by non-violent rather than violent encounters. The territory was marked by a line of

short burrows which was respected by subordinate mice when the dominant was out of the burrow and is probably respected at all times in nature. A dominant-subordinate relationship consisted of one dominant individual and the group of subordinates within which no ranking was observed.

A variable pattern of courtship ended in copulation which involved the two animals lying on their sides while in-copulo. Two gestation periods of 32 and 34 days each were observed in non-lactating females and litter size of sex litters averaged 3.78 individuals with a sex ratio of 52 females to 48 males. Development of behavior and the pattern of juvenile-adult molt was observed in six litters. Homosexual behavior was never observed.

A wide variety of insects and other animal food was eaten by the mice. Feeding postures differed in no way from those of other small mammals. Coprophagy was observed in four juvenile mice.

Eliminative behavior was not directly observed, but one corner of the cage was used for elimination.

Individual grooming followed a definite pattern in which head and face grooming was much more frequent than either whole body or mutual grooming. Eleven per cent of the time was spent in grooming.

Olfactory communication played a part in sex recognition as indicated by the accuracy of like-sex and unlike-sex circling which was of a wider diameter in the former than the latter. Anal gland secretions were probably used in marking territories.

Auditory communication included: (1) squeaks from the young and adults during a fight, (2) a high-pitched chirping call given as an alarm note, (3) one prolonged call used as a means of locating other grasshopper mice, and the other (4) given if another mouse was located but contact could not be made. Postures assumed while these calls were being given were quite variable.

The tail was used as a "third leg" while a mouse was sitting on his haunches.

Swimming was found not to be a part of investigative behavior but did serve as a means of escape.

Studies indicated that the mice had to learn to use the vibrissae as sensory tools. No evidence for hibernation was found.

Onychomys differed from Peromyscus in that the nest entrance was not protected, females were attacked whenever they entered the territory of a male-female pair, the agonistic-submissive posture involved the animal lying on its side, pair bonds were probably permanent, copulation involved lying on the side, and localization calls were recorded.

The behavior patterns supported the evolution of the arid-land, carnivorous, predatory habit of Onychomys as indicated by tooth structure and other morphological structures. All aspects of the ethogram served to enhance the development of this habit.

LITERATURE CITED

Allee, W.C., A. Emerson, O. Park, T. Park, and K. Schmidt. 1949. Principles of animal ecology. W.B. Saunders Co., Philadelphia. 837 pp.

Armitage, K.B. 1962. Social behavior of a colony of the yellow-bellied marmot (Marmota flaviventris). Animal Behavior 10: 319-331.

Asdel, S.A. 1946. Patterns of mammalian reproduction. Comstock Publ. Co., Ithaca. 437 pp.

Bailey, V. 1926. A biological survey of North Dakota. N. Amer. Fauna 49, 226 pp.

_____. 1931. Mammals of New Mexico. N. Am. Fauna 53, 412 pp.

_____. 1936. The mammals and life zones of Oregon. N. Amer. Fauna 55, 416 pp.

_____ and C.C. Sperry. 1929. Life history and habits of the Grasshopper mice, Genus Onychomys. U.S. Dept. Agr. Tech. Bull. 145, 19 pp.

Baird, S.F. 1858. Mammals. Repts. Expl. Surv. 8:458.

Baker, R.H. 1956. Mammals of Coahuila, Mexico. Univ. Kansas Publ. Mus. Nat. Hist. 9: 125-335.

Balph, D.F. and A.W. Stokes. 1963. On the ethology of a population of Vinta Ground Squirrels. Amer. Midl. Nat. 69:106-126.

Barnes, C.T. 1927. Utah mammals. Bull. Univ. Utah 17, 183 pp.

Barnes, R.H. 1959. Effects of the prevention of coprophagy in the rat. J. Nutrition. 68:121-130.

Beach, F.A. 1945. Current concepts of play in animals. Amer. Nat. 79:523-541.

