THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

SOME ASPECTS OF THE ETHOECOLOGY OF RICHARDSON'S GROUND SQUIRREL IN EASTERN NORTH DAKOTA

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

BY

WALTER ROY QUANSTROM

Norman, Oklahoma

1968

SOME ASPECTS OF THE ETHOECOLOGY OF RICHARDSON'S GROUND SQUIRREL IN EASTERN NORTH DAKOTA

APPROVED BY

DISSERTATION COMMITTEE

ACKNOWLEDGEMENTS

Few tasks of any magnitude are accomplished without assistance. This one is no exception. Field studies by their nature require more than the usual amount of assistance.

I am grateful to Mr. and Mrs. Teddy R. Erbele, Lehr, North Dakota; Mr. and Mrs. Chet Burley, Blanchard, North Dakota; Mr. and Mrs. Swede Johnson, Hunter, North Dakota; and Mr. and Mrs. Merton L. Sheldon, Mapleton, North Dakota, for use of their land while making this study. The Erbeles were especially kind and helpful during the two years we worked on their land. Mr. Merton L. Sheldon was willing to lend a hand in many ways, and provided a place to stay during the study. Mr. Sheldon's sensitivity to nature is refreshing. Mrs. Sheldon served meals many days to save more time for field work.

I am grateful to the Department of Zoology, University of Oklahoma, and the National Aeronautics and Space Administration (N.A.S.A.) for financial help. The research funds from N.A.S.A. made possible the filming many of the observations.

I am indebted to Dr. Charles C. Carpenter, Professor of Zoology, for so many things that it would be most

difficult, indeed, to list them all. Dr. Carpenter's love of all forms of animal life is deeply imbedded in my impressions of him. One of the largest contributions to my graduate program that Dr. Carpenter has made is that I have always felt free to speak with him on any matter. Much of the basic concepts of this study were gained from Dr. Carpenter.

I am also grateful to Dr. George Mitsch Sutton, Research Professor, not so much for actual help in this study but for teaching me the value of careful field observations. Dr. Sutton's constant attention to detail has helped me to strengthen a weak point. Professor Sutton's deep love for animals in their natural environment is something that I shall never forget.

I am grateful to Drs. Charles C. Carpenter, Cluff E. Hopla, George J. Goodman, and Howard B. Haines for reading the manuscript and for making many helpful suggestions.

I would also like to thank my wife, Fay, for her help in every aspect of this study. Without Fay's encouragement this study would not have been completed.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES


RAMONA KAATZ
•1967•

SOME ASPECTS OF THE ETHOECOLOGY OF RICHARDSON'S GROUND SQUIRREL IN EASTERN NORTH DAKOTA

CHAPTER I

INTRODUCTION

From the time of Aristotle, who thought that every animal had its unique slot to fill and that the degree of perfection of a thing could be measured by how well it fit into this slot, man has recognized some basic zoological concepts of a particular animal's adaptation to its environment. These early natural historians recognized many obvious examples of these relationships such as gills for breathing in water, and lungs for breathing in air. Much present day research, still concerned with these adaptations, unearths some incredulously subtle animal-environmental relationships.

It can be noted that in the past biologists have been primarily concerned with morphological adaptations. Such things as the rigid tail feathers of a woodpecker, or the stiff hair fringe on the hindfoot of a water shrew are pointed out as examples of structures which enable an animal to adapt to a particular environment. More recently, however, studies show that animals have evolved the ability to

use (i.e., behavior patterns) its morphology in ways that are advantageous. These behavior patterns must compliment the morphological structures in order for the organism to be successful. The associated behavior pattern is just as important as the morphological structure that it compliments, and the more specific the structure the more specific its behavioral pattern is liable to be. The American Avocet, Recurvirostra americana, with its unique bill structure, uses it to obtain food in a very specific manner; however, the virginia opossum, Didelphis marsupialis, is a generalized animal and its feeding behavior is quite variable.

A mature behavior pattern that compliments a specific anatomy can be accomplished by at least two means; an inherited behavior characteristic or behavior modified by experience. The type of behavior attempted, and also the amount of time spent performing a motor pattern can be genetically influenced (Scott and Fuller, 1951). Learning as a method of achieving at a particular behavior which compliments a structure has been suggested by Hinde (1958, 1959, 1961). Selander (1966) has pointed out that this mechanism of learned behavior can work to separate populations of the same species by allowing them to select different food items, and thereby reduce competition.

Selander's studies on the woodpecker genus Centurus demonstrate that the bills of the males are significantly larger than those of the females, and the types of behavior

used differ between sexes. The females are obtaining a different type of food than the males, reducing competition within the species. This is an excellent example of a very close working partnership between structure and behavior to aid in the survival of this woodpecker.

The study of animal behavior is not new; however, the use of the scientific approach, avoiding anthropomorphic interpretations and a lack of objectivity in observing animals, is the modern trend. The objective study of animal behavior is termed ethology.

This study is concerned with the autecology and ethology of Richardson's Ground Squirrel, Citellus richardsoni richardsoni (Sabine, 1822). This northern ground squirrel, known as the flickertail, has many behavioral and morphological adaptations to its environment. The fact that ground squirrels are diurnal and, in this species, somewhat colonial makes them excellent subjects for investigation into behavioral ecology.

Citellus richardsoni is a member of the family Sciuridae. This family contains about 50 extant genera, and 1300 known forms (Walker, 1964). The Sciuridae are cosmopolitan except for Australia, Madagascar, and southern South America. The Sciuridae show a breadth of adaptive radiations, invading many habitat niches.

Richardson's ground squirrel is a member of the genus Citellus. This species has been historically termed the

flickertail. This genus has been in a confusing taxonomic condition for some time with respect to generic and subgeneric relationships.

It is generally agreed that the North American ground squirrels fall into eight groups (Howell, 1938). It is unknown if these groups differ sufficiently from one another to be placed in separate genera, or if they should be considered subgenera. The latter choice has been used by most workers, including Howell. Richardson's ground squirrel belongs to the type subgenus of Citellus and therefore will be included here in the genus Citellus.

The genus Citellus is credited to Oken, in his "Lehrbuch der Zoologie." The use of Oken names for valid scientific nomenclature has been reviewed by Herschkovitz (1949). Herschkovitz states: "Names in Oken's 'Lehrbuch der Zoologie', published in 1816 in Jena, are non-Linnaean and not available in scientific nomenclature." Since Oken did not use the term Citellus as a generic name, and since he did not follow the Linnaean system, the name would seem invalid. The next published report is that of Cuvier (1825), placing ground squirrel in the genus Spermophilus.

The American Society of Mammalogists' Committee on Nomenclature (1960), acting on this question, recommended the conservation of the term Citellus. The majority recognized the validity of Spermophilus "on a strictly priority basis." The committee felt that the preponderance of use of

Citellus warranted its conservation. The recommendation was accepted by the Society; therefore Citellus is now the accepted generic name.

In contrast with research interest in the genus Citellus, work on the species Citellus richardsoni is amazingly scarce. The anatomy of the cheek area, including the pouch, has been described by Sleggs (1926) and Quay (1965). Other than these papers, there are three works of note concerning the ethoecology of Citellus richardsoni. First of these is the section in Ernest Thompson Seton's Lives of Game Animals (1929) dealing with the flickertail, which was helpful in understanding the original environment of this ground squirrel. Brown and Roy (1943) determined the agricultural significance of Richardson's ground squirrel in southern Alberta, Canada, and their study is mainly concerned with the eradication of flickertails on the grounds that they may be a vector of plague. Many of the items mentioned in this article concerning the life history of the flickertail do not agree with findings of this study. Dean Gunderson (1961) studied Citellus richardsoni in South Dakota, and his paper is useful in making comparisons with the present study.

Other research of lesser significance concerning the life history would include Soper (1926) and Kolstoe (1966).

CHAPTER II

METHODS AND MATERIALS

Squirrels were trapped and then marked so that they could be identified visually. Trapping was done either by a noose (McCarley, 1966) or by means of a National live trap. Since Richardson's ground squirrels have more than one entrance to their burrow systems, the live trap was the more successful. Noosing was most useful in capturing young squirrels. The traps were set on the top of the ground and baited with shelled corn. Squirrels could usually be captured in less than ten minutes. It was rare to capture more than one squirrel in a trap at the same time. Certain individuals in the main study area were captured several times in a single day. After they made an association between the corn and the trap, certain animals, especially dominant individuals, moved toward a trap as soon as it was sighted. These individuals were captured repeatedly. If the temperature was 80° F. or higher, trap mortality could result in less than one-half hour. Trap mortality rose with the temperature and the time of the year. Extremely fat squirrels succumbed to the heat most rapidly. Squirrels that were

approaching death or were already dead due to heat, showed excessive salivation which wet a considerable part of the head.

Captured squirrels were weighted to the nearest one-tenth gram. The measurements taken were total, tail, hind-foot, and ear. The total measurement of a live ground squirrel can only be approximate because of the difficulty in laying the animal out straight.

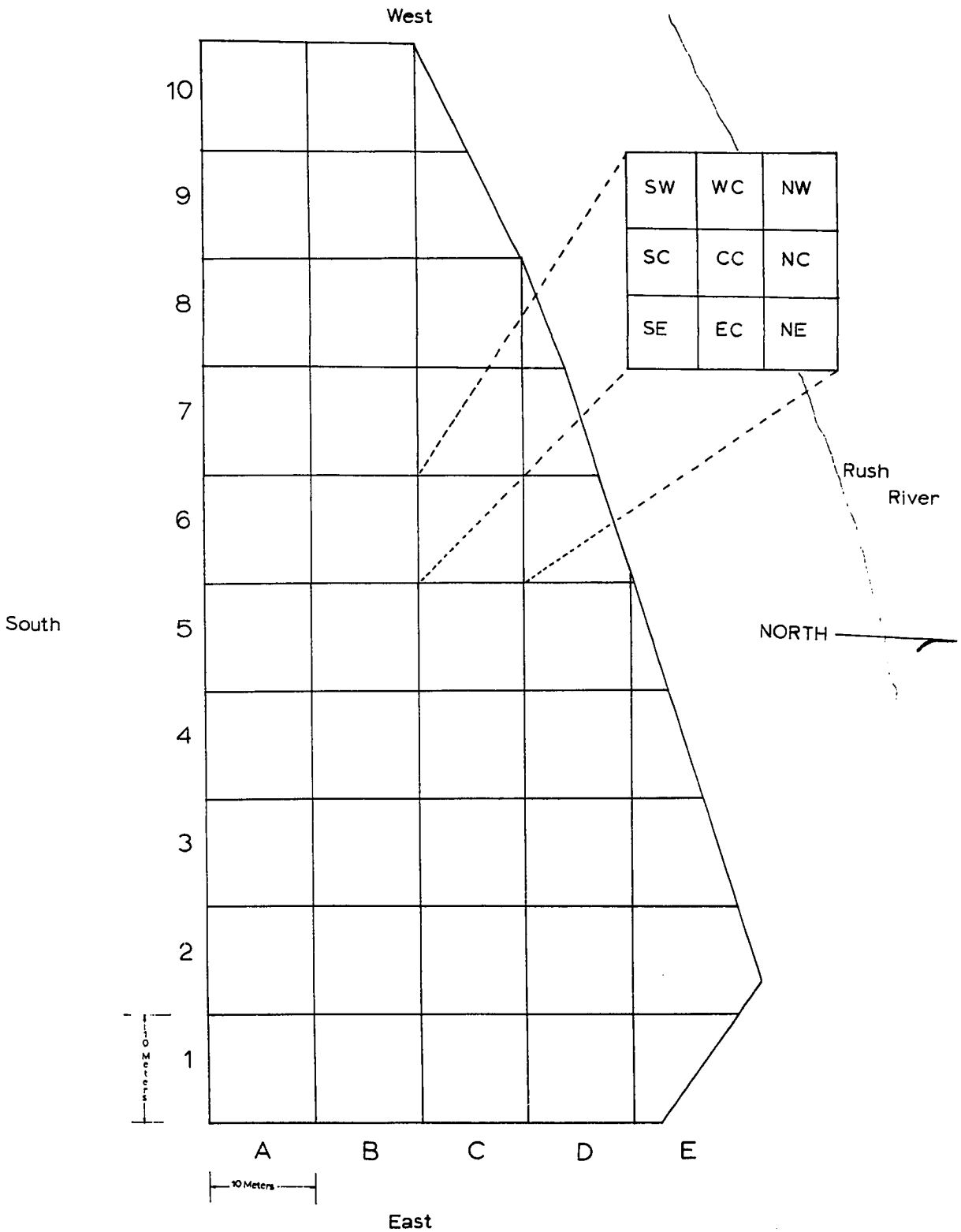
The toes of the animals during the first year of the study, 1965, were clipped for a permanent identification. During all three years of the study the squirrels were permanently marked with fingerling ear tags obtained from the Salt Lake City Stamp Company, Salt Lake City, Utah. This tag was placed in the squirrel's left ear. An effort was made to make sure that the top of the tag did not protrude from the edge of the pinna so the tag would not catch on objects that brush by the squirrel. The pinna of Citellus richardsoni is much reduced and tough and holds the ear tag firmly in place. After the first year, only ear tags were used for permanent identification.

Squirrels were also marked with a cattle dye, Nyanzol D, from Nyanza Inc., Lawrence, Massachusetts, for visual identification. A stock solution (prepared in the laboratory) was fixed for use in the field by adding a small amount of 30% hydrogen peroxide and then applied to the animal with a paint brush. The resulting black mark is not

lost until the hair is molted. The squirrels were dye-marked in such a way that each mark symbolized a certain number. The method described by Balph and Stokes (1963) of marking actual numbers on the sides of the animal was tried and found to be unsatisfactory for this situation. The areas used to symbolize numbers were as follows: right front leg was one, left front--two, right hind--three, left hind--four, left front and hind--five, right front and hind--six, right front, left hind--seven, left front and right hind--eight, left and right hind--nine. Then in order to provide for ten more places a center back mark added then to the leg number. In most cases the dye number corresponded to the last part of the ear tag number.

The squirrels were observed the first year from a 10 foot tower erected on the study area in quadrate C3 (Fig. 1). During the second two years of the study the back of a pickup truck with a shell camper was used for observations. The truck was more convenient because it could be moved from one place to another. Observations were made using a 7 x 35 power Busnell binoculars or a 20 power Swift spotting scope. During 1966 and 1967 motion pictures were taken of all types of behavior observed with the use of a Bolex Rex 4, H-16 movie camera with a 150 mm. macro-Yvar lens. Over 5,000 feet of black and white and 3,000 feet of color film were exposed.

Figure 1. Quadrates of the Mapleton study are, Section 14, Harmony Township, Cass County, North Dakota. The inset shows the method of dividing the quadrates for visual plotting of a squirrel's position.



Layout Of Study Area

The effect of marking the squirrel seemed to be minimal, for no significant difference in behavior was observed between the marked and unmarked colonies. The presence of the observer in the colony had some effect, to be sure, but this also seemed to be small. During 1965, a test was made to determine the effect of the observer's presence. For several days observations were made from a considerable distance and from a position that was out of the squirrel's view. The only noticeable difference was the including of quadrate C3, the quadrate that contained the tower, in the territory of one of the adult females. The squirrels apparently recognized me and paid far less attention and showed less alarm than to the presence of some other person.

Five study areas were used: Mapleton, Hunter, Blanchard, Lehr East and Lehr West. In only the Mapleton study area were the squirrels marked and observed as individuals. The other four areas were used to study the colony rather than the individual. Every effort was made to determine if the squirrels in the other colonies displayed the same types of behavior as the ones in the marked colony.

The main study colony, Mapleton, was on Section 14, Harmony Township, Cass County, North Dakota, along the southern edge of the Rush River. This area has had a colony of flickertails for at least 20 years. The study area was laid out on an east-west axis (Fig. 1). Each of the

quadrates was ten meters on a side (100 square meters). The corners of the quadrates were permanently marked by placing a buried brick at each corner, and for observational purposes, wires with a piece of bright cloth attached to the top were placed at each corner. On the east-west axis each quadrate was given a number, and the north-south axis of each quadrate was assigned a letter. Thus, each quadrate had a symbol such as C4, D6, E8, etc. It was possible to quickly determine the position of a squirrel in the colony in relationship to the quadrates. By visually estimating smaller units of each quadrate, such as southwest, west-central, northwest, etc., the position of a given squirrel could be plotted within a given 10 square meters.

The Hunter study area was located on Section 23, Hunter Township, Cass County, North Dakota. This colony had a very dense population. The Blanchard study area was located on Section 25, Blanchard Township, Traill County, North Dakota. The Lehr East study area was located on Section 35, Range 67, Logan County, North Dakota, and the Lehr West area on Section 32, Range 69, Logan County, North Dakota.

This study began on May 25, 1965, and ended on August 1, 1967. Approximately six months of daily observations were made: from May 25 to August 2, 1965; May 28 to August 1, 1966; and from March 29 to April 4; and from May 29 to July 15, 1967.

Plants from all the areas were collected, identified, and compared with the specimens of the Bebb Herbarium of the University of Oklahoma.

CHAPTER III

THE ABIOTIC ENVIRONMENT

An animal must cope with the abiotic environment in which it finds itself. Such abiotic factors as insolation, temperature, and moisture are important in determining just what kinds of plants and animals can be present in a given location. The flickertail, primarily a herbivore, is dependent on plants for food. The types of plants will in turn be determined by the geological history, the climate, and the pedogensis of an area.

Geological History

The Wisconsin ice age is responsible for some of the major differences in the two habitat types in the eastern half of North Dakota. The Red River Valley, which represents one habitat type, was formed as the bottom of a prehistoric lake, Lake Agassiz. Since the Red River of the North drains northward into the Hudson Bay, the receding glaciers blocked the flow of its own melting water. This created a fresh water lake which extended over the eastern part of the state. The silt of the bottom of Lake Agassiz is now the soil of the Red River Valley. It is characterized

as a deep, black soil with very few rocks. The main study area, Mapleton, is part of this formation. This region is very flat.

The region that was the shore of Lake Agassiz laid down a soil of a much different type. These are characteristically more sandy, and usually contain rocks. The land in this region is not flat, but rather gently rolling with small, flat bottomed depressions throughout, termed coulees. In this region, two areas have been under study: Hunter and Blanchard, North Dakota. The coulees are a favorite habitat location for the squirrels and offer a means of dispersion from one pasture to another.

In the east central part of the state rolling hills are present. This is the situation at Lehr, North Dakota. These hills were created by the pushing and receding of the glaciers. The soil in this region is much harder and is rocky. The rocks vary from the size of golf balls on up. The low areas between the hills are mesic to hydric. The latter areas are commonly known as wetlands, and offer breeding grounds for waterfowl and shorebirds.

The larger rocks are used by squirrels as observation posts. Some rocks present a considerable climbing problem, but once a squirrel is standing on top in an upright posture it serves as an excellent lookout. Flickertails will frequently dig burrows under the rocks. This behavior affords them some protection against a major predator the badger, Taxidea taxus.

Climate

North Dakota is typical of the northern plains area, and is located near the center of the North American continent. The climate is a continental type with large fluctuations in summer and winter mean temperatures. The mean January temperature for Fargo is 7.1° F. while the mean for July is 71.3° F. There are well developed spring and fall seasons. The mean average spring freeze date is May 5; mean average fall freeze date, September 26. The ground squirrels emerge four weeks before the last spring mean freeze date, but hibernate before the first fall freeze. The average growing season is 121 days, varying from 110 days in the north to 135 days in the south. Precipitation in the eastern third of the state, including three of my study areas (Mapleton, Blanchard, Hunter) averages about 19 inches per year.

The original vegetation of this area is considered to be tall grass prairie (Kuchler, 1964). The reason that North Dakota is able to support a tall grass prairie community on so much less rainfall than other areas is the lesser rate of evaporation of soil moisture, due to a much lower average temperature and the lesser evaporation of water held in the form of ice and snow.

The temperatures recorded at the Fargo, North Dakota, U. S. Weather Bureau station for 1965, 1966, and 1967 are recorded in Table 1. The Fargo recording station is

TABLE 1.--Maximum, minimum, and average air temperatures (° F.) taken at Fargo (Hector Airport), North Dakota during 1965, 1966, 1967

Month	Week	1965 Max.	1965 Ave.	1965 Min.	1966 Max.	1966 Ave.	1966 Min.	1967 Max.	1967 Ave.	1967 Min.
January	1.	19.0	7.1	- 7.4	4.1	- 4.9	-13.6	21.0	10.6	- 0.1
	2.	- 2.7	-11.3	-19.4	11.7	1.1	- 9.9	28.0	16.6	4.6
	3.	18.9	6.9	5.3	5.9	- 2.3	- 9.7	11.1	- 0.1	-11.7
	4.	8.4	1.3	-11.1	- 9.9	-22.1	-27.0	15.1	6.0	- 3.1
February	5.	.3	-12.7	-25.4	6.9	4.9	-16.4	24.0	13.0	1.6
	6.	23.6	12.7	1.4	27.9	20.2	12.0	11.9	0.9	- 9.7
	7.	20.3	10.0	5.7	3.6	- 6.1	-15.4	10.6	2.8	-15.4
March	8.	13.3	2.6	- 7.7	12.9	.1	-12.4	13.8	2.9	- 7.6
	9.	23.7	14.7	5.0	31.7	25.3	18.6	32.0	15.0	23.7
	10.	32.0	20.4	8.6	29.0	19.3	11.9	30.1	17.6	4.7
	11.	25.1	16.6	7.4	44.3	36.9	29.0	24.3	15.3	5.7
	12.	16.9	3.9	-10.7	35.4	27.6	19.4	40.7	34.9	28.6
	13.	29.3	20.9	11.9	49.9	39.4	28.4	52.4	40.9	28.9
April	14.	38.0	35.0	31.4	38.9	33.8	28.4	48.9	36.4	24.3
	15.	48.9	42.6	35.9	47.9	39.0	29.7	50.6	43.0	35.0
	16.	50.9	41.6	31.6	49.0	37.1	24.6	45.0	37.1	28.6
	17.	61.9	47.9	33.4	46.9	39.6	31.9	48.7	39.6	30.0
May	18.	72.3	50.4	43.7	58.0	44.9	30.9	44.1	35.0	25.6
	19.	70.0	55.7	41.3	51.3	41.6	31.4	54.0	43.4	32.3
	20.	65.4	54.3	42.7	64.4	51.7	38.6	66.0	51.3	36.1
	21.	52.4	45.1	37.7	77.6	63.3	48.4	77.3	62.0	46.4
	22.	61.7	53.0	43.9	74.3	60.1	45.4	76.4	63.4	50.0
June	23.	74.4	62.7	50.9	70.4	58.0	45.3	72.1	61.0	49.6
	24.	77.6	65.4	52.7	73.1	60.7	47.6	72.9	64.3	55.3
	25.	79.1	65.6	51.4	85.4	73.9	61.6	71.0	60.1	48.7
	26.	74.4	64.1	53.4	85.7	75.0	63.7	77.9	63.7	49.0

TABLE 1--Continued

Month	Week	1965 Max.	1965 Ave.	1965 Min.	1966 Max.	1966 Ave.	1966 Min.	1967 Max.	1967 Ave.	1967 Min.
July	27.	79.4	66.4	53.1	84.0	73.1	61.7	75.0	63.6	49.1
	28.	75.4	65.6	55.3	86.6	74.8	62.4	79.6	65.1	50.6
	29.	84.3	72.7	60.6	87.1	74.9	61.9	88.1	74.9	60.9
	30.	82.6	69.6	56.1	84.1	71.4	58.1	85.0	69.7	53.7
August	31.	81.1	70.4	63.3	86.7	74.1	60.9	85.4	66.0	54.0
	32.	82.1	70.0	57.4	74.4	63.3	51.9	79.6	64.7	49.4
	33.	84.7	72.1	58.7	75.4	64.0	51.8	84.7	70.4	55.7
	34.	77.1	64.7	52.0	70.6	60.0	48.9	80.7	67.3	53.4
	35.	66.1	56.4	46.0	84.0	70.7	57.0	78.3	63.4	48.0
September	36.	66.3	55.0	43.1	77.3	64.1	50.3	81.7	67.0	51.9
	37.	59.9	51.9	43.3	73.9	60.4	46.7	71.7	62.6	52.9
	38.	53.7	47.6	41.0	75.3	59.3	42.7	71.9	60.0	48.7
	39.	49.6	41.3	32.6	59.7	48.0	35.7	70.5	53.9	36.4
October	40.	60.0	47.7	35.0	64.0	50.3	36.3	63.7	52.9	41.6
	41.	58.7	46.3	33.4	59.4	47.7	35.4	51.1	43.3	34.9
	42.	63.8	53.7	43.1	55.0	41.4	27.6	57.4	29.7	43.9
	43.	56.7	41.9	26.6	52.3	40.3	27.6	46.7	29.0	38.1
	44.	62.6	47.1	31.3	40.3	29.9	18.9	43.9	26.4	35.4
November	45.	43.7	32.1	20.0	27.9	19.4	10.4	46.7	34.3	21.3
	46.	35.6	25.3	14.4	34.0	23.0	12.0	42.7	32.4	21.4
	47.	34.3	26.1	17.1	40.3	28.9	17.0	37.6	29.7	21.7
	48.	20.6	12.3	3.6	23.1	15.1	6.7	22.6	15.6	8.4
	49.	39.0	29.0	18.9	27.3	15.7	3.7			
	50.	26.3	23.3	19.7	23.9	15.3	6.3			
	51.	24.4	15.0	5.4	26.0	15.8	5.1			
	52.	24.6	13.6	2.0	11.4	2.9	- 6.0			

approximately 12 miles from the main study area. The year was divided into 52 seven day weeks and an average of the daily maximum, average, and minimum temperatures are shown.

Flickertails make their burrows in areas of heavy grass cover, away from trees. The trees during the winter tend to slow the wind and large deposits of snow and ice usually accumulate at the base of the trees. These snow deposits can linger until May, and would severely limit the amount of time the squirrels could spend above ground if their burrows were near the trees. The minimum temperatures under grass sod were somewhat higher than under more bare areas (Potter, 1956). This may be due to the insulating value of organic material (Benninghoff, 1952). The insulating value of sod not only helps in reducing the extreme of the minimum temperatures of the soil under it, but also helps to stabilize soil temperature during the spring. As a result the "grass and sod was frost-free 4 to 8 weeks earlier than the other sites of comparable snow depth in 1952" (Potter, 1956). Thus the reduced minimum temperature and the lesser amount of snow cover due to the lack of trees may permit the squirrels to emerge from hibernation much earlier than would otherwise be possible.

Flooding of the colony occurred during two of the three year of the study. The flooding in 1965 may have been responsible for the late arousal of the squirrels since they could not have come to the surface of the ground while the

area was water covered. On April 7, 1965, the main study area was flooded by the adjacent Rush River. The entire area of the ground squirrel colony was covered by water from April 7 to April 15, 1965. The minimum depth of the water during this eight days was 5 cm.; the maximum depth was 46 cm. On April 15 the water receded rapidly, leaving the area exposed to the sun. One week later, on April 22, ground squirrels were observed coming out of their burrows in the same area. There were 12 adult females emerging from burrows that had been covered by water.

CHAPTER IV

THE BIOTIC ENVIRONMENT

The biotic environment of a species is the total component of both plants and animals that are found where the species lives. The biotic environment of Richardson's ground squirrels is a varied one. In the eastern part of North Dakota the areas in which the squirrels live is quite moist, while in western Montana it is nearly desert. Even within the four study areas of the eastern half of North Dakota there is a wide variance in the animal and plant life.

North Dakota has a less varied topography than many states, and the ecological situations present are more homogeneous than that of most other states. These of ecological characteristics limit the number of species of plants found in the state, only about 1,000, which is approximately one-half the number in many other states (Stevens, 1963). A partial list of the species of plants found in the four main study areas is given in Table 2. This list is not exhaustive, but contains the major plants.

It is apparent that the Mapleton, Hunter, and Blanchard study areas are closely related with respect to

plant species composition. Lehr is more different from Mapleton, Blanchard, and Hunter than the latter are from each other. Hunter and Mapleton are the most alike, with Blanchard slightly different. Part of the reason for these differences may be the geology. Mapleton and Hunter were part of the bottom of pre-historic Lake Agassiz and therefore are very fertile with very few rocks. Blanchard was part of the shore of Lake Agassiz and has more rocks, while Lehr was never part of Lake Agassiz and was formed by the Wisconsin glacier.

The Mapleton study area is an overgrazed pasture. The dominant species of plant are Bromus inermis, Poa pratensis, and Hordeum jubatum. The physiognomy of this area is much like a mowed lawn. The grazing of the cattle is very important in maintaining the area in a suitable condition for ground squirrels. Mapleton was part of the bottom of Lake Agassiz.

The Hunter study area has many of the same dominant species as does Mapleton. Hunter is more overgrazed than any of the other areas. Much of the ground is bare, and many more borrows occur per unit area than in any other of the areas. Hunter was part of Lake Agassiz.

The Blanchard study area was also an overgrazed pasture area interspersed with coulees. The dominant plants in this area are Bromus inermis, Agropyron cristatum, and Symphoricarpos occidentalis. The Symphoricarpos formed

barriers in the view of many squirrels and tended to grow on old burrow mounds because it was not eaten by the squirrels. Koford (1958) pointed out a similar case in which mustard, Brassica sp., not eaten by prairie dogs, would grow on mounds.

The Lehr study area was mostly composed of mature prairie grasslands. The most abundant grasses were Agropyron repens, Agropyron cristatum, Koeleria cristatum, Bouteloua gracilis, Stipa viridula, and Stipa comata. There was also a greater variety of other plants than in the Mapleton, Hunter, or Blanchard study areas (Table 2).

North Dakota's fauna of amphibians and reptiles is a rather limited one. Table 3 gives the amphibians found living in association with flickertails, and Table 4 shows the reptiles.

The bird list of North Dakota reflects the abundance of the northern prairie ponds that are used as breeding ponds by many species of the ducks, sandpipers, plovers, and rails. Many strictly prairie-breeding species are also present among the flickertails. Table 5 shows the birds observed in or near flickertail colonies during this study.

Mammals are found living in the same area as do the flickertails. The prairie vole, Microtus ochrogaster, and the deer mouse, Peromyscus maniculatus, could be trapped in considerable numbers on the prairie during most of the three study years. An expanded list of the mammals found living in the same areas as flickertails is given in Table 6.

TABLE 2.--Partial list of plants found in association with Richardson's ground squirrel in eastern North Dakota

	LEHR	BLANCHARD	MAPLETON	HUNTER
GRAMINEAE				
Bromus inermis	x	x	x	
Glyceria grandis			x	
Poa pratensis	x	x	x	x
Agropyron repens	x	x	x	
Agropyron cristatum	x	x		
Hordeum jubatum	x	x	x	x
Elymus macounii			x	
Koeleria cristata	x	x		x
Phleum pratense	x			
Calamovilfa longifolia	x			
Stipa comata	x			
Stipa viridula	x			
Beckmannia syzigachne	x			
Bouteloua gracilis	x			
Phalaris arundinacea			x	
CYPERACEAE				
Eleocharis calva	x	x	x	
Scirpus americanus	x			
JUNCACEAE				
Juncus balitcus	x	x		
Juncus bufonius			x	
SALICACEAE				
Salix sp.			x	

TABLE 2--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
POLYCONACEAE				
Rumex crispus	x	x	x	x
Rumex occidentalis	x	x	x	x
CHENOPODIACEAE				
Chenopodium album	x	x	x	x
AMARANTHACEAE				
Amaranthus sp.		x	x	x
CARYOPHYLLACEAE				
Lychnis alba			x	
Paronychia sessiliflora	x			
Cerastium arvense	x	x		
RANUNCULACEAE				
Ranunculus cymbalaria	x	x	x	x
BRASSICACEAE				
Thlaspi arvense		x	x	x
Descurainia sophia	x	x	x	x
Rorippa islandica		x	x	x
Capsella bursa-pastoris	x	x	x	x
ROSACEAE				
Potentilla anserina	x	x	x	
Rosa arkansana	x		x	

TABLE 2--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
FABACEAE				
Trifolium pratense			x	
Trifolium repens		x	x	x
Melilotus alba		x	x	
Astragalus goniatus			x	
Medicago sativa	x			
Astragalus flexuosus	x			
Amorpha canescens	x			
Psoralea esculenta	x		x	
Vicia americana			x	
POLYGALACEAE				
Polygala alba	x			
MALVACEAE				
Malva rotundifolia		x	x	x
APOCYNACEAE				
Apocynum sibiricum	x			
ASCLEPIADACEAE				
Asclepias syriaca		x	x	
BORAGINACEAE				
Asperugo procumbens			x	
Onosmodium occidentale	x			
CONVOLVULACEAE				
Convolvulus arvensis	x	x		

TABLE 2--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
LAMINACEAE or LABIATAE				
Stachys palustris	x	x		x
SCROPHULARIACEAE				
Bacopa rotundifolium		x		
PLANTAGINACEAE				
Plantago major			x	
CAPRIFOLIACEAE				
Symphoricarpos occidentalis	x	x	x	x
ASTERACEAE				
Ratibida columnifera	x			
Gaillardia aristata	x	x		
Achillea lanulosa	x	x		x
Senecio plattensis			x	
Artemisia ludoviciana	x			
Cirsium vulgare		x	x	
Taraxacum officinale	x	x	x	x
Lactuca serriola	x	x	x	x

TABLE 3.--Amphibians found in association with Richardson's ground squirrel in eastern North Dakota

	LEHR	BLANCHARD	MAPLETON	HUNTER
AMBYSTOMIDAE				
Gray Tiger Salamander *Ambystoma tigrinum diaboli*	x	x	x	x
BUFONIDAE				
Great Plains Toad *Bufo cognatus*		x	x	x
Dakota Toad *Bufo hemiophrys*		x	x	x
Rocky Mountain Toad *Bufo woodhousei woodhousei*	x			
HYLIDAE				
Boreal Chorus Frog *Pseudacris triseriata maculata*			x	
RANIDAE				
Northern Leopard Frog *Rana pipiens pipiens*	x	x	x	x

TABLE 4.--Reptiles found in association with Richardson's ground squirrel in eastern North Dakota

	LEHR	BLANCHARD	MAPLETON	HUNTER
COLUBRIDAE				
Western Plains Garter Snake *Thamnophis radix haydoni*	x	x	x	x
Red-sided Garter Snake *Thamnophis sirtalis parietalis*	x	x	x	x
CHELYDRIDAE				
Common Snapping Turtle *Chelydra serpentina serpentina*			x	
TESTUDINIDAE				
Western Painted Turtle *Chrysemys picta belli*			x	

TABLE 5.--Birds found in association with Richardson's ground squirrel in eastern North Dakota

	LEHR	BLANCHARD	MAPLETON	HUNTER
PODICIPEDIDAE				
Pied-billed Grebe *Podilymbus podiceps*			x	
PELECANIDAE				
White Pelican *Pelecanus erythrorhynchos*	x			
ARDEIDAE				
Great Blue Heron *Ardea herodias*			x	
Black-crowned Night Heron *Nycticorax nycticorax*	x			
ANATIDAE				
Mallard *Anas platyrhynchos*	x		x	
Gadwall *Anas strepera*	x			
Pintail *Anas acuta*	x	x		
Green-winged Teal *Anas carolinensis*	x			
Blue-winged Teal *Anas discors*	x		x	
Cinnamon Teal *Anas cyanoptera*	x			
Shoveller *Spatula clypeata*	x		x	

TABLE 5--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
Redhead *Aythya americana*	x			
Canvas Back *Aythya valisineria*	x			
Ruddy Duck *Oxyura jamaicensis*	x			
CIRCINAE				
Marsh Hawk *Circus cyaneus*	x	x	x	x
FALCONINAE				
Sparrow Hawk *Falco sparverius*			x	
PHASIANIDAE				
Hungarian Partridge *Perdix perdix*	x			
Ring-necked Pheasant *Phasianus colchicus*	x	x	x	x
RALLIDAE				
Sora Rail *Porzana carolina*	x		x	
American Coot *Fulica americana*	x			
CHARACRIIDAE				
Killdeer *Charadrius vociferus*	x	x	x	x

TABLE 5--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
SCOLOPACIDAE				
Spotted Sandpiper *Actitis macularia*		x		
Pectoral Sandpiper *Erolia melanotos*	x			
Marbled Godwit *Limosa fedoa*	x			
RECURVIROSTRIDAE				
Avocet *Recurvirostra americana*	x			
PHALAROPODIDAE				
Wilson's Phalarope *Steganopus tricolor*	x			
LARIDAE				
Franklin's Gull *Larus pipixcan*			x	
STERNINAE				
Black Tern *Chlidonias niger*	x			
COLUMBIDAE				
Domestic Pigeon *Columba livia*	x	x	x	x
Mourning Dove *Zenaidura macroura*	x	x	x	x

TABLE 5--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
PICICAE				
Yellow-shafted Flicker *Colaptes auratus*		x	x	x
Red-shafted Flicker *Colaptes cafer*		x	x	x
Red-Headed Woodpecker *Melanerpes erythrocephalus*			x	
TYRANNIDAE				
Eastern Kingbird *Tyrannus tyrannus*	x	x	x	x
Arkansas Kingbird *Tyrannus verticalis*	x	x	x	
Wood Pewee *Contopus virens*	x	x	x	
ALAUDIDAE				
Horned Lark *Eremophila alpestris*	x	x	x	
HIRUNDINIDAE				
Tree Swallow *Iridoprocne bicolor*	x		x	
Barn Swallow *Hirundo rustica*	x	x	x	
CORVIDAE				
Blue Jay *Cyanocritta cristata*	x			
Common Crow *Corvus brachyrhynchos*	x	x	x	x

TABLE 5--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
TROGLODYTIDAE				
House Wren *Troglodytes aedon*			x	
MIMIDAE				
Brown Thrasher *Toxostoma refum*	x	x	x	x
TURDIDAE				
Robin *Turdus migratorius*	x	x	x	x
BOMBYCILLIDAE				
Cedar Waxwing *Bombycilla cedrorum*	x			
PARULIDAE				
Yellow-throad *Dendroica petechia*		x	x	
PLOCEIDAE				
English Sparrow *Passer domesticus*	x	x	x	x
ICTERIDAE				
Bobolink *Dolichonyx oryzivorus*	x	x	x	
Western Meadowlark *Sturnella neglecta*	x	x	x	x
Yellow-headed Blackbird *Xanthocephalus xanthocephalus*	x		x	

TABLE 5--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
Red-wing *Agelaius phoeniceus*	x	x	x	x
Orchard Oriole *Icterus spurius*			x	
Baltimore Oriole *Icterus galbula*			x	
Purple Grackle *Quiscalus quiscula*		x	x	x
Brown-headed Cowbird *Molothrus ater*			x	
FRINGILLIDAE				
Dickcissel *Spiza americana*			x	
Common Goldfinch *Spinus tristis*	x	x	x	x
Lark Bunting *Calamospiza melanocorys*	x	x	x	x
Grasshopper Sparrow *Ammodramus savannarum*	x			
Baird's Sparrow *Ammodramus bairdii*	x			
Vesper Sparrow *Pooecetes gramineus*		x	x	x
Clay-colored Sparrow *Spizella pallida*	x			
White-throated Sparrow *Zonotrichia albicollis*	x			
Song Sparrow *Melospiza melodia*		x	x	x
Chestnut-collared Longspur *Calcarius ornatus*	x			

TABLE 6.--Mammals found in association with Richardson's ground squirrel in eastern North Dakota

	LEHR	BLANCHARD	MAPLETON	HUNTER
SORICIDAE				
Shorttail shrew *Blarina brevicauda*			x	
LEPORIDAE				
White-tailed jackrabbit *Lepus townsendi*			x	
Eastern cottontail *Sylvilagus floridanus*			x	
SCIURIDAE				
Thirteen-lined ground squirrel *Citellus tridecemlineatus*	x	x	x	x
Franklin's ground squirrel *Citellus franklini*		x	x	x
Fox squirrel *Sciurus niger*			x	x
GEOMYIDAE				
Northern pocket gopher *Thomomys talpoides*		x		x
Plains pocket gopher *Geomys bursarius*		x	x	x
CRICETIDAE				
Deer mouse *Peromyscus maniculatus*	x	x	x	x
White-footed mouse *Peromyscus leucopus*	x	x	x	x

TABLE 6--Continued

	LEHR	BLANCHARD	MAPLETON	HUNTER
Prairie vole *Microtus ochrogaster*			x	
MURIDAE				
House mouse *Mus musculus*	x			
CANIDAE				
Red fox *Vulpes fulva*			x	
Gray fox *Urocyon cinereoargenteus*	x			
PROCYONIDAE				
Raccoon *Procyon lotor*			x	x
MUSTELIDAE				
Mink *Mustela vison*	x	x	x	x
Striped skunk *Mephitis mephitis*	x	x	x	x
Badger *Taxidea taxus*	x	x	x	x
CERVIDAE				
White-tailed deer *Odocoileus virginianus*	x		x	

CHAPTER V

BEHAVIOR

Growth and Pelage

The physical size and color of a flickertail can be used to determine age and, to some extent, sex. The color of flickertails varies considerably from individual to individual. Brown and Roy (1943) wrote: "There is a very definite intermingling of size and colour in this species throughout the whole of southern Alberta; in fact, so much so that one is led to believe that there are numerous subspecies of this animal inhabiting the same range." Seton (1929) felt that all squirrels were similar and described one as "a warm yellowish buff, deepening along the cheeks, shoulders, and flanks, and thigh to a strong buffy yellow. On the crown and back it is thickly peppered with brownish black, giving the effect of a gray mantle. On the rump, these markings faintly suggest cross pencilling, or faint dapplings of lighter colour. The tail above is brown, peppered like the back; below, clear pale sienna; finished with a blackish edging, which again has a broad tipping of pale yellow." The observations made of squirrels collected

from all parts of the range of the sub-species Citellus richardsoni indicate that there is indeed quite a variance in color from individual to individual squirrel. This variance is however not random, but somewhat determined by the age and sex of the individual. The following color descriptions of flickertails are based upon Ridgeway's Color Standard (1912). Immature squirrels, those less than one year old, can be distinguished from older squirrels on the basis of color. Young squirrels during June are much smaller than adults and their color is much lighter. About the beginning of July young squirrels become large enough to be confused with adults, even though they weigh less. Immature males during July and August are cinnamon buff on the ventral side with a small blackish spot on the tip of the tail. The sides of the head from the base of the forelimbs to the area under the eye are yellow ochre. The sides of the immature males fade from yellow ochre anteriorly to cream buff along the sides of the body. The back of the immature males is blackish with spots of cream buff. The immature females are cinnamon buff from anterior to posterior. It is very difficult to distinguish between immature males and females on the basis of color.