Benson, S.B. 1933. Concealing coloration among some desert rodents of the Southwestern United States. Univ. Calif. Publ. Zool. 40, 70 pp.

Blair, W.F. 1939. Faunal relationships and geographic distribution of mammals in Oklahoma. Amer. Midl. Nat. 22:85-133.

_____. 1943a. Ecological distribution of mammals in the Tularosa Basin, New Mexico. Cont. Lab. Vert. Biol., Univ. Mich. 20:1-40.

_____. 1943b. Populations of the deer-mouse and associated small mammals in the mesquite association of Southern New Mexico. Cont. Lab. Vert. Biol., Univ. Mich. 21, 40 pp.

_____. 1953. Population dynamics of rodents and other small mammals. In: Adv. in Genetics. New York: Academic Press. 5:1-41.

Bodenheimer, F.S. 1957. The ecology of mammals in arid zones. Human and Animal Ecology (Reviews of Research), UNESCO. pp. 1-53.

Booth, Y.S. 1956. Shrews (Crocidura cassiteridum) on the Scilly Isles. Proc. Zool. Soc. London 126:167-170.

Bourliere, F. 1954. The natural history of mammals. Alfred A. Knopf, New York. 364 pp.

Burt, W.H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool., Univ. Mich. 45, 58 pp.

_____ and R.P. Grossenheider. 1952. A field guide to the mammals. Houghton Mifflin Co., Boston. 200 pp.

Cahalane, V.H. 1947. Mammals of North America. The Macmillan Co., New York. 682 pp.

Carpenter, C.R. 1958. Territoriality: A review of concepts and problems. In: Behavior and Evolution. Edited by: A. Roe and G.G. Simpson. Yale Univ. Press, New Haven. pp. 224-250.

Cary, M. 1911. A biological survey of Colorado. N. Amer. Fauna. 33, 256 pp.

Clark, L. D. 1962a. A comparative view of aggressive behavior. Amer. J. Psychiatry 114:336-341.

_____. 1962b. Experimental studies of the behavior of an aggressive, predatory mouse, Onychomys leucogaster. In: Roots of Behavior. Paul B. Hoeber, Inc., New York. pp. 179-186.

Cloudsley-Thompson, J. L. 1960. Animal behaviour. London: Oliver and Boyd, Ltd. 162 pp.

Cockrum, E. L. 1952. Mammals of Kansas. Univ. Kansas Publ. Mus. Nat. Hist. 7, 306 pp.

Crowcroft, P. 1952. Refection in the common shrew. Nature 170:627.

Cutter, W. L. 1958. Food habits of the swift fox in northwestern Texas. J. Mammal. 39:527-532.

Dalquest, W. W. 1948. Mammals of Washington. Univ. Kansas Publ. Mus. Nat. Hist. 2:1-444.

Davis, W. B. 1960. The mammals of Texas. Bull. 41., Texas Game and Fish Comm. 252 pp.

Dice, L. R. 1930. Mammal distribution in the Alamagordo region, New Mexico. Occ. Papers Mus. Zool., Univ. Mich. 213, 32 pp.

_____. 1932. The prairie Deer-mouse. Bull. Cranbrook Inst. Sci. 2:1-8.

Egoscue, H. J. 1960. Laboratory and field studies of the northern grasshopper mouse. J. Mammal. 41:99-110.

_____. 1962. Ecology and life history of the kit fox in Tooele County, Utah. Ecology 43:481-497.

_____. 1963. Color phases and their inheritance in the northern grasshopper mouse. J. Mammal. 44:74-79.

Eibel-Eibesfeldt, I. and S. Kramer. 1958. Ethology, the comparative study of animal behavior. Quart. Rev. Biol. 33:181-211.

Eisenberg, J. F. 1962. Studies on the behavior of Peromyscus maniculatus gambelii and Peromyscus californicus parasiticus. Behaviour 14:177-207.

_____. 1963. Intraspecific behavior of some cricetine rodents of the genus Peromyscus. Amer. Midl. Nat. 69:240-246.

Fautin, R.W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecol. Monogr. 16:251-310.