The adult males and females are quite different from the young squirrels. The adult females are cinnamon rufous to tawny olive on the undersides of the tail. This is quite variable. The sides are pale smoke gray anteriorly

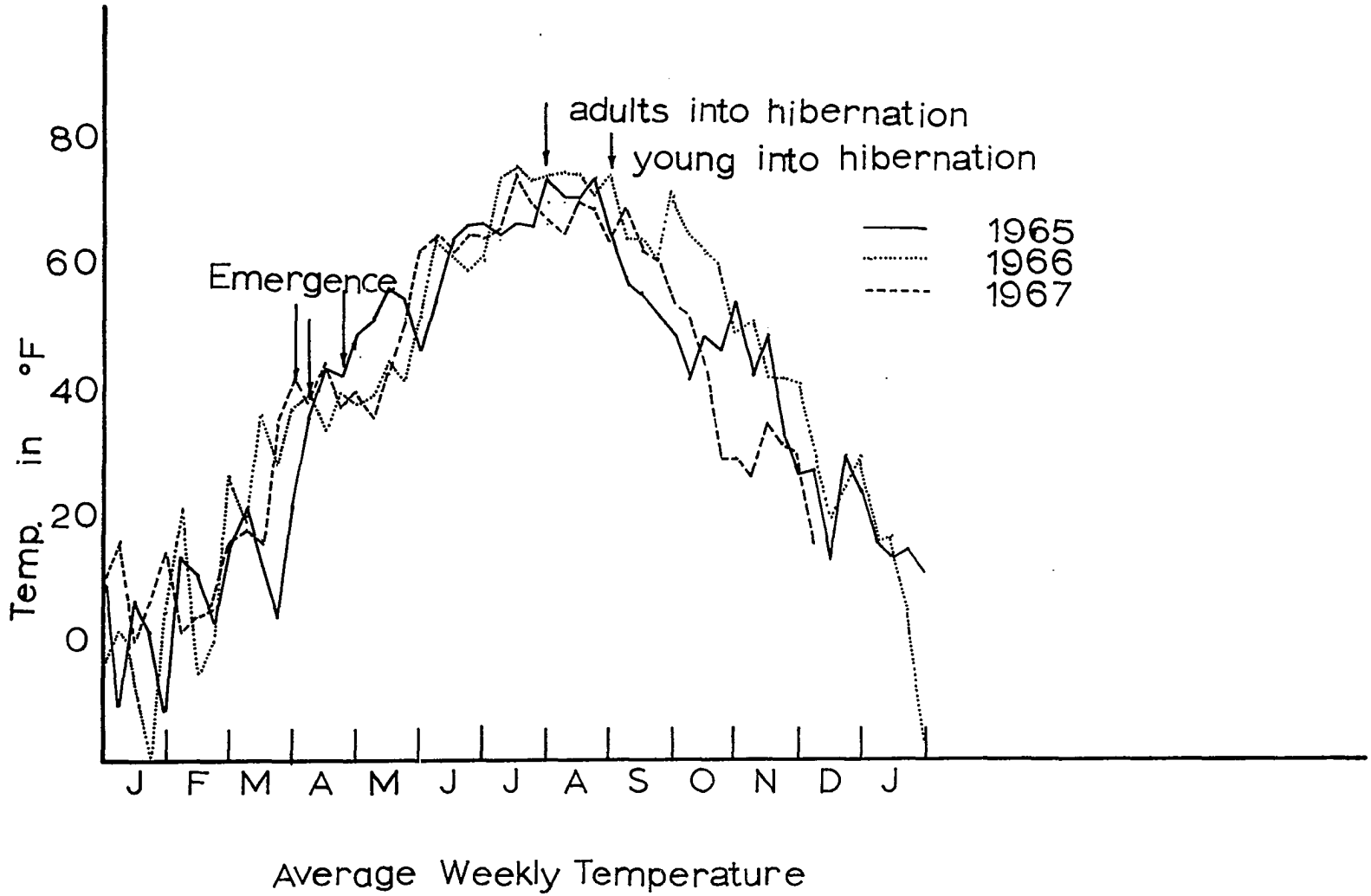
fading to light buff along the sides of the abdomen. The adult males are larger and stockier than the adult females. They are much broader in the neck region and give a more square appearance. The adults of both sexes are much lighter and whiter than are the immature animals. A specimen of each group is deposited in the Stovall Museum of the University of Oklahoma. The very young animal is U.O.M.Z. 3151, the immature male U.O.M.Z. 3152, immature female U.O.M.Z. 3153, and mature female U.O.M.Z. 3154.

The size and weight of the various groups of squirrels is given in Table 7. Young squirrels increase in size regularly during the summer. Young males start out smaller than young females but are larger after the middle of June.

Yearly Cycles

Citellus richardsoni spends much of the year in hibernation and the types of behavior shown by members of a population vary considerably from one season to another. The ground squirrels emerged from hibernation on April 22, 1965, April 8, 1966, and April 1, 1967. The 1965 date might have been delayed by the flood. These arousal dates are not as uniform as those reported for Citellus tridecemlineatus (McCarley, 1966). The arousal of the ground squirrels from hibernation comes when the sharpest rise in air temperature is seen (Fig. 2). This air temperature rise is in a general way suggested by McCarley (1966). Figure 3 gives the underground temperatures of the soil at Fargo,

AVERAGE WEEKLY TEMPERATURE AT FARGO, NORTH DAKOTA (HECTOR AIRPORT) DURING 1965, 1966, 1967



Average Weekly Temperature

Figure 2

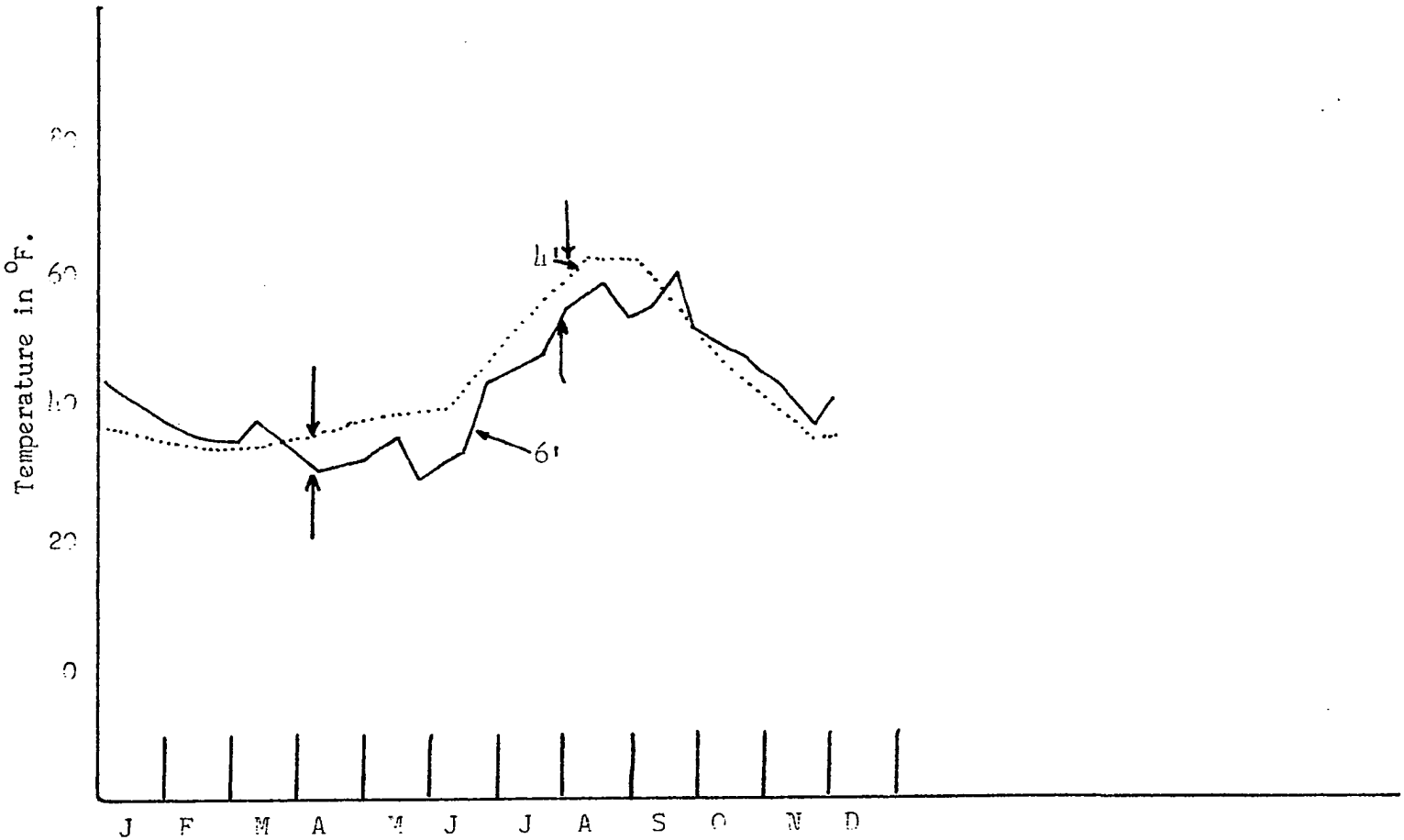
TABLE 7.--Mean weights and lengths of selected groups of Richardson's ground squirrels

TIME		N	Lengths (m.m.) TOTAL	TAIL	HIND-FOOT	EAR	WEIGHT (gms.)
May 29, June 7	Immature females	9	230.7	60.0	40.7	10.4	113.3 g.
	Immature males	10	221.0	56.7	41.8	10.6	123.3 g.
	Mature females	6	307.0	87.8	43.1	11.5	365.4 g.
June 8, June 14	Immature females	10	237.6	65.2	41.2	10.5	No Measurement
	Immature males	10	221.0	56.7	41.8	10.6	123.3 g.
	Mature females	8	297.6	81.0	42.8	11.0	314.0 g.
June 15, June 21	Immature females	16	234.3	65.7	40.4	10.2	171.0 g.
	Immature males	12	237.5	63.8	42.7	11.1	163.5 g.
	Mature females	4	292.2	77.6	46.9	10.3	325.2 g.
June 22, June 27	Immature females	4	262.5	77.5	43.8	11.5	No Measurement
	Immature males	7	271.2	76.2	47.3	12.5	223.3 g.
	Mature females	5	316.5	77.0	44.5	12.3	425.5 g.
June 28, July 30	Immature females	3	301.3	82.7	44.3	12.3	270.0 g.
	Immature males	2	310.0	77.0	48.0	11.0	No Measurement
	Mature females	3	No Measurements				

North Dakota, during 1953 and 1954 (Potter, 1956). Even though the cited years of the soil temperatures are not for the same years as the air temperatures, it would seem that both would be similar year after year. The arousal of ground squirrels is probably not due to air temperatures, for their burrows are tightly plugged during the winter, preventing any cold air from coming down the shaft, and thus these squirrels have no apparent way of sensing the air temperature from deep in their burrow systems. It seems probable that the squirrels have evolved the ability to sense some other environmental factor which occurs simultaneously with the rise in air temperature. This other factor is related to the rise in temperature during the spring which allows the squirrels to arrive at the surface of the soil after the air temperature is warm enough to permit above-ground activity.

The nest cavities in which the squirrels spend the winter are usually from four to six feet below the surface of the soil. Comparison of Figures 2 and 3 indicates that the temperature of the soil lags behind the air relative to warming and cooling. The coolest part of the year at a depth of six feet is during April and May, while the coolest air temperatures are during December and January. The warmest soil temperatures at a depth of six feet are during August and September while the warmest air temperatures are during July and August. The period of lag is longer for the cooling of the soil than for warming.

Figure 3. UNDERGROUND SOIL TEMPERATURES TAKEN AT FARGO, NORTH DAKOTA (Potter, 1956)



The temperature in the soil surrounding the nest becomes cooler during January, February, and March, and reaches a near low for the year during the first part of April. This corresponds with the time of emergence of the ground squirrels. It seems more likely that the squirrels might use the lowering temperatures of the nest as the clue for arousal rather than the environmental air temperatures per se. Further studies will be needed to demonstrate if this lowering of temperatures can arouse a squirrel from hibernation.

Potter (1956) also pointed out that the soil has a spring and fall temperature overturn. During this time there is no actual vertical movement of soil as there is water in a lake overturn, but all levels of soil have the same temperature. During this spring and fall overturn all temperature lines coincide as the reversal of the temperature at different levels occurs. This time of the spring overturn is approximately the first week of May, and the fall overturn the first week of October. The presence of ground squirrels after initial hibernation has been observed. Flickertails have been observed above ground during the first week in October. What connections there is, if any, between these two variables is unknown.

Adult squirrels begin hibernation about the first of August. The onset of hibernation is not a sudden event, but a gradual one. Squirrels usually come out each morning in a

fairly predictable manner. Each adult squirrel was observed each day during June, but by the middle or latter part of July, certain squirrels were not observed.

Table 8 shows which females were observed during the days of July, 1965. On July 9, it was noted that the adult female animals were quite fat and that they were beginning to come out and feed more sporadically during the day. Some individuals, such as number 4, disappeared for hibernation in a fairly sudden manner. Female 4 was out on July 16 and again on July 23. After that she was not seen. Other individuals have a more gradual retirement into hibernation. Female 16 was observed on July 16, not on July 17 or 18, but then reappeared on the nineteenth of July. Female 16 was not observed for 3 days, or until July 23, and then was not observed again during that summer.

The young animals are not as fat as adults during this time and remain active above ground during all of August and some of September. Most of the young squirrels cease above-ground activity about September 5.

The behavior of the adult squirrels is different during the various parts of the annual cycle. After the squirrels resume their above-ground activity, an intensive period of feeding takes place. A week later mating activity occurs. After May 1 the young squirrels are born, but they do not come up from the burrows until the first of June. During May, perhaps because nursing pressure is great, much

TABLE 8.--Appearance of adult females above ground, July 1965

	Females											
DATE	#1	#2	#3	#4	#6	#7	#10	#11	#12	#13	#14	#16
July 16	x		x	x				x				x
July 17		x						x			x	
July 18	x						x		x			
July 19					x					x	x	x
July 20		x							x			
July 21			x							x	x	
July 22	x						x					
July 23				x								x
July 24					x							
July 25								x				
July 26						x			x			
August 3						x						

of the female's time is spent feeding. Consequently social interactions are reduced. Young squirrels appear above ground within a period of four days.

Emergence and Movement of Young Squirrels

The young ground squirrels were first observed above ground on June 3, 1965, May 28, 1966, and May 30, 1967. On June 3, 1965, the first young flickertail made its appearance at 7:28 A.M. The first hour above ground was spent just looking out of the burrow entrance; at first the young did not completely emerge. After an hour the young appeared on the mound. They were observed to dig, stand upright, and feed on grass at the edge of the mound. Female 12 was observed to groom the young squirrel by licking the entire back, one hour and 20 minutes after it first appeared. The young squirrels commonly stand by the edge of the burrow entrance, then they may lose their footing and tumble back into the burrow. For the first three days only two young squirrels were observed at any burrow opening at one time. On June 6, 1965, however, four of the young animals were poking their heads from a single burrow. They were then observed for the first time to feed on grass while in the picket pin position. On June 7, 1965, the young flickertails began to show the early signs of agonistic behavior, and to move further from their burrows. The young squirrels at this stage show an alarm response much more readily than do the adults. The young animals seem to have more body

contact between themselves than do the adults. They touch each other quite freely, leaning on each other and demonstrating a considerable amount of mutual grooming.

From the time the young squirrels emerge from their burrows they move progressively further from the maternal burrow mound. Figure 4 shows the progressive distances from the burrow that the young of female 6 moved during 1965. The young squirrels of female 6 emerged on June 3 at 7:28 A.M. They picket pinned for the first time on the same day, 2 hours and 10 minutes later. On June 6, three days after emergence, they were moving up to 2 feet from the burrow entrance. On June 7, they were observed up to 10 feet from the burrow entrance, on June 8, up to 12 feet, and on June 11, up to 30 feet from the burrow. While some movements were made to these distances, most of the activity remained on or very near the mound. By June 17, the young were moving up to 50 feet and into the territory of other adult females. On June 23 the central tendency of the family seemed to break down and the squirrels demonstrated more adult-like behavior. On June 28, one young squirrel was observed 120 feet from the home burrow, and on June 30, several animals were observed from 500 to 700 feet away, and one animal was seen one mile from the home range of its mother.

On July 7, 1965, a young male flickertail was tagged in the afternoon. This individual was shot by Mr. Baxstrom

MOVEMENT OF YOUNG RICHARDSON'S GROUND SQUIRRELS
FROM THEIR HOME BURROW

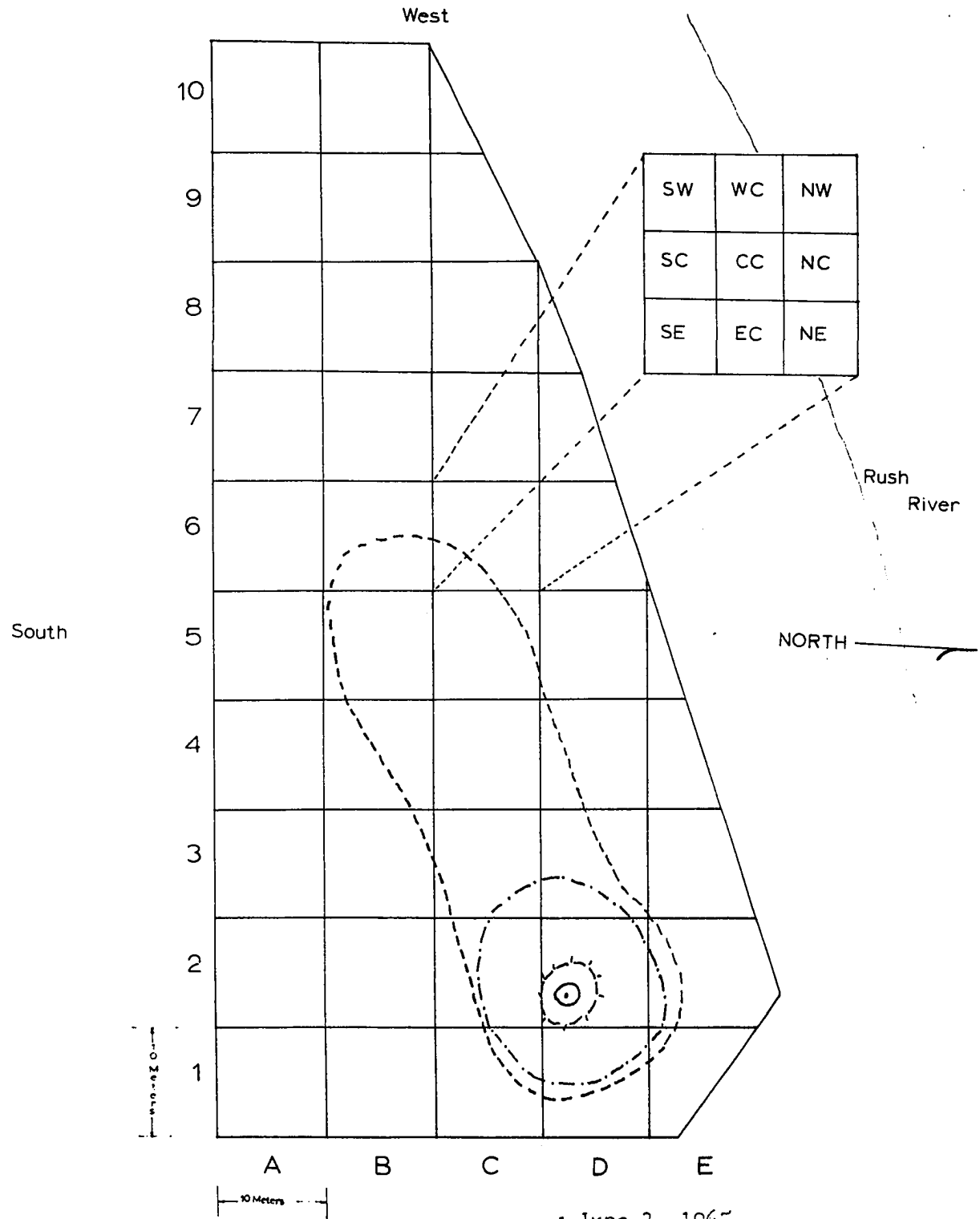


Figure 4

Layout Of Study Area

on July 11, six miles from the place that it was released. This particular male had moved six miles in less than 72 hours. During these first two weeks of July it was common to see young squirrels several miles from the nearest colony. The sex of 35 young squirrels that had become road fatalities was examined and 33, or 94 per cent were males.

The females are able to distinguish between their own offspring and those of another by sight. When a young squirrel enters the territory of a non-maternal female, this non-maternal female will usually stand upright. After visually examining the strange young squirrel she will immediately chase it. On July 10, 1967, a young squirrel was lacerated on the side of the head when caught by the adult female. The adult females will periodically move from one part of their territory to another giving each of their own young a kiss by touching the mouth with the heads at approximately right angles to each other. (Figure 5)

Daily Cycle

During April and May much of the activity was confined to the afternoon, which was the warmest part of the day. Table 9 shows the numbers of the squirrels observed active during the days of June 3 and June 8, 1965. The squirrels were out from 6:45 A.M. until 6:50 P.M. Peaks in activity were seen in the morning, and in the afternoon after approximately 3 P.M. Late in the summer, during late

IDENTIFICATION KISS

Figure 5

TABLE 9.--Number and per cent of total squirrels above ground at half hour intervals on June 8, and June 10, 1965

TIME	JUNE 8, 1965		JUNE 10, 1965	
	N	%	N	%
7:00 A.M.	6	20	6	20
7:30	8	27	22	73
8:00	8	27	24	80
8:30	10	33	22	73
9:00	11	37	15	50
9:30	9	30	22	73
10:00	11	37	18	60
10:30	13	43	15	50
11:00	4	13	5	17
11:30	11	37	8	27
12:00	5	17	5	17
12:30	14	47	7	23
1:00	24	80	10	33
1:30	2	7	9	30
2:00	6	20	7	23
2:30	2	7	13	43
3:00	6	20	24	80
3:30	16	53	27	90
4:00	14	47	19	63
4:30	14	47	30	100
5:00	7	23	27	90
5:30	13	43	25	83
6:00	17	57	25	83
6:30	4	13	10	33
7:00	0	0	0	0

July, more squirrels were observed in the morning than in the afternoon.

Posturing

A position that an animal frequently assumes can be termed a posture. Flickertails have several important postures, and these positions give the other animals in the colony clues to the attitude of another animal.

The basic posture is used for many purposes. The animal has its axis parallel to the ground in this posture. The front limbs are quite straight with a bend at the wrist so the front paws are plantigrade on the ground. The back is straight, with the head lifted above the back somewhat. Feeding takes place in the basic posture. The postures of agonistic behavior, identification kiss, and digging are modifications of the basic posture.

In the medium alert posture the animal is supported by the hind limbs only. The back is bent strongly and the front limbs are held out in front of the body. The medium alert is also used as a feeding posture. It is not basically used as a social posture except between the adult female and her offspring. The young squirrels will groom the female while both animals assume the medium alert posture. The medium alert posture is produced by mild stages of excitement. It may be held for considerable lengths of time.

In the low high alert posture the back is held straight and the support of the body is entirely on the hind

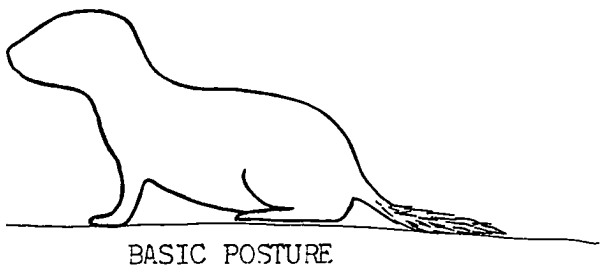
limbs. The front limbs are held out from the body, and the animal is tilted slightly forward. The low high alert posture is not used for social interactions, but is for feeding and visual examination of the surroundings. It may be held for up to several minutes. Squirrels can turn around by movement of the feet while in any of the three high alert postures, making possible the viewing of their whole realm without altering their stance. During feeding the forelimbs may or may not assist the food into their mouth.

The medium high and high alert postures are very similar. The back is held straight, the weight entirely on the hind limbs, and the forelimbs are held tightly against the body. In the medium high the feet are plantigrade, and in the high the feet are digitigrate (Figure 6). The medium high and high alert postures are not usually used for feeding or any social interactions. They are used only as alert postures.

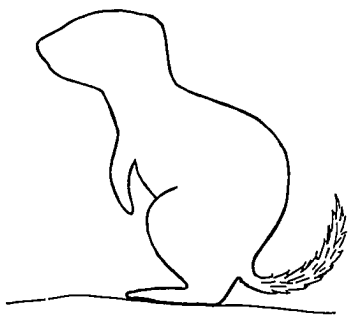
Locomotion

Locomotion in flickertails is accomplished either by running or walking. This movement is rather uniform from individual to individual, as suggested by Gray (1944). Walking is the primary form of movement for short distances and running for longer distances. While walking, all four feet are either on the ground or in the process of moving to a new position. The front foot is moved forward, followed by the opposite hind foot; then the other front foot,

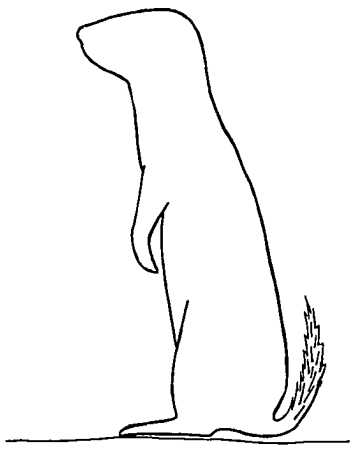
POSTURES GIVEN BY RICHARDSON'S GROUND SQUIRREL



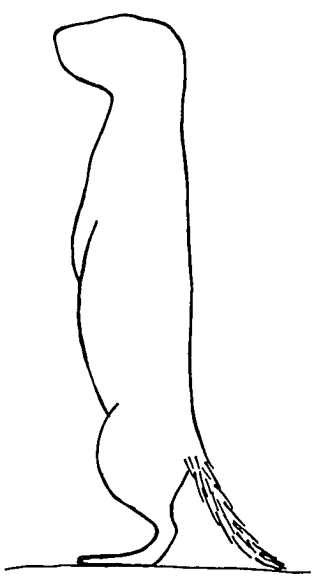
BASIC POSTURE



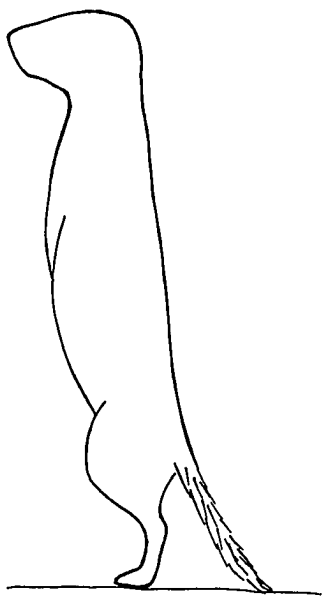
MEDIUM ALERT



LOW HIGH ALERT



MEDIUM HIGH ALERT



HIGH ALERT

Figure 6

followed by the opposite hind foot. The sequence may be stopped at any point and the animal remain still for several minutes. Walking is accomplished with the abdomen on the ground and with the body off the ground. When walking is performed with the abdomen on the ground, the squirrel is rarely in a state of alarm. Feeding on roots, rhizomes, cattle feces, and other ground foods is accomplished while walking with the ventral surface of the body on the ground. Walking with the body raised off the ground is performed when the squirrel is more directed in his movement, such as walking toward a burrow, toward another squirrel, or toward a particular group of plants. Walking with the body off the ground is jerky.

Running is the major means of locomotion. If the squirrel moves over 10 meters, it will usually run. Figure 7 shows the normal running postures. The animal uses both front and hind feet together instead of separately, as in walking. The front limbs are brought under the animal, as it leaps propelled by the push of the hind limbs, which are then brought up to the position of the front limbs. The front legs then extend to meet the ground followed by the hind legs, and the sequence is repeated.

Burrows and Digging Behavior

Burrows are of major significance when considering the ethoecology of flickertails. The squirrels are in their burrows from the first of August until about the first of

SEQUENCE OF POSITIONS ASSUMED WHILE RUNNING

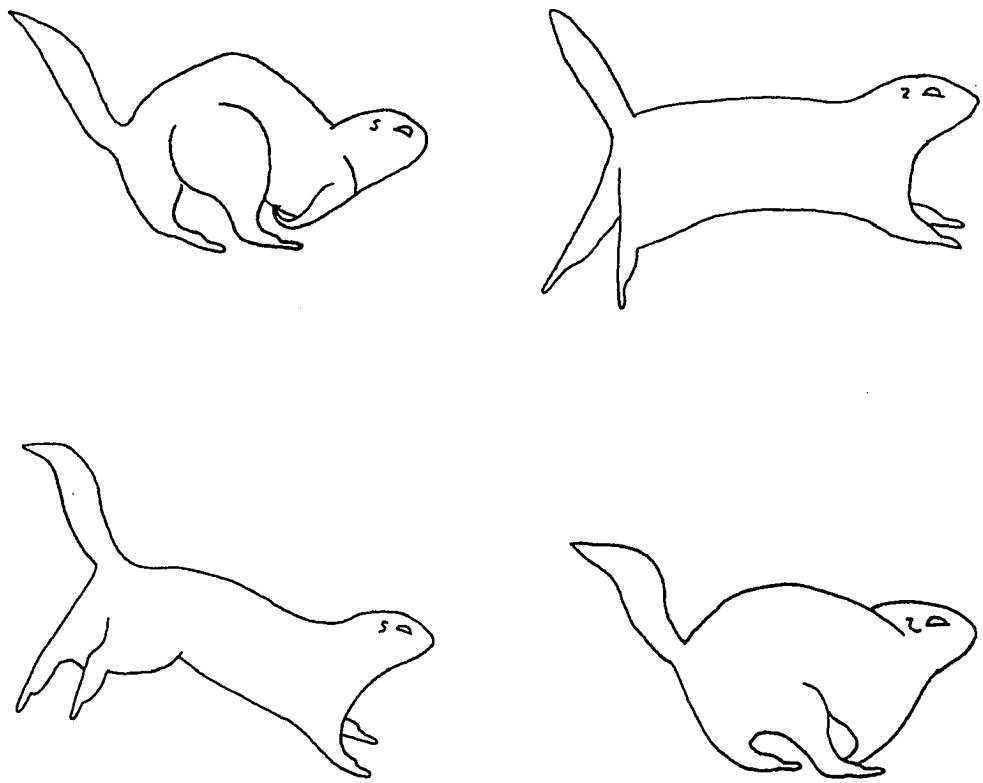


Figure 7

April, or 8 months. During the 4 months they are active they are never out at night, adding 2 more months to burrow time. During the hours of daylight, the individual may be active only 6 to 8 hours per day.

The location of the burrows is not random, but clumped. At Blanchard the burrows were located on flat areas above the coulees and the crests of the ridges near the coulees. No burrows were located on the bottom or the lower sides of the coulee walls. At Lehr the burrows were not located near the prairie ponds, or in any low area that would become quite wet. Most of the burrows were on the sides of the larger ridges, but usually not on the top. These burrow areas have the best drainage, and are somewhat sheltered from the wind. Burrows are also located in proximity of other burrows. Seldom is a burrow located a considerable distance from other squirrels.

There are three different types of burrow openings. All three types may be present in the same system. The type 1 burrow has an opening with a mound. This mound is not formed in a complete circle around the burrow entrance, but is an incomplete arc. This arc is usually more than 180° and usually approximately 270°. Some of these mounds obtain a considerable size. The mound is used for many purposes. The squirrels will frequently lie out on the mounds early in the morning and orient themselves at 90 degrees to the sun while basking on the mound. The mound

is also used as an observation post, and many of the social interactions of the young squirrels and the young squirrels with the adult females take place on the mound.

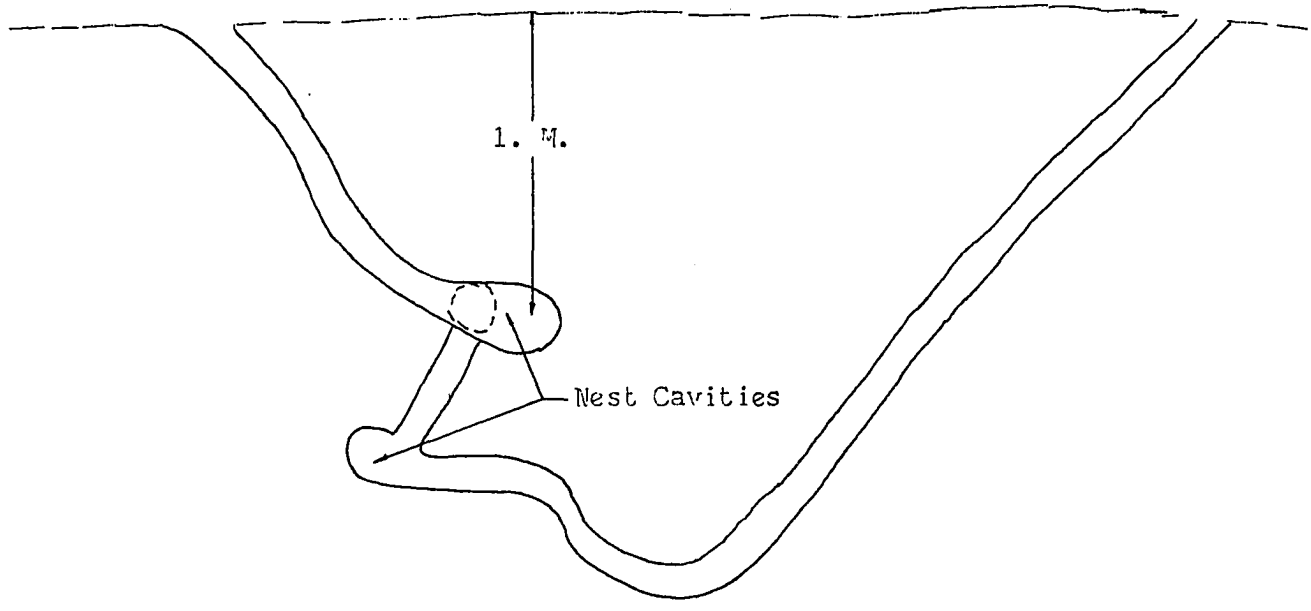
The type 2 burrow entrance is one in which there is very little or no mound present. The entrance in this type is quite large, up to 8 inches in diameter. These burrows are used for quick retreat in emergency situations.

The type 3 burrow is a small round hole very much like that of Citellus tridecemlineatus. It is usually without any dirt and the grass cover makes it well camouflaged.

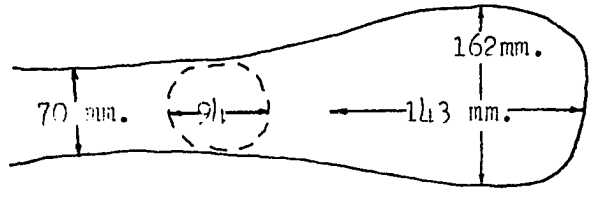
One burrow system was excavated July 25, 1965, during this study. It was a burrow of an adult male squirrel living about 100 meters from the colony (Figure 8). This burrow system had two entrances, a type 1 and a type 2. The burrow descended from the type one burrow entrance to the nest chamber which was approximately one meter from the surface of the soil. The tunnel then traveled straight west as it descended to approximately 1 3/4 meters deep. It then dipped to a 2 meter depth and then the tunnel ascended to the type two burrow entrance. Two chambers were found in the system, one approximately one meter deep, and the other at 1 1/2 meters depth. The shallow nest chamber had a nest constructed mostly of shredded smooth brome grass, Bromus inermis. The deep chamber did not contain a nest.

Digging activity in flickertails is one behavior that is practiced by all squirrels, nearly every day. During

SKETCH OF AN EXCAVATED BURROW



Side view of a burrow system of a male Richardson's ground squirrel excavated July 25, 1965.



Side view of the nest cavity of a male Richardson's ground squirrel excavated July 25, 1965. The dotted area is the entrance into the east west tunnel. This cavity contained a grass nest.

Figure 8

certain times of the year more digging is carried on than others. The first part of July is a period of burrow cleaning. The squirrels usually bring up considerable amounts of fecal material, dirt, and other debris. This material is a result of both cleaning of burrow tunnels and making of new tunnels. The digging done on the surface is accomplished in a rather uniform fashion. The squirrel emerges from the entrance of the burrow head first. The animal then proceeds slowly outward and then turn around 180 degrees until facing the entrance of the burrow (Figure 9A). The squirrel then begins to dig, doing so in two separate motions. First it will scoop up dirt with the forelimbs which are held together to make a sort of shovel (Figs. 9B and C). This process is repeated 5 or 6 times and creates a small pile of dirt up under the abdomen of the squirrel. The hind limbs are then brought forward under the body with the hind paws pointed laterally from the body and the dirt pushed out from under the squirrel (Figure 9D and E). Then the squirrel moves forward into the burrow entrance and repeats this process over and over. The size of the arc of the type 1 burrow entrance is determined by the angle from which the squirrel makes these approaches to the burrow entrance. Some squirrels will make three such paths, while others will make as many as 5 or 6.