Finley, R.B., Jr. 1954. Notiosorex crawfordi and Antrozous pallidus from southeastern Colorado. J. Mammal. 35:110-111.

Geyer, R.P. 1947. Growth studies with rats kept under conditions which prevent coprophagy. J. Nutrition 33:129-142.

Glass, B.P. 1953. A second Notiosorex from Oklahoma. J. Mammal. 34:118.

Gotteschang, J.L. 1956. Juvenile Molt in Peromyscus leucopus noveboracensis. J. Mammal. 37:516-520.

Grubitz, G., III. 1963. The social behavior of the thirteen-lined ground squirrel (Citellus tridecemlineatus). M.S. Thesis. University of Oklahoma. 57 pp.

Hall, E.R. 1946. Mammals of Nevada. Berkeley: Univ. Calif. Press. 710 pp.

_____. 1955. Handbook of the mammals of Kansas. Univ. Kan. Mus. Nat. Hist., Misc. Publ. 7:1-303.

_____ ed. 1957. Vernacular names for North American mammals north of Mexico. Univ. Kan. Mus. Nat. Hist., Misc. Publ. 14:1-16.

_____ and K.R. Kelson. 1959. The mammals of North America. The Ronald Press Co., New York. 2 v.

Harris, V.T. 1952. An experimental study of habitat selection by prairie and forest races of the deermouse, Peromyscus maniculatus. Cont. Lab. Vert. Biol., Univ. Mich. 56:1-53.

Hediger, H. 1950. Wild animals in captivity. Butterworths Scientific Publications, London. 207 pp.

Hibbard, C.W. 1944. A checklist of Kansas mammals. Trans. Kan. Acad. Sci. 47:61-88.

Hildebrand, M. 1961. Voice of the grasshopper mouse. J. Mammal. 42:263.

Hill, J.E. 1944. Singing Mice. Nat. Hist. 53:436.

Hinde, R.A. and N. Tinbergen. 1958. The comparative study of species-specific behavior. In: Behavior and Evolution. Edited by: A. Roe and G.G. Simpson. Yale Univ. Press, New Haven. pp. 251-268.

Hoffmeister, D.F. 1944. Phylogeny of the Nearactic Cricetine Rodents, with especial attention to variation in Peromyscus truei. Ph. D. Thesis. Univ. of California. pp. 423.

_____ and W.W. Goodpaster. 1954. The mammals of the Huachuca Mountains, southeastern Arizona. Ill. Biol. Monog. 24:1-152.

Holdenried, R. 1957. Natural history of the bannertail kangaroo rat in New Mexico. J. Mammal. 38:330-350.

Hollister, N. 1915. A systematic account of the grasshopper mice. Proc. U.S. Nat. Mus. 47:427-490.

Horner, B.E. 1947. Paternal care of young mice of the genus Peromyscus. J. Mammal. 28:31-36.

_____. 1954. Arboreal adaptations of Peromyscus, with special reference to use of the tail. Cont. Lab. Vert. Biol., Univ. Mich. 61:1-85.

Howard, W.E. 1948. Dispersal, amount of inbreeding and longevity in a local population of prairie deer mice on the George Reserve, southern Michigan. Contr. Lab. Vert. Biol., Univ. Mich. 43:1-40.

Ingles, L.G. 1961. Reingestion in the mountain beaver. J. Mammal. 42:411-412.

Ivey, R.D. 1957. Ecological notes on the mammals of Bernalillo County, New Mexico. J. Mammal. 38:490-502.

Jackson, H.H.T. and H.E. Warfel. 1933. Notes on the occurrence of mammals in the regions adjacent to the salt plains of Northwestern Oklahoma. Publ. Univ. Okla. Biol. Sur. 5:65-72.

Johnson, C. 1944. Selective adaptation for color phases of the terrestrial snail Helicina arbiculata. Tex. Jour. Sci. 11:366-370.