SEQUENCE OF POSITIONS ASSUMED WHILE DIGGING

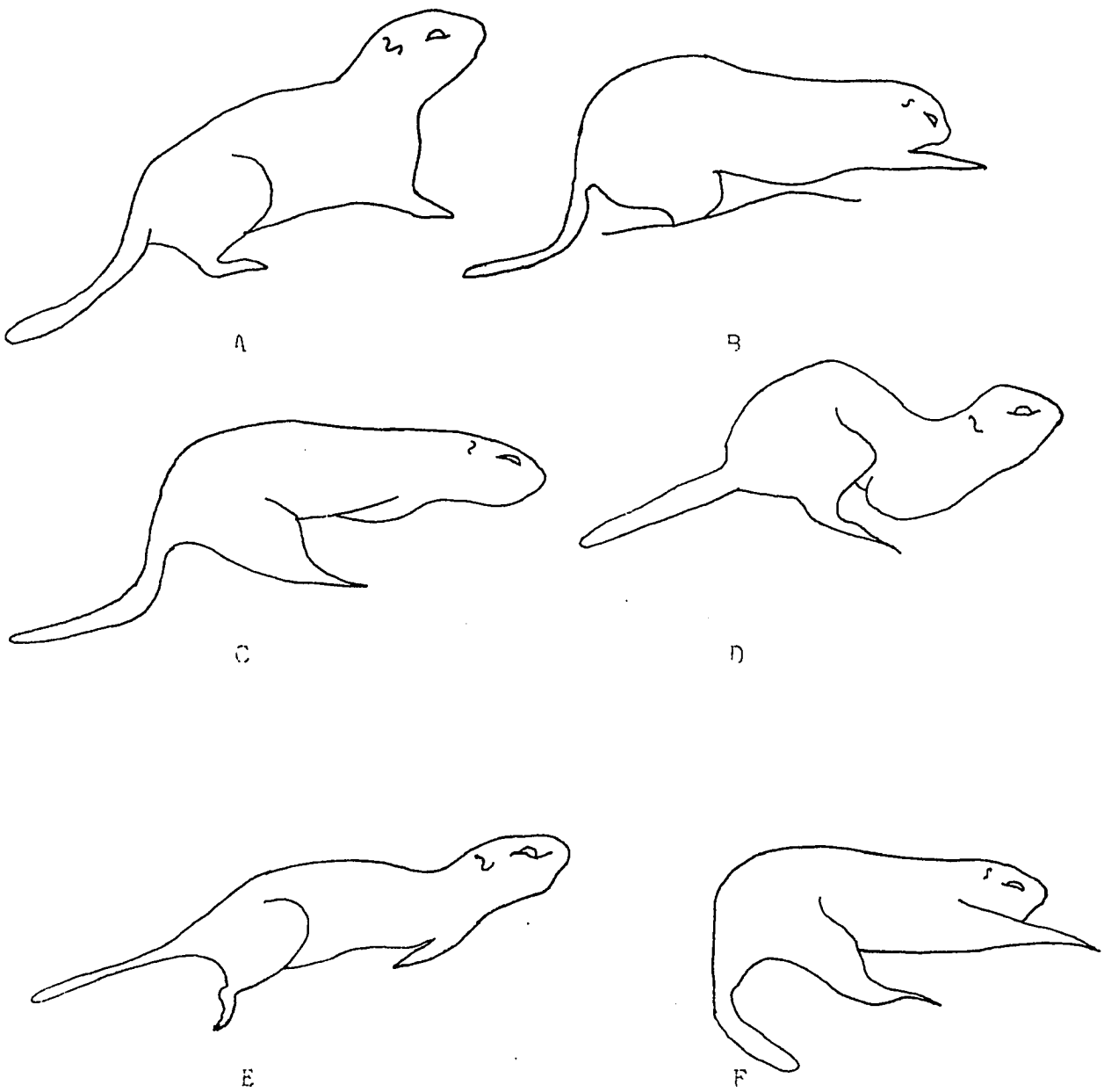


Figure 8

Tail Flicking

The habit of tail flicking is the basis for the common name flickertail. Tail flicking is demonstrated in all types of squirrels: males, females, and even young squirrels their first day out of the burrow. Flickertails precede most movement with tail flicking. Flickertails move their tails both horizontally and vertically. Critical examination of motion pictures indicates that the tail is raised up, then brought approximately half way down, brought back up in a circular motion and then placed back down on the ground.

The tail is significant in copulation, mutual grooming and in self grooming. When the squirrels are in an agonistic situation, it is common for the tail to be in a bottle brush configuration, the hairs of the tail erected resembling a bottle brush.

Nest Building

Nest material is gathered above the ground and taken down into the burrow systems. Grass, rushes, and corn stalks are the main items used by the Mapleton squirrels in making their nests. The larger material is cut with the incisors in long, narrow strips. These strips are then placed sideways in the mouth as far back as the lips will permit. Then the squirrel folds the strips over and over by running the front paws along the side of the head. This is repeated until a compact bundle of strips is contained within the

mouth behind the incisors. The squirrel will then run to the burrow entrance, usually stop for several seconds, and then disappear into the burrow. The excavated nest was made entirely of Smooth Brome. It was a loosely woven structure approximately 6 inches long, 4 inches wide and 2 inches deep.

Grooming

The squirrels groom frequently. Grooming consists of biting, clawing, and rubbing of the fur. The act systems of grooming are quite uniform, but the sequence in which they are combined is variable. Squirrels will groom themselves and others. Self grooming is the most common, however; a female grooming her offspring or vice versa is frequent. A female grooming another female or a male is rare, but both were observed.

Self grooming includes both dusting and manipulations of the fur by teeth and paws. Most squirrels will dust on the type 1 burrow mounds. The nose is pushed under loose dirt, which has been dug with the forelimbs, and the ventral surface of the body is dragged over this soft dirt. Sometimes the squirrels will roll over on their backs and rub in loose dirt. Grooming with the teeth and paws usually occurs near the home burrow, but can be observed almost anywhere in the home range of the animal. Self grooming frequently follows a flight; sometimes it may occur during a pause in the middle of a flight, for example: chase, fight, groom, flight, chase. This represents a form of displacement

behavior. They groom their back by pulling the skin with their forepaws and biting through the hair with the incisors. They groom the ventral surface by using both paws and teeth. Grooming on the sides of the body from behind the ear posteriorly to just in front of the hind legs is accomplished by scratching with the hind foot. The sides of the hind legs are groomed with the teeth and forelimbs; the squirrel either bending around sideways to the posterior or rolling into a ball.

The area just posterior to the ear is of unusual interest in grooming, for most of the grooming of one squirrel by another is concerned with this area. Squirrels will also rub this area on the ground around their burrows. During 1965, female #6 made rounds of the burrows of other squirrels and rubbed her posterior ear area on the edges of their burrows. These areas seem to be unusually strong in odor and perhaps contribute to some sort of chemical communication.

Elimination

There are no observed special postures for elimination. The squirrels apparently carry on other activities while eliminating. Occasionally feces were observed along the boundaries of the home ranges of a squirrel. This condition is rare, but did occur.

Flickertails must defecate a great deal in their burrow systems. During certain times of the year (June 29 and 30, 1965, were noted particularly), great quantities

(calculated to be more than 5 gallons) of fecal material are brought up from the burrows.

When captured in a trap or handled, flickertails will defecate copiously. The fecal material forms a soft, dark green pellet.

Sexual Behavior

Copulation was observed three times, once in the Animal Behavior Laboratory on October 29, 1965, and twice in the field on April 5, 1967. Following is a description of one copulation observed in the field.

Running has a significance in the approach of the males to the females just before copulation. Males approach the females with a modified run (Figure 10). It begins identically to the normal run, but then the male pushes harder and in a more upward position to create a high leap with the head directed upward. This is very conspicuous in the running of the male squirrels during the mating season. This modification of running is not observed in females and infrequently in males during the non-breeding season.

It seems to me that the precopulatory run reduced the aggressive level of the female to allow the male to approach the female for copulation. Females will usually chase out any male in the colony.

At close range the male approaches the female almost perpendicularly, with his head about at the area of the female's ear (Figure 11A). The male stops momentarily at this

SEQUENCE OF POSITIONS
ASSUMED IN THE PRE-COPULATORY RUN OF THE MALE

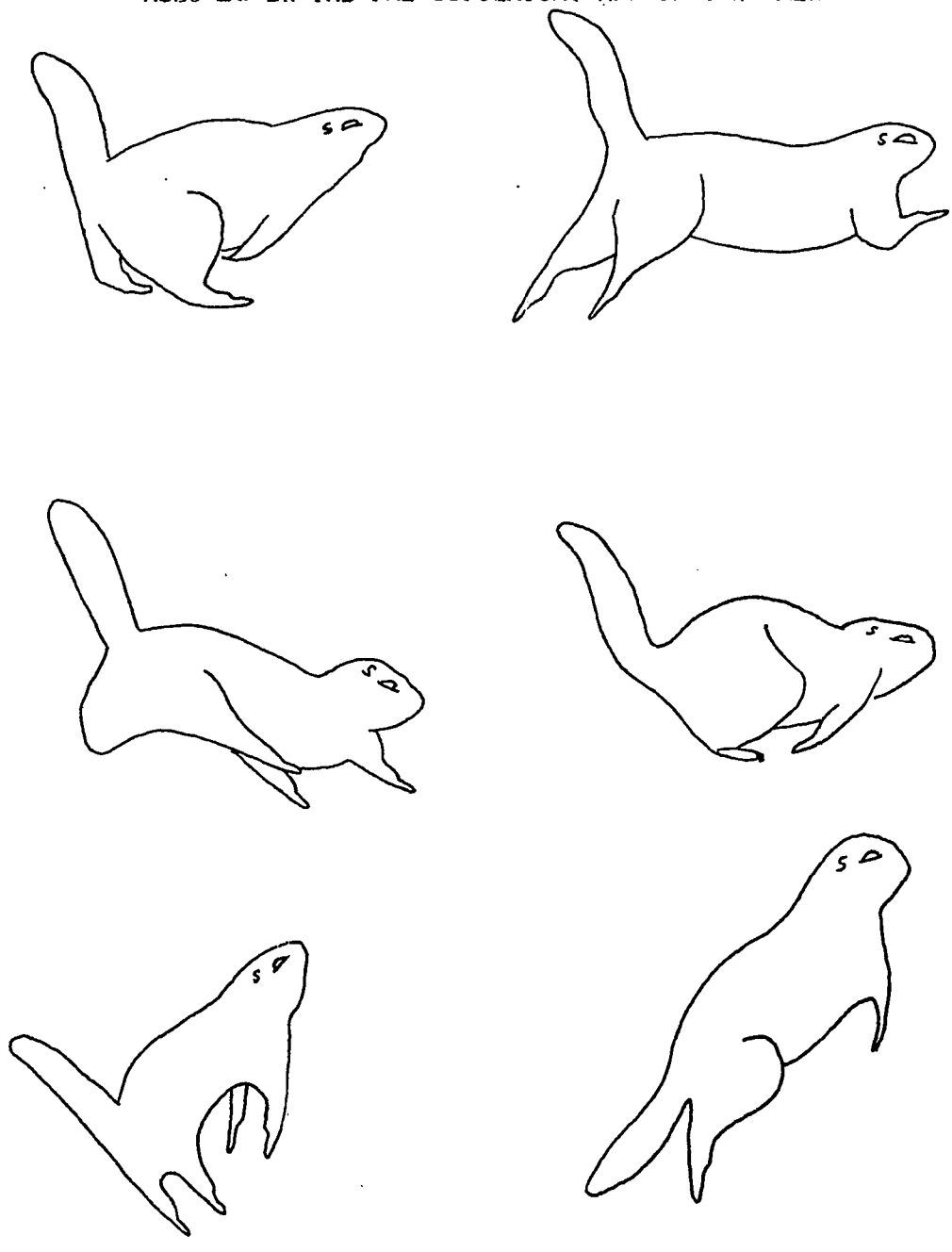


FIGURE 10

point being at about a 70 degree angle to the female (Figure 11B). The male then approaches closer with his body lateral to that of the female and his head opposite the female's posterior. Both squirrels stop a few seconds in this position (Figure 11C). The backs of both the male and female are arched; the belly of each is off the ground, while the tails remain on the ground. Then both animals place the entire ventral side of their bodies on the ground and the female begins to groom the posterior dorsal regions of the male (Figure 11D). The female continues grooming the male moving anteriorly until she is in the region of the ear (Figure 11E). The two animals then lie sideways on the ground with the same orientation, anterior to posterior. The female then begins to stretch; both tails are flat on the ground. The female begins to groom the tail of the male and both crawl forward (Figure 11F). Since they are not facing each other, this results in separation. The female flattens on the ground and moves 2 or 3 meters from the male (Figure 11G). The female then turns and approaches the male. The male jumps on the anterior of the female. The male places the tail, which is now in the bottle brush configuration, over the back of the female (Figure 11H). Both squirrels then lie side to side, but this time they have a head to head orientation. The male and the female then begin to box each other with the front feet. The female then backs up a step and the male pushes. The male then places his

SEQUENCE OF POSITIONS ASSUMED BEFORE AND DURING COPULATION

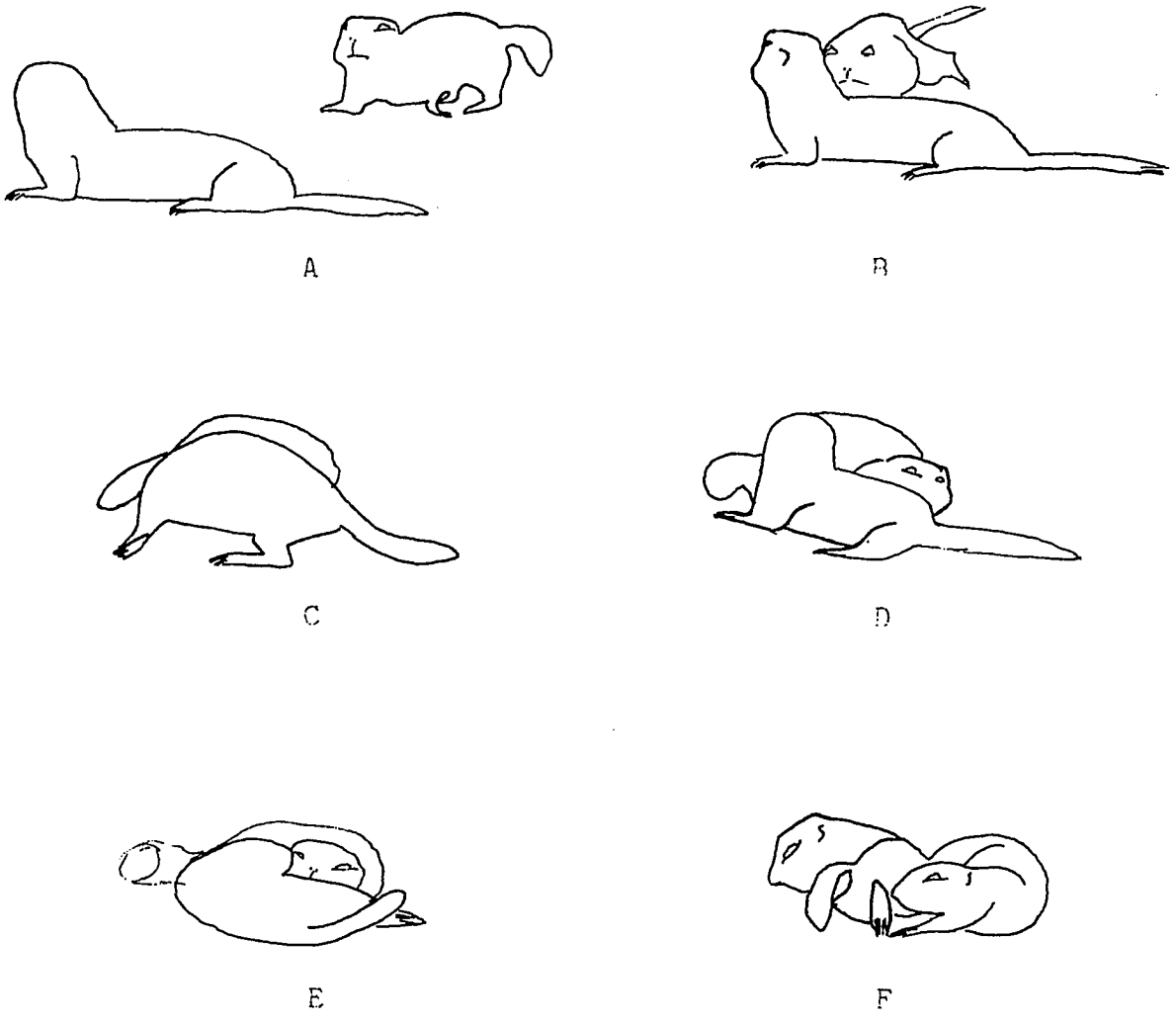
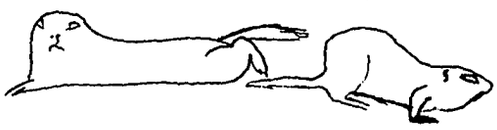


Figure 11

SEQUENCE OF POSITIONS ASSUMED BEFORE AND DURING COPULATION



G

H

I

J

K

Figure 11

head under the head of the female. The male next removes his tail from over the female, rolls over on his back and gives the identification kiss (Figure 11I). The squirrels then separate briefly (Figure 11J). The female then moves off some distance and they approach each other again. This time the tails are bottlebrushed and the squirrels lie down close together in a head to head orientation, and copulation takes place (Figure K). The male leaves quickly after copulation. The copulatory acts observed took about 20 seconds.

Parturition

One female Richardson's ground squirrel was observed giving birth on April 24, 1966, at 10:20 P.M. at the Animal Behavior Laboratory. When first observed two young had already been born; one was lying near the female, while the other was being handled by her. The third squirrel came from the vagina posterior end first; young squirrel and vulva were bloody. The female picked up the third and began to lick it vigorously, then licked her vulva. The fourth young squirrel emerged; the female licked it and then herself. The female rested, licking at the cords and vulva, getting some blood on her nose. The young squirrels, after being licked by the female, became quite vigorous in their movements. Three umbilical cords remained attached to the female. The female then began to pull cotton up under herself and the young squirrels, then she licked them and herself again. The female scratched her nose with the hind paw. The female then

licked the young squirrels and seemed to chew something; then she lifted the umbilical cords with her teeth. The activity of the young varied considerably: some squirmed, others were limp and sluggish. The fifth young was then born after about 3 contractions of the trunk region. The female licked vigorously, then she turned the young animals over and over with her front paws. She again licked herself and the cords. The female strained again twice and the sixth young was born head first. The female grasped the newly born squirrel and pulled it away from her vagina. Seven more contractions of the body occurred and she resumed licking of the young squirrels. Five more body contractions. The female licked her paws. There were two more muscular strains of the abdomen and the seventh young squirrel was born posterior first. The actual birth of this squirrel took about 2 seconds, and occurred about 3 minutes after the first body contractions before this birth. The female rested with nose on the floor of the cage, and breathed heavily. The female kept her paws pressed to her chest and licked herself energetically. The young squirrels wiggled and moved away from the adult. She strained once more, then two more vigorous strains and a bit of blood appeared at the vulva. She resumed vigorous licking after straining six more times. Female rested; strained twice and the eighth young was born head first in two seconds. The female licked the newest squirrel. The afterbirth then appeared and the

female began to eat it. She resumed licking herself. The body then contracted strongly and the posterior of a young squirrel appeared. The female began to lick this emerging squirrel before the anterior was out of the vagina. This squirrel, number nine, required one minute 55 seconds to emerge completely.

The female worked with the umbilical cords and cut them with her teeth. The young squirrels were cold to the touch. The young were able to raise their heads and forelimbs at birth. The female rested with nose on cage floor. The female then began to retrieve the young squirrels which were crawling away. She grasped them around the neck with her mouth and placed them in a nest of cotton nearby. The young squirrels squeaked softly.

The size and weight of the young squirrels just after birth is given in Table 10. The young squirrels were born naked, without any visible hair. This observation does not agree with that of Brown and Roy (1943). The eye appeared as a dark area under the skin. The gestation of Richardson's ground squirrel is given as 18 days by Denniston (1957).

Social Structure

The Mapleton colony consisted of only adult females and offspring during 1965 and 1966. The males were located from 50 to 500 meters from the edge of the colony. The colonies at Hunter and Blanchard showed a strong tendency to

TABLE 10.--Size and weight of Richardson's ground squirrels shortly after birth
April 24, 1966

NUMBER	WEIGHT (grams)	TOTAL (mm.)	TAIL (mm.)	HINDFOOT (mm.)
1	5.3	60	8.0	7.5
2	6.0	59	8.5	7.5
3	6.7	61	8.5	7.5
4	6.0	58	8.5	7.0
5	5.8	60	8.5	8.0
6	5.8	60	8.5	8.0
7	6.3	62	9.0	8.0
8	5.2	58	9.0	7.5
9	5.6	58	9.0	7.0

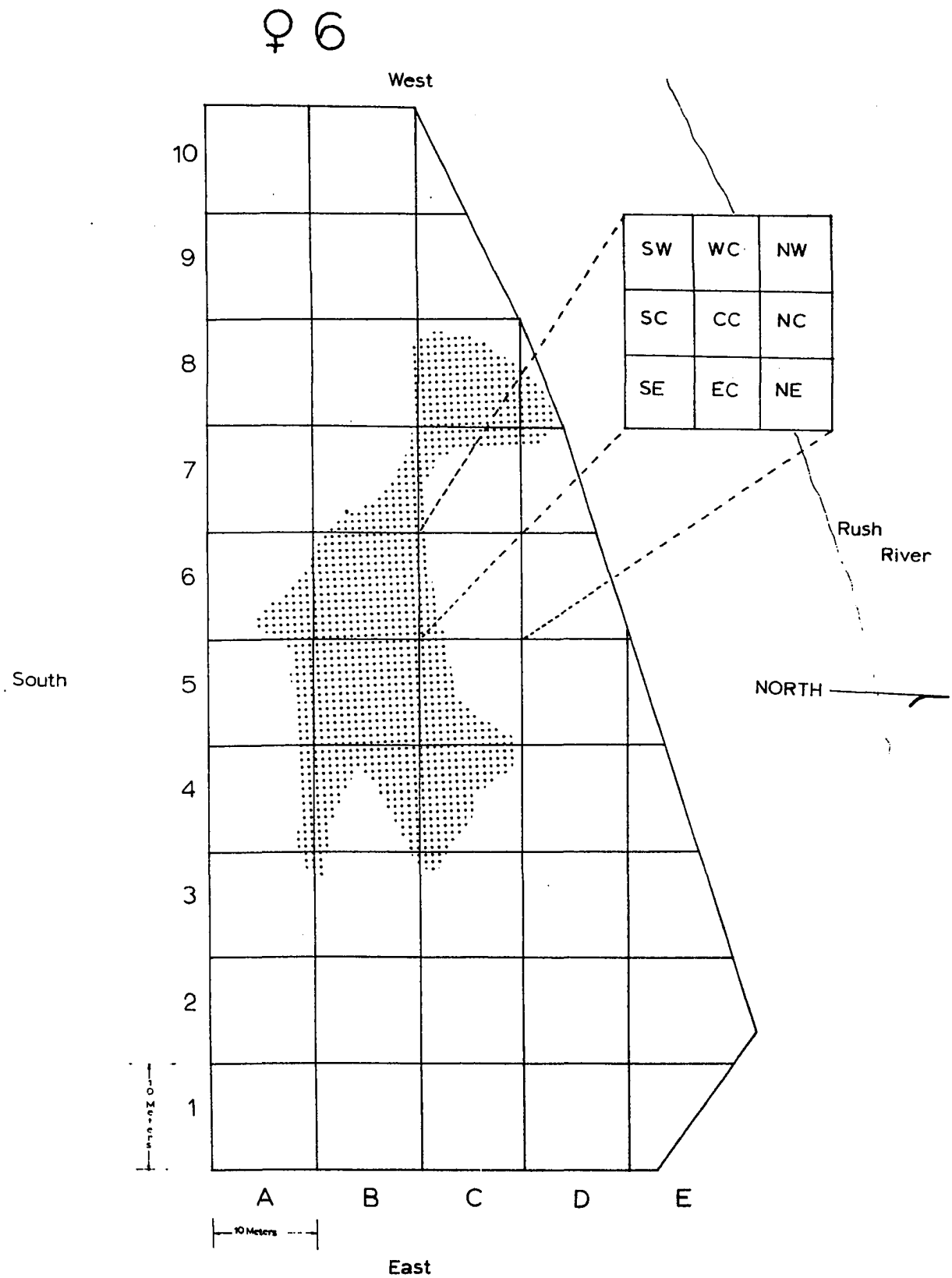
consist exclusively of females, with the males around the periphery of the colony. In 1967, however, two males were captured in the Mapleton colony. These males stayed in the colony during that summer. There were 13 adult females in 1965, 9 in 1966, and 13 in 1967.

Each year there was a female which was considered dominant because of her ability to win agonistic encounters. This squirrel was in the colony only one year in each case. The dominants during the study were female 6 in 1965, female 15 in 1966, and female 12 in 1967. Females 6 and 15 were not in the colony following the year of their dominance. The dominant females occupied a central position in the colony (Figures 12 and 13).

Most other squirrels were subordinate to these adult females, and would lose most agonistic encounters with the dominant. Many of the encounters between two subordinates would end in a stalemate, neither squirrel chasing the other from a particular area.

Home Range and Territoriality

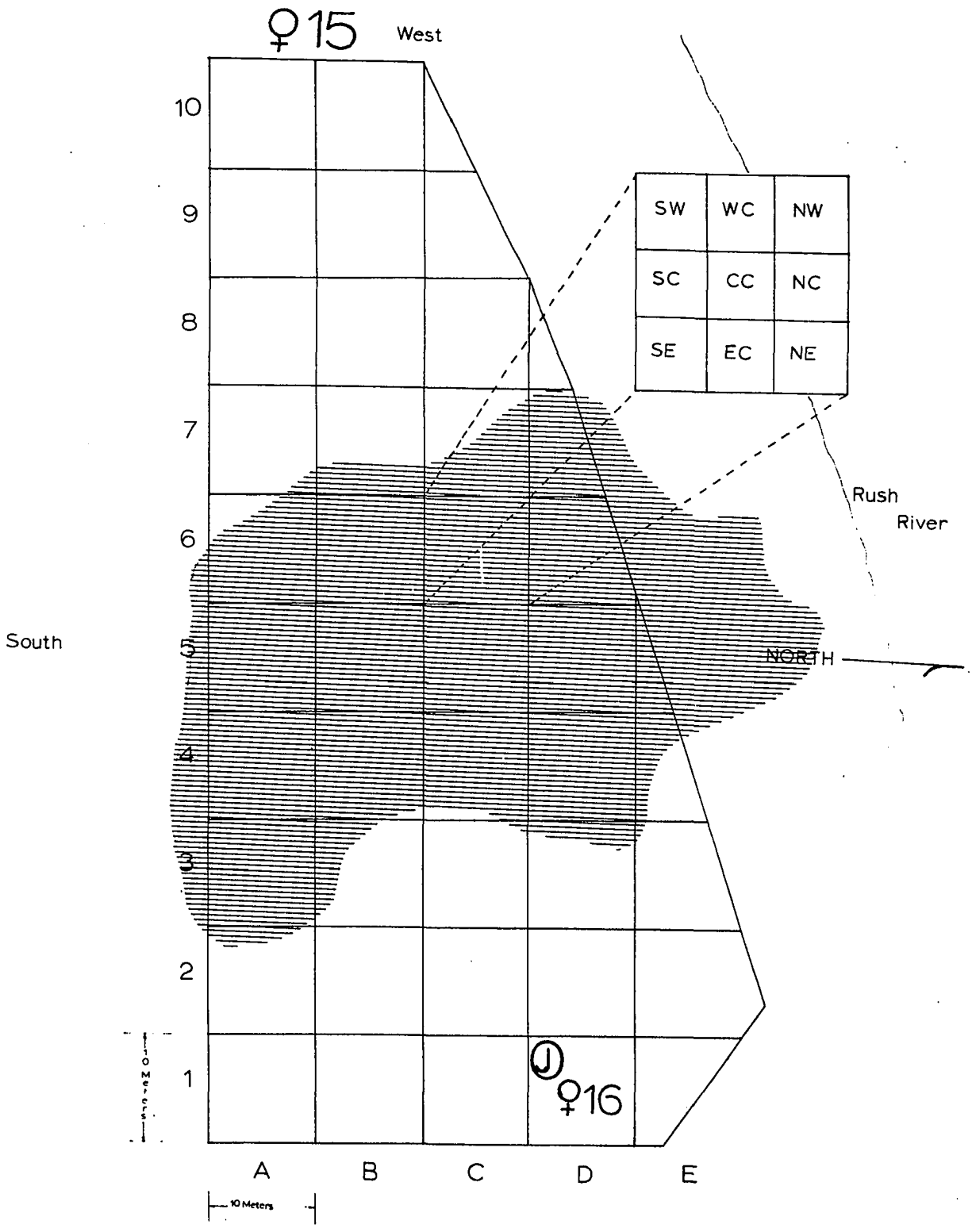
The home range of Richardson's ground squirrels varies in space and time. The squirrels are not spaced at random, but rather are associated with particular locations in the colony, and with particular groups of squirrels. Large variations in the area used by a particular individual can be shown from one year to the next (Figures 14, 15, 16, 17, 18 and 19). Adult females during the first week of June