Jones, C.J., E.D. Fleharty, and A.H. Harris. 1960. Unusual habitats of grasshopper mice in New Mexico. J. Mammal. 41:275-276.

Justice, K.E. 1957. The pigmy mouse in southeastern Arizona. J. Mammal. 38:520-521.

Kelson, K.R. 1951. Fluctuations in populations of small mammals in Utah. J. Mammal. 32:113-114.

Kaye, S.V. 1961. Laboratory life history of the Eastern Harvest Mouse. Amer. Midl. Nat. 66:439-451.

Lechleitner, R.R. 1957. Reingestion in the black-tailed jack rabbit. J. Mammal. 38:481-485.

Long, C.A. and W.C. Kerfoot. 1963. Mammalian remains from owl pellets in Eastern Wyoming. J. Mammal. 44:129-131.

Martin, A.C., H.S. Zimm and A.L. Nelson. 1951. American wildlife and plants. McGraw-Hill, New York. 500 pp.

Mayr, E. 1958. Behavior and systematics. In: Behavior and Evolution. Edited by: A. Roe and G.G. Simpson. Yale Univ. Press, New Haven. pp. 341-362.

Merriam, C.H. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the little Colorado. N. Amer. Fauna. 3, 136 pp.

_____. 1892. The geographic distribution of life in North America with special reference to the Mammalia. Proc. Biol. Soc. Wash. 7:1-64.

McCabe, T.T. and B.D. Blanchard. 1950. Three Species of Peromyscus. Santa Barbara: Rood Associates. 136 pp.

McCarley, W.H. 1958. Ecology, behavior and population dynamics of Peromyscus nuttalli in Eastern Texas. Tex. Jour. Sci. 10:147-171.

_____. 1959. A study of the dynamics of a population of Peromyscus gossypinus and P. nuttalli subjected to the effects of X-irradiation. Amer. Midl. Nat. 61:447-469.

Noble, G.K. 1939. The role of dominance in the life of birds. Auk 56: 263-273.

Olin, G. and J. Cannon. 1954. Mammals of the southwest deserts. Southwestern Monuments Assn., Popular Ser. 8:1-112.

Orr, H.D. 1959. Activity of white-footed mice in relation to environment. J. Mammal. 40:213-221.

Petter, F. 1957. Note preliminaire sur l'ethologie et l'ecologie de Meriones libycus. Mammalia 17:281-294.

Preston, J.R. and R.E. Martin. 1963. A gray shrew population in Harmon County, Oklahoma. J. Mammal. 44:268-270.

Quay, W.B. 1953. Seasonal and sexual differences in the dirsal skin gland of the kangaroo rat (Dipodomys). J. Mammal. 34:1-14.

Richardson, R.G. 1958. The comparative behavior of some Oklahoma mice of the families Heteromyidae, Cricetidae, and Muridae and its ecological implications. M.S. Thesis. University of Oklahoma. 49 pp.

Richmond, N.D. and H.R. Rosiund. 1952. A mid-ventral dermal gland in Peromyscus maniculatus. J. Mammal. 33:103-104.

Ridgway, R. 1912. Color standards and color nomenclature. Washington, D.C., Privately Published. 43 pp. 53 plates.

Ruffer, D.G. 1960. The effect of flooding on a population of white-footed mice (Peromyscus leucopus noveboracensis ((Fischer))). M.A. Thesis. Bowling Green State University. 53 pp.

_____. 1961. Effect of flooding on a population of mice. J. Mammal. 42:494-502.

Russell, R.J. and F.S. Findley. 1954. Swimming ability of the grasshopper mouse. J. Mammal. 35:118.

Schenkel, R. 1947. Ausdrucks -- Studien an Wolfen. Behaviour 1:81-129.

Scott, J.P. 1958a. Aggression. Univ. Chi. Press, Chicago. 148 pp.