HOME RANGE OF DOMINANT FEMALE, 1965

Layout Of Study Area

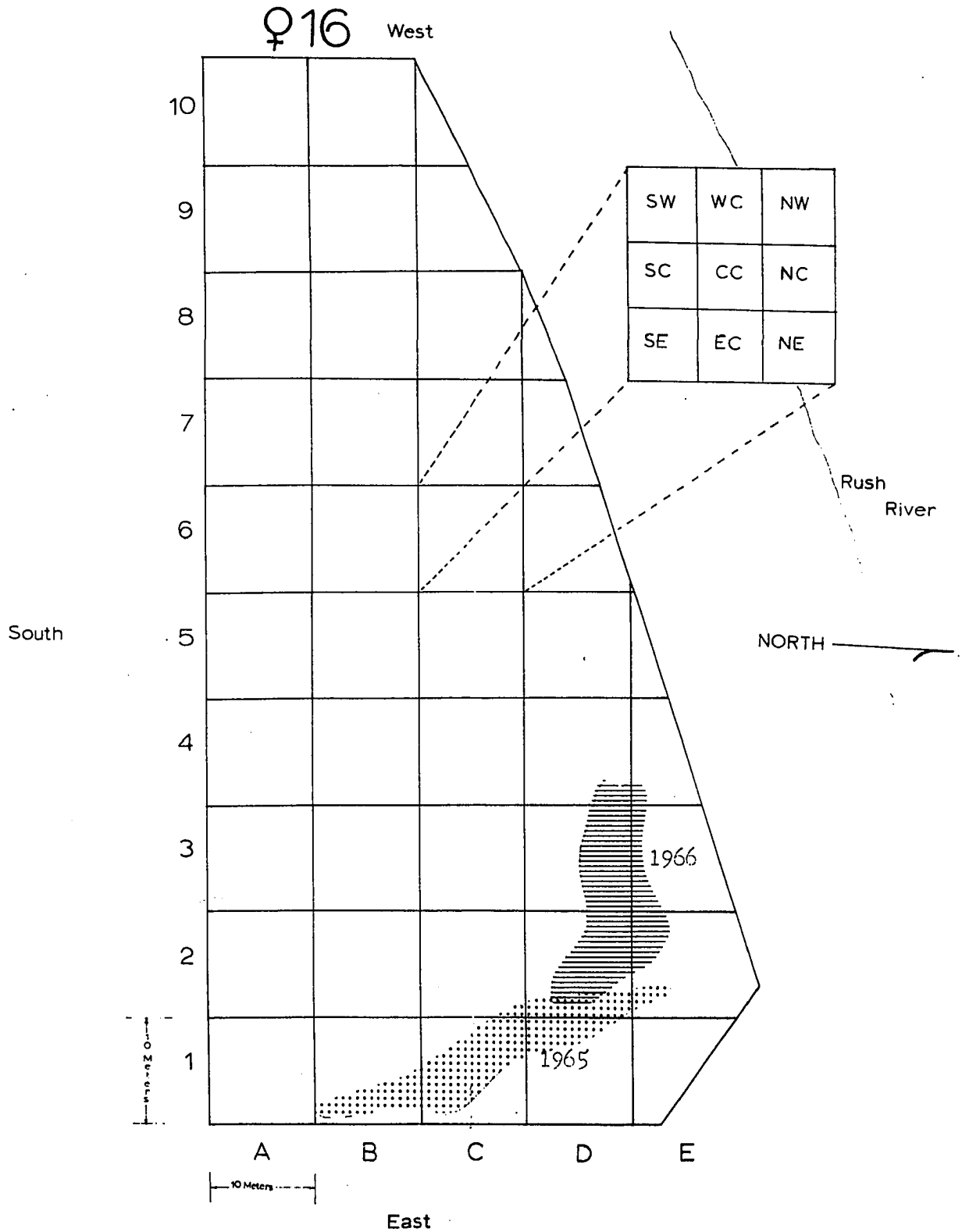
Figure 12



HOME RANGE OF DOMINANT FEMALE, 1966

Layout Of Study Area

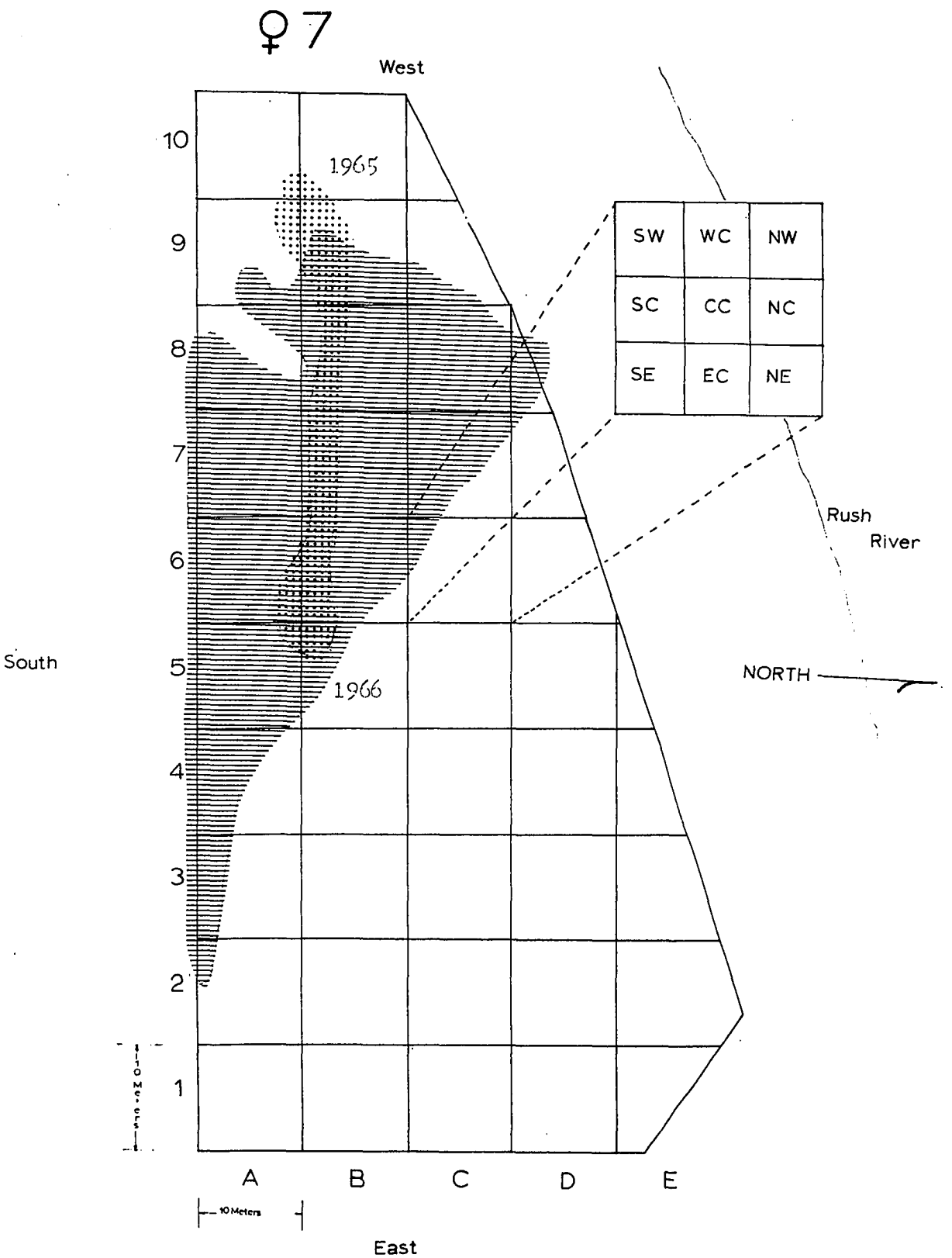
Figure 13



HOME RANGE OF FEMALE 16 DURING 1965 and 1966

Layout Of Study Area

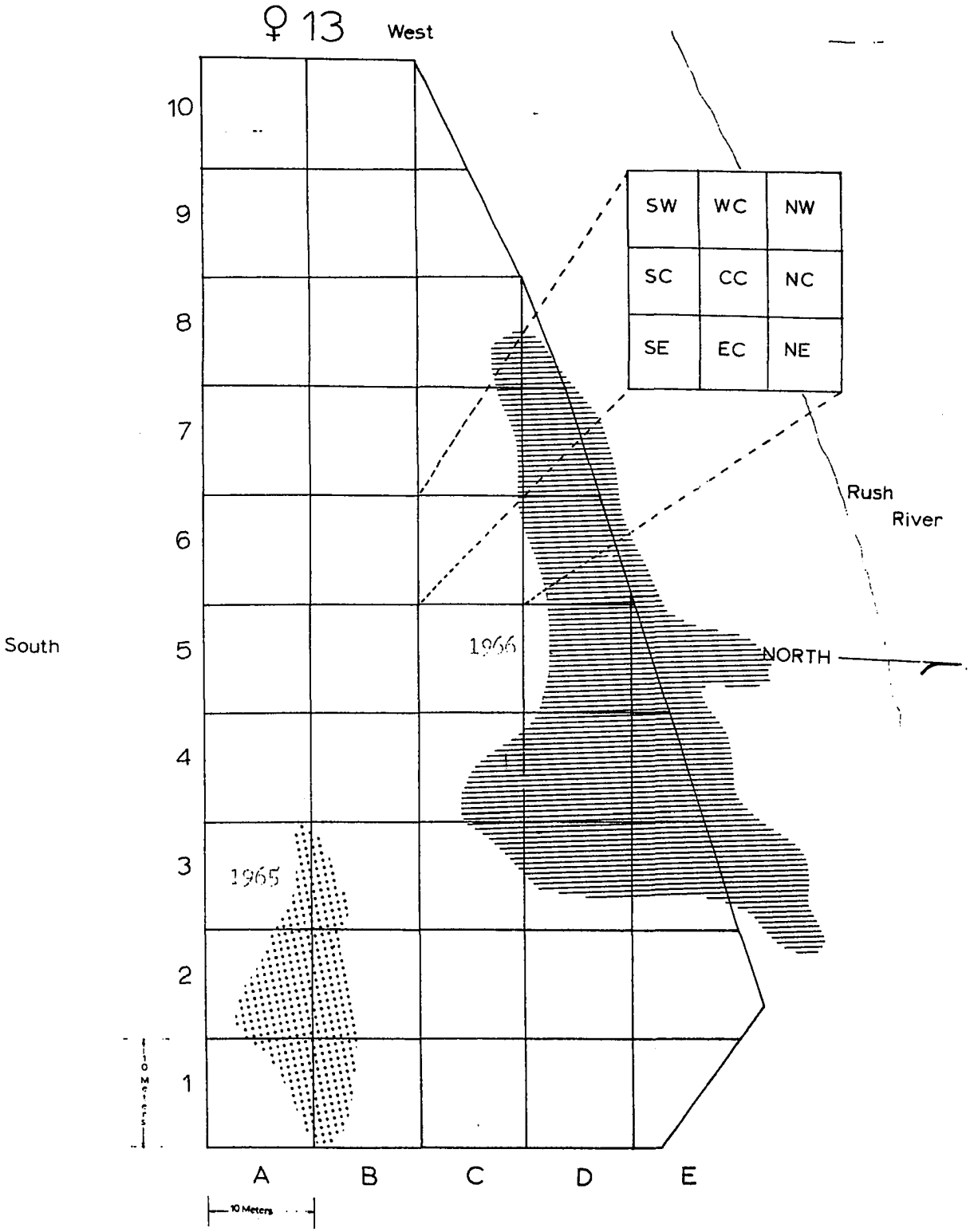
Figure 14



HOME RANGE OF FEMALE 7 DURING 1965 AND 1966

Layout Of Study Area

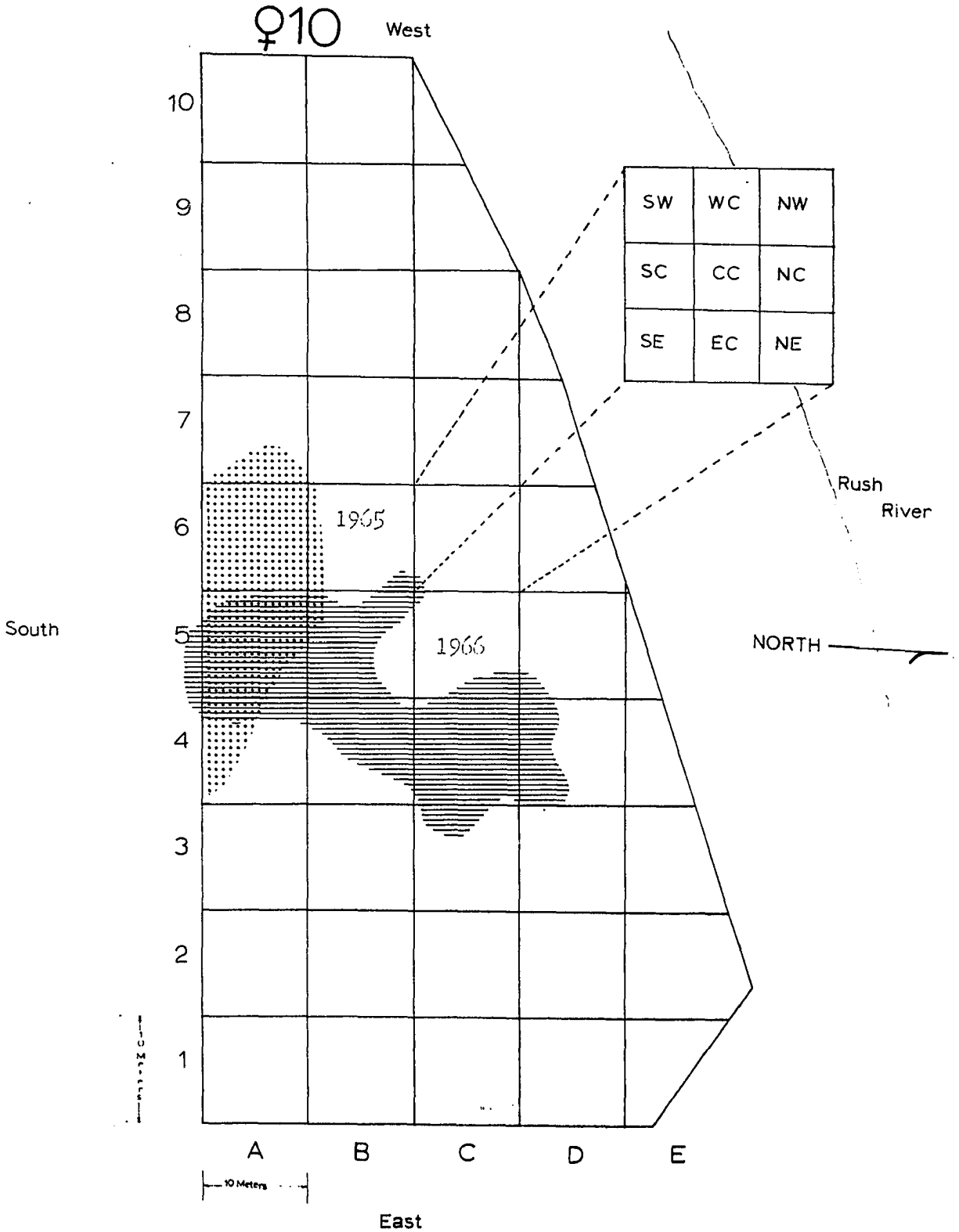
Figure 15



HOME RANGE OF FEMALE 13 DURING 1965 AND 1966

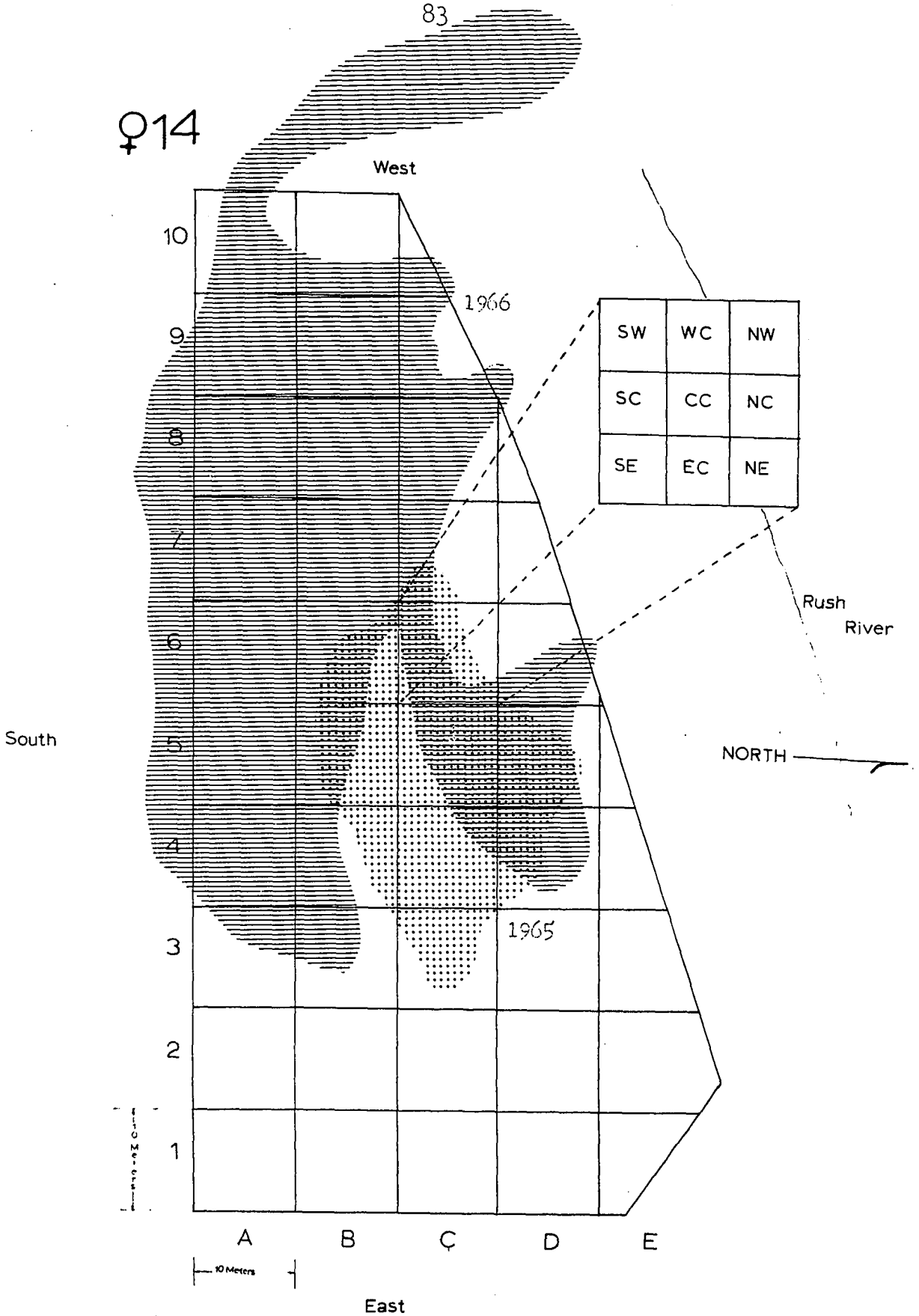
Layout Of Study Area

Figure 16



HOME RANGE OF FEMALE 10 DURING 1965 AND 1966

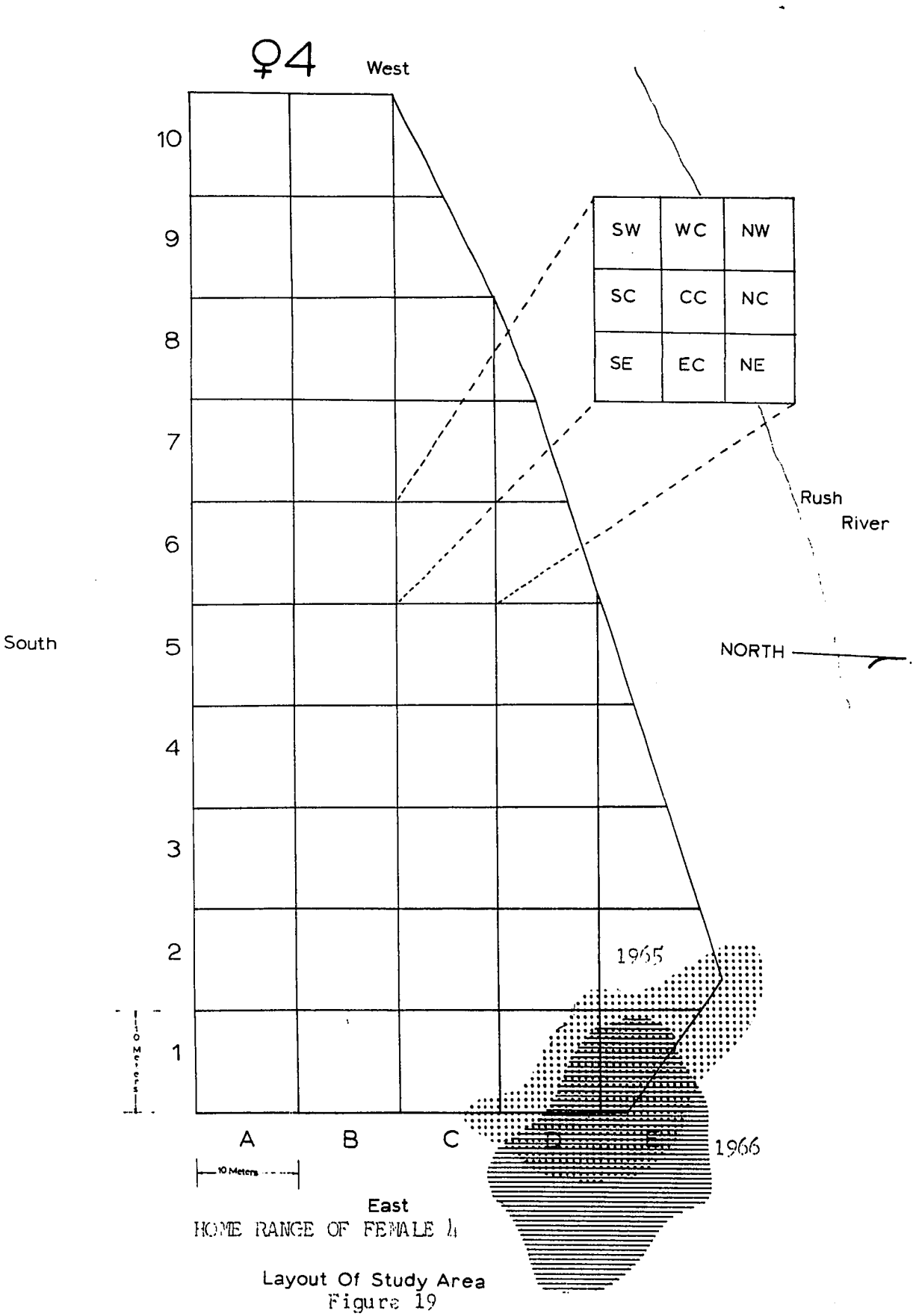
Layout Of Study Area
Figure 17



HOME RANGE OF FEMALE 14 DURING 1965 AND 1966

Layout Of Study Area

Figure 18



HOME RANGE OF FEMALE 4

Layout Of Study Area
Figure 19

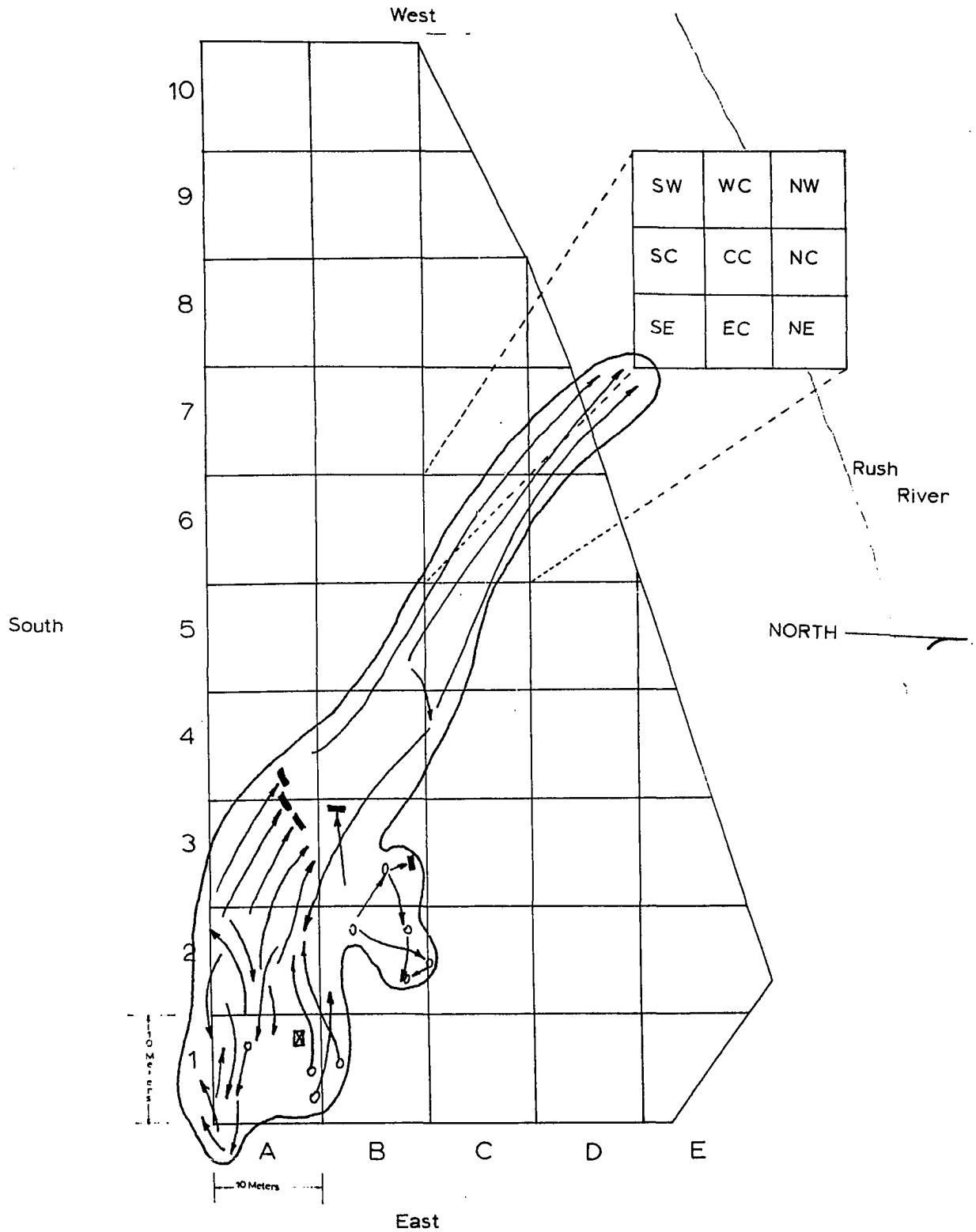
are presumably under pressure to obtain enough food to supply the milk needs of the litter. The young squirrels at this time weigh approximately 80 to 100 grams, and there may be as many as 11 per litter. Females at this time usually weigh 300 to 400 grams. The litter sizes of females in 1965 are given in Table 11.

This lactation pressure on the female apparently affects various aspects of her behavior. The need for almost continual feeding and nursing reduces the home range and territory. Agonistic behavior between females diminishes because of a lack of contact. Since food is usually abundant, it is not normally necessary for a female to travel far from her home burrow to obtain nourishment. Except during hibernation, the home range is at a minimum during this early part of the summer.

The territory, the defended area, in all cases is smaller than the home range of the female and represents a portion of the home range around the home burrow. It is usually approximately half the home range in the subordinate females. Figure 20 shows the home range of subordinate female 11 during 1965. This female defended the area around her burrow, up to the bars (appearing as dark lines perpendicular to the arrows in Figure 20), but moved a considerable distance beyond the territory, indicated by the arrows which do not lead to bars. The home range and territory of dominant female 6, 1965, is shown in Figure 21. The

TABLE 11.--Number of young Richardson's ground squirrels observed above ground for each female in 1965

FEMALE	YOUNG
1	6
2	0
3	11
4	11
6	9
7	0
10	9
11	11
12	9
13	8
14	6
16	11



HOME RANGE AND TERRITORY OF FEMALE 11, 1965

Layout Of Study Area

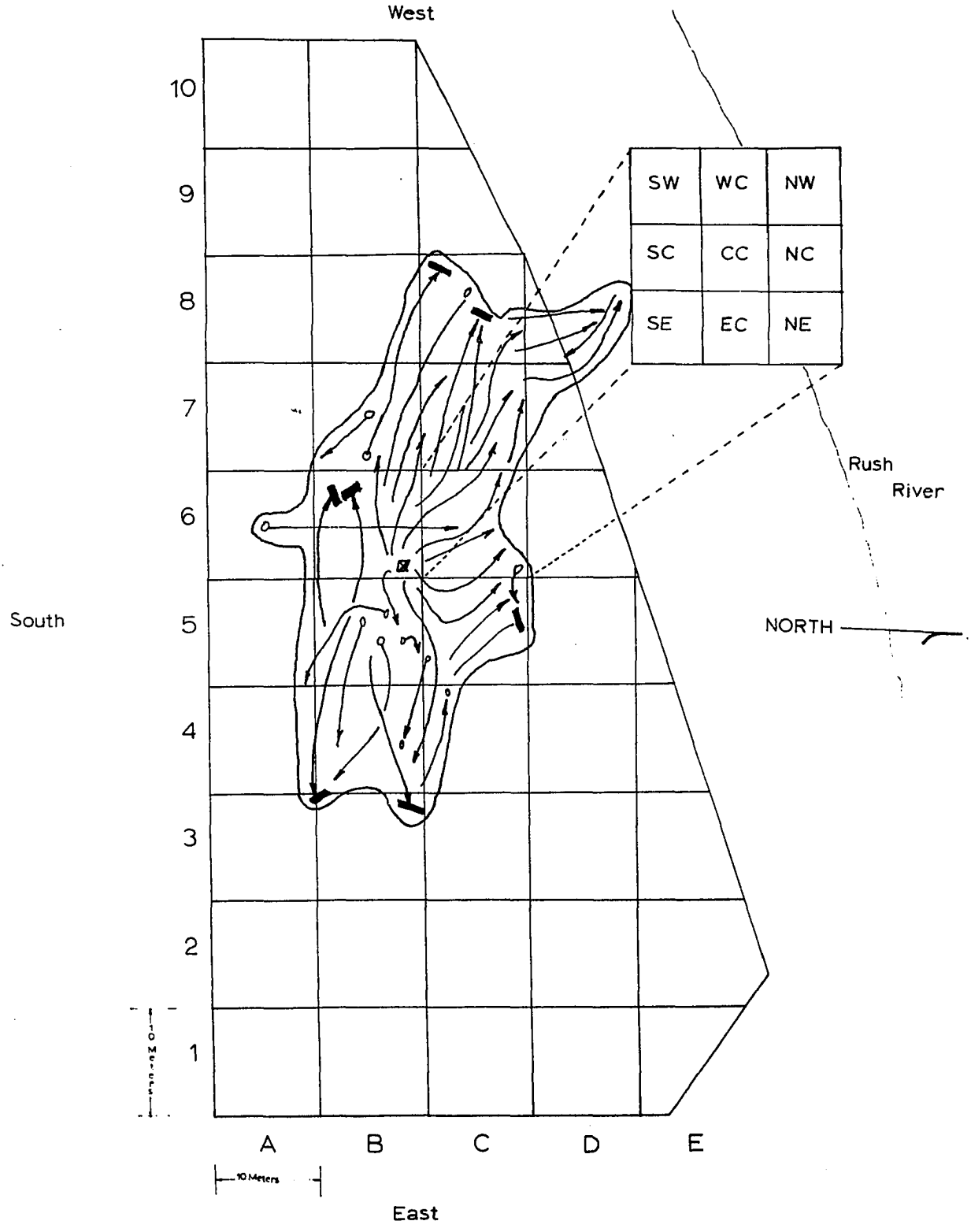
Figure 20

defended territory, the area within the bars, is almost as large as the home range. During all three years, the dominant female did not stop at the territory of the other squirrels. She would frequently go directly to the home burrow of a subordinate female and rub the nape of her neck, just behind the ear, on the edge of the subordinate's burrow. It is rare to observe a subordinate female trespassing on the territory of another, but this sometimes occurs.

No grid pattern was made to observe the home ranges of males, but observations indicate males have much larger home ranges than females, at least 50,000 square meters.

The home range of the females varied from 95 to 2,259 square meters. There seemed to be a tendency for the squirrels to have their home ranges as near the center of the colony as possible (Figure 22). The central position of the dominant female was present all three years. The dominant female in 1965 (#6) had the second largest home range and the dominant in 1966 (#15) had the largest home range of any squirrel. This is in part due to a function of the dominant role played by this squirrel and to the freedom of the dominant to enter the territory of another squirrel (Figures 12 and 13).