_____. 1958b. Animal Behavior. Univ. Chi. Press, Chicago. 281 pp.

Seton, E.T. 1909. Life histories of northern animals. New York: Charles Scribner's Sons. 2v. 1267 pp.

Shillito, E.E. 1963. Exploratory behaviour in the short-tailed vole Microtus agrestis. Behaviour 21:145-154.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist. 85:1-350.

_____. 1958. Behavior and evolution. In: Behavior and Evolution. Edited by: A. Roe and G.G. Simpson. Yale Univ. Press, New Haven. pp. 507-535.

Sperry, C.C. 1941. Food habits of the coyote. U.S. Dept. Int., Wildl. Res. Bull. 4:1-70.

Svihla, R.D. 1936. Breeding and young of the grasshopper mouse (Onychomys leucogaster fuscogriseus). J. Mammal. 17:172-173.

Tamsitt, J.R. 1961. Mating behavior of the Peromyscus truei species group of white-footed mice. Amer. Midl. Nat. 65:501-507.

Taylor, J.M. 1962. Breeding biology of the grasshopper mouse, O. torridus. Amer. Zool. 2:451-452.

Tinbergen, N. 1951. The study of instinct. Clarendon Press, Oxford. 228 pp.

Verplanck, W.S. 1957. A glossary of some terms used in the objective science of behavior. Phychol. Rev. 64:1-42.

Viek, P. and G.A. Miller. 1944. The cage as a factor in hoarding. J. Comp. Phychol. 37:203-210.

Warren, E.R. 1942. Mammals of Colorado. Univ. Okla. Press, Norman. 330 pp.

Whitman, C.O. 1899. Animal behavior. In: Biological lectures delivered at the Marine Biological Laboratory at Woods Hole in 1898: 329-331.

Wight, H.M. 1931. Reproduction in the eastern skunk (Mephitis mephitis nigra). J. Mammal. 12:42-47.

Williams, O. 1955. Home range of Peromyscus maniculatus rafinus in a Colorado pondorosa pine community. J. Mammal. 36:42-45.

Wood. A.E. 1955. A revised classification of the rodents. J. Mammal. 36:165-187.

_____. 1959. Eocene radiation and phylogeny of the rodents. Evolution 8:354-361.

Young, S.P. and E.A. Goldman. 1944. The wolves of North America. Washington, D.C.: American Wildlife Institute. 636 pp.

APPENDIX

Study skins and skulls of 20 individuals used in the present study were prepared and the measurements are presented in Table 3. These 20 adult individuals (8 males and 12 females) had an average body length of 104.13 mm. and an average tail length of 43.53 mm. Thus, the tail averaged 41.80 per cent of the body length and, as stated in the section on Taxonomic Relationships, this was characteristic of the species O. leucogaster. Other measurements in the table also fell within the range of those given for the species O. leucogaster. These skins and skulls were deposited either in the mammal collection at the University of Oklahoma Biological Station or in my personal collection.

TABLE 3

SKIN AND SKULL MEASUREMENTS OF 8 MALE AND 12 FEMALE

ONYCHOMYS LEUCOGASTER USED IN THIS STUDY

	TOTAL LENGTH	TAIL LENGTH	BODY LENGTH	HIND FOOT LENGTH	LEFT EAR
Male	149.75	43.50	106.25	20.89	15.33
Female	144.64	43.55	102.00	21.17	15.10
Mean	147.20	43.53	104.13	21.03	15.22
	GREATEST LENGTH	BASILAR LENGTH	ZYGOMATIC BREADTH	ZYGOMATIC LENGTH	GREATEST WIDTH
Male	29.26	23.05	15.63	20.15	12.85
Female	28.89	22.80	14.03	19.87	12.65
Mean	29.08	22.93	19.83	20.01	12.75
	NASAL LENGTH	DIASTEMA LENGTH	MAXILLARY TOOTH ROW	INTERORBITAL BREADTH	
Male	11.79	7.44	4.56	4.86	
Female	11.74	7.41	4.57	4.79	
Mean	11.77	7.43	4.57	4.82	