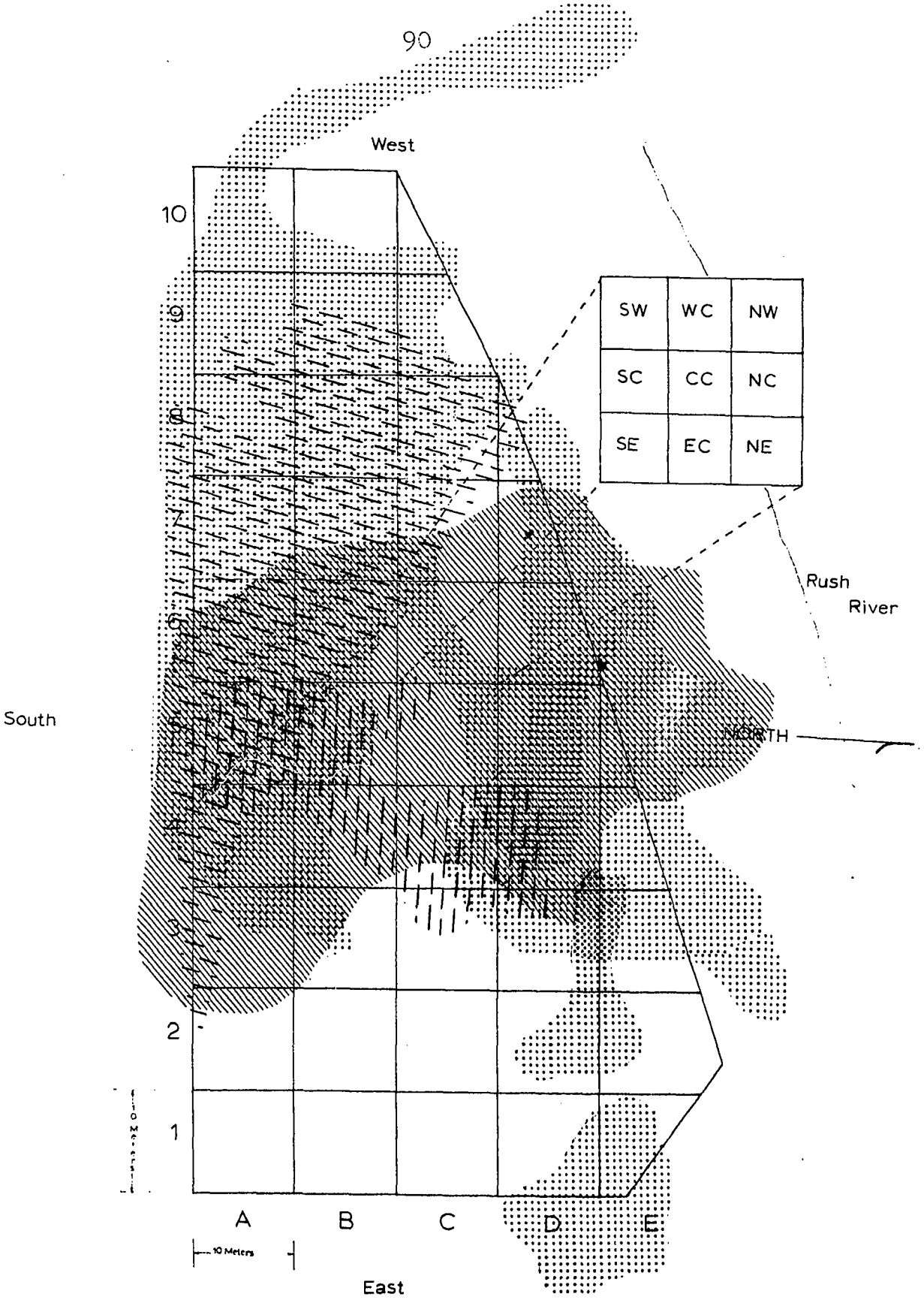
The home ranges also changed for an individual between 1965 and 1966. Seven females were present two years. Five of these increased and two decreased their home ranges.



HOME RANGE AND TERRITORY OF FEMALE C, 1965

Layout Of Study Area

Figure 21



HOME RANGES OF ALL FEMALES, 1965
Layout Of Study Area

Figure 22

The increase varied from 11.3 per cent to 91.12 per cent. The decreases were 62.66 per cent and 72.03 per cent. There were ten females during 1965, and only 8 females during 1966. The average home range during 1965 was 339.8 square meters, and the average during 1966 was 770.62 square meters. The average home range dropped as the population density increased (Table 12).

In other areas of eastern North Dakota some observations were made to detect differences from the overgrazed pasture environment. In areas having more open spaces, my observations indicate that the home ranges are larger than those in the colony studied.

Agonistic Behavior

Agonistic behavior can be observed between any two or more squirrels. Occasionally four or five individuals will be involved in a single agonistic interaction. Usually, however, only two squirrels participate in any single interaction.

The agonistic encounters of flickertails are made up of rather uniform act systems, which may be sequenced in a variety of ways. The most common encounter would be for one squirrel to chase another (Figure 23), followed by the squirrels' stopping in various positions (Figure 24). Then the squirrels will face off, line up in an anterior to posterior orientation with their backs arched (Figure 25A). One squirrel may then roll over, lying on its back (Figure 25B).

TABLE 12.--Home ranges of Richardson's ground squirrels (square meters)

NUMBER OF FEMALE	1965	1966
1	975	270
2	175	
3	350	625
4	310	340
6	560	
7	95	1,070
10	215	385
11	375	140
12	200	
14	143	745
15		2,590
Average	339.8	770.62

SEQUENCE OF POSITIONS ASSUMED WHILE CHASING

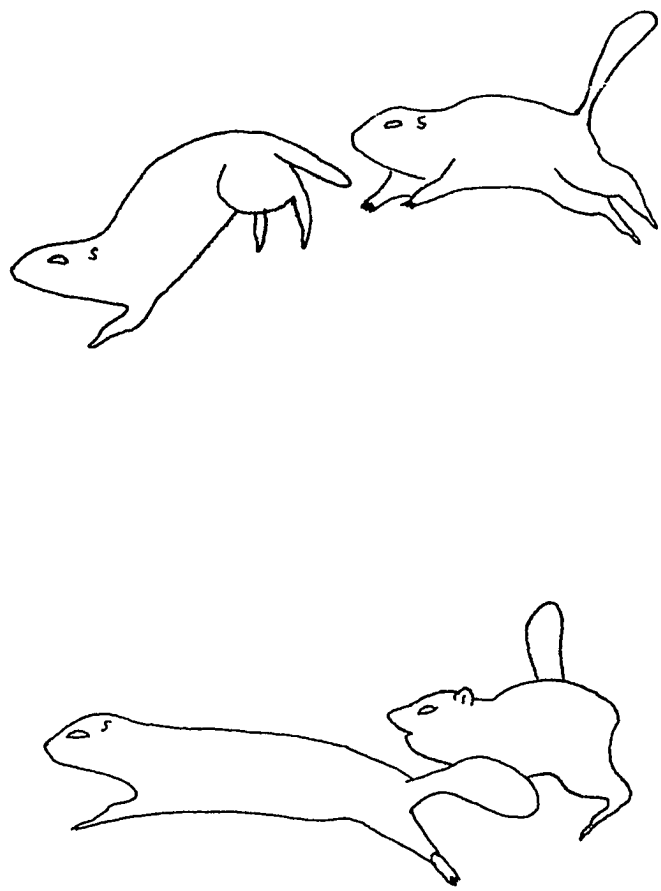
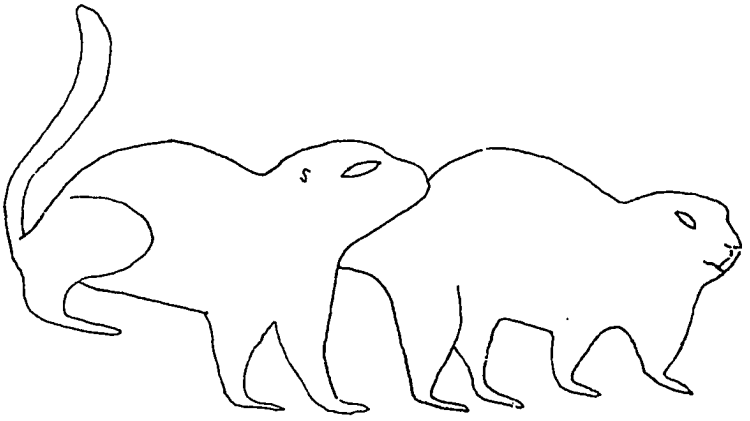


Figure 23

POSTURES ASSUMED AFTER CHASE



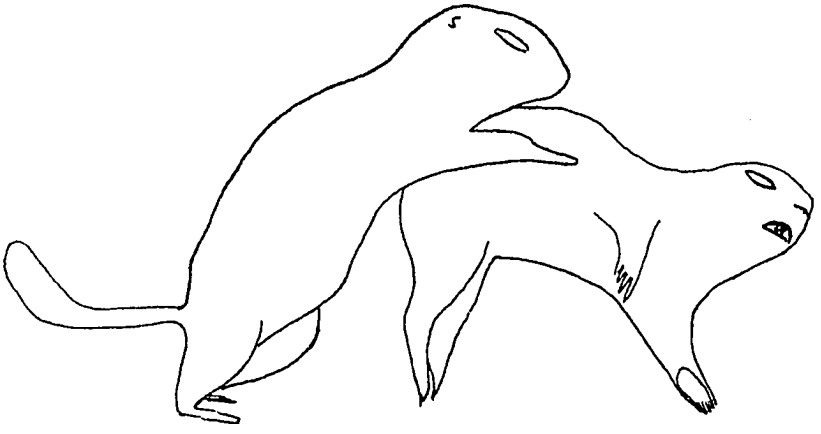
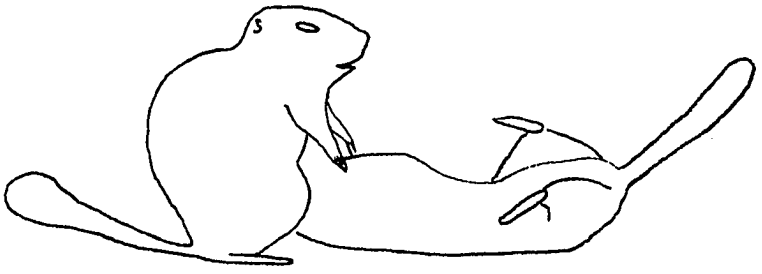


Figure 24

FACE OFF

A

SUBMISSION-AGGRESSION POSTURE



B

Figure 25

This behavior stops the aggressions of the aggressor animal, who usually runs away. When the two aggressive squirrels are close together, the feet may be used to "box" the other animal (Figure 26A).

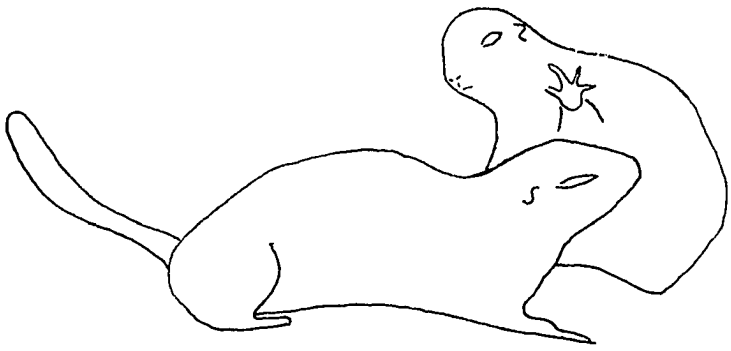
The face off may be held for several seconds, with the animals either remaining in one spot or circling. They circle in the direction in which they are facing. Many variations of this basic plan are observed. The addition of a third animal (Figure 26B), and a series of chases with more than one face off interspersed, are common.

Young of the year squirrels begin to demonstrate various components of the agonistic display from the first day they emerge from their burrow systems. This is correctly termed play. The young flickertails are very uncoordinated, and are unable to carry out certain parts of the agonistic display properly. However, as the animals grow they increasingly show the adult agonistic pattern.

Food, Water, and Associated Behavior

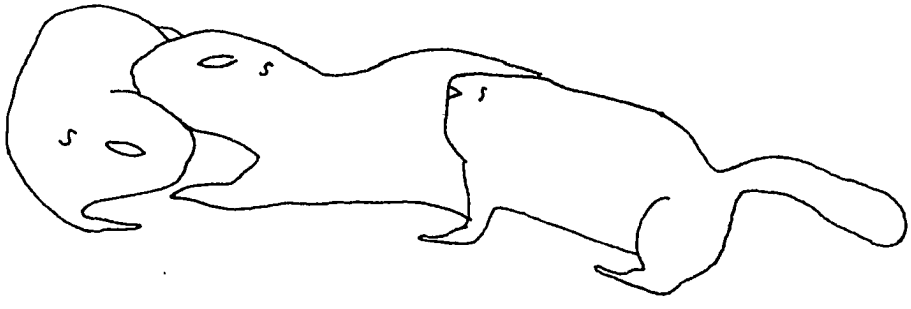
Feeding is the most frequent activity. Squirrels usually feed in the morning and in the late afternoon, but may feed for short periods at any time. The lactating adult females will feed almost constantly, when above ground during late April, except when nursing the young. Feeding is usually sporadic or discontinued when it is excessively cloudy, windy, or rainy. Lactating females, however, were observed feeding during a rather heavy rainfall.

"BOXING"



A

THREE SQUIRREL INTERACTION



B

Figure 26

The food is either taken into the mouth directly or put into the mouth with the forelimbs. The heads of grasses are eaten directly by clipping the floret off with the incisors and then pulled into the mouth with the teeth and tongue. Flickertails are able to feed on long objects such as a blade of grass without touching the blade with their forelimbs. The blade is cut off with the incisors, and then through actions of the tongue and teeth the blade can be drawn into the mouth without any additional aid. Rhizomes and roots are dug up with the forelimbs and eaten directly with or without aid of the paws. Feeding occurs in all postures except the high intensity alert.

It can not be assumed that ground squirrels will eat all plants present in the area in which they live. Observations indicate that the flickertails are very selective in the plants they eat.

Bromus inermis Smooth Brome is a very common grass in the eastern part of North Dakota. It is found as the main pasture grass in the three eastern study areas, Mapleton, Hunter, and Blanchard. Smooth brome is the main item of food of the squirrels observed in these areas. The leaves and stems are eaten during April and May, and the glumes, lemmas, and other floral parts are consumed during the time between mid-June and mid-July. When this grass flowers its floral parts are sought after by the flickertails. They are commonly observed during this time of the year standing

in the middle high intensity position and reaching out with their forelimbs in order to bring the florets to the mouth. Sometimes a squirrel stretches too far to reach other heads, and occasionally will lose its balance and fall over. After the brome grass has grown higher, the floral parts are above the squirrels' reach, even when high on their hind feet. They then move the forelimbs "hand over hand" until they bend the stem far enough so they can grasp the spiklets with their paws and proceed to eat.

It is interesting to note, especially in light of the fact that this grass is the main food item during most of the year, that this is an introduced grass, first planted around 1890 (Stevens, 1963). Therefore the major portion of the summertime diet of flickertails before this time could not have been Bromus inermis but would have had to have been some other plant or plants.

Glyceria grandis Tall Mannagrass is found in shallow water or in very wet places. Observations do not indicate this grass to be used as food by the squirrels. It is a rather "woody" grass and the microhabitat in which it grows is generally avoided by the squirrels.

Poa pratensis Kentucky Bluegrass, commonly known as Junegrass, is a very abundant grass in all areas. Like Bromus inermis it matures in mid-June. The florets and leaves are both used as food. During the second week in June the heads begin to mature and soon after are sought as

food. Since Junegrass does not grow nearly as tall as smooth brome, Bromus inermis, it is not usually necessary for the squirrels to bend the plants to eat the florets. Much of the eating of the spikelets was done in the medium high intensity position.

Junegrass was probably introduced from Europe (Stevens, 1963, and Hitchcock, 1951). Therefore it could not have been in the diet of the flickertails on the original prairie.

Agropyron repens Quackgrass is considered a weed (Hitchcock, 1951). It is found in the three eastern study areas. Although not usually common over the entire colony, it is found in rather dense mats with the plants connected by rhizomes. In the microhabitat of a particular family group of squirrels it may be a very important item of diet during the latter part of June and the first half of July.

The Mapleton study area has a patch of Quackgrass which contains about 30 square meters and is located near the junction of quadrates A 9 and B 10. For the squirrels that have their home ranges in this area Agropyron repens becomes a very important item of diet.

Agropyron cristatum Crested Wheatgrass is found in only two study areas, Blanchard and Lehr. It is most important at Lehr where it is planted as a pasture grass, however it is very abundant at Blanchard. This species begins growth very early in the spring and is used as food

during this time, but later in the summer it becomes tough and wiry. The leaves probably make up a significant portion of the diet of squirrels at both study areas.

Hordeum jubatum Foxtail is found in all areas; it grows in low prairie and in pastures. The awns are long and stiff, with barbs along the edges. These barbs can do damage to the mouths of cattle. The squirrels have been observed to eat foxtail, but it is not a common food. When they do feed on it they usually do not eat the heads, thus avoiding the stiff awns.

Elymus macounii Macoun Wild-Rye was found only in colonies at Mapleton. Even though it was not seen at Blanchard it is reportedly common in coulees (Stevens, 1963). It is not abundant in flickertail colonies and does not make up a significant portion of the diet.

Koeleria cristata Prairie June grass was found only at the Lehr area. It was quite common. Prairie Junegrass develops early in the year and may be used for food at this time.

Phleum pratense Timothy was found only in the Lehr study area, but should be present in all four. Its use as food by the squirrels is not known.

Calamovilfa longifolia Big Sandgrass is common in dry sandy soils. It is found only at the Lehr area. Sandgrass is a large species which is too wiry and stiff to be used as forage and is not eaten by flickertails.

Both Stipa comata, Needle and Thread, and Stipa viridula, Green Needlegrass, are found only at the Lehr study area. They are very common, with Needle and Thread being more so than Green Needlegrass. It is not known if flickertails use these species for food because of a lack of observations.

Beckmannia syzigachne American Sloughgrass is found in low places near many of the colonies at Lehr. The area around the roots of this grass is often very wet with a small amount of standing water. Flickertails are almost never found in the micro-habitat required by American Sloughgrass and therefore it is not eaten.

Bouteloua gracilis Blue Grama is found in abundance in the Lehr colonies of squirrels. It is used as food by the squirrels. Grama blooms during late July and the heads are used by young squirrels at that time.

Like American Sloughgrass, Phalaris arundinacea, Reed-canary grass, is found in areas that are not frequented by flickertails and is therefore not used as a source of food.

The two members of the Cyperaceae that are found near squirrel colonies are Eleocharis calva, Spike Rush, and Scirpus americanus, Three-square, Chairmaker's Rush. The latter is found growing along the edges of the Rush River. During the winter the lower parts of the plant become frozen in the ice. When the spring thaw comes, it floods the ice

containing the rush onto the land in the middle of the flickertail colonies. After all melting has taken place, pieces of the lower part of this plant are frequently found in the area of the burrows of the ground squirrels. These dry as the season progresses and the squirrels will then split them up into long, narrow strips by running their incisors along the length of the rush. These are then folded in the mouth and taken down the burrows to be used as nest material.

The two Juncaceae found in the area are Juncus balticus Baltic Rush and Juncus bufonius Toad Rush. They are found in wet areas along the edges of the colonies. They are not eaten.

Salix sp. is found in the shelter belts along the edge of the Mapleton colony. It is this plant which creates a physical barrier which prevents squirrels from moving into the area of the shelter belts.

The two members of the Polygonaceae that are found in flickertail colonies are Rumex crispus, Curled Dock, and Rumex occidentalis S., Western Dock. The former is rare and the latter rather common. Neither is used as food.

The only member of the Chenopodiaceae found is Chenopodium album, Lamb's-quarters. It is very common and usually is the first plant to appear in a primarily bare area. Such a spot was found the first year of the study in quadrate D 2 of the main study area. Since the squirrels

seek out this species and feed on it readily, the Lamb's-quarters was soon eaten out and the area was taken over by Thlaspi arvense, Brassica arvensis, Rorippa islandica, Capsella bursa-pastoris, and Descurainia sophia. In other areas near, but not in the colony, Lamb's-quarters also was the first to invade. However, since in these areas the squirrels did not feed on the Lamb's-quarters it grew thick and high, preventing the other plants from growing in these areas. Thus the squirrels, by selectively feeding on Lamb's-quarters have affected the course of plant succession.

Amaranthus sp., Pigweed, is found in the three eastern colonies and is used as food by the squirrels.

The members of the Caryophyllaceae and Ranunculaceae do not seem to be very important in the ecology of flicker-tails.

The family Brassicaceae is an abundant and important family in eastern North Dakota. There are five species of mustards found in flickertail colonies: Brassica arvensis, Field or Yellow Mustard, Descurainia sophis, Flixweed, Rorippa islandica, March Yellow Cress, Capsella bursa-pastoris, Shepherd's Purse, and Thalspi arvense, Field-Pennycress. None of these plants has ever been observed to be eaten by ground squirrels. There is a definite selection of the squirrels against these plants as food.

The two members of the Rosaceae that are found in flickertail colonies are Potentilla anserina Silverweed, and

Rosa arkansana, Prairie Wild Rose. Both are conspicuous members of the prairie community and are quite beautiful, but are not eaten by ground squirrels according to our observations.

Trifolium pratense, Red Clover, Trifolium repens, White Clover, and Melilotus alba, White Sweet Clover, all members of the Fabaceae, are usually found along the perimeter of the colonies. They are planted and escape frequently to other areas. The ground squirrels in the Mapleton colony during 1966 would travel up to 50 yards to feed on these species. Other members of the Fabaceae are also important food sources for flickertails. Astragalus goniatus, Astragalus flexuosus, Slender Milkvetch, are found in the prairie community. These are low plants which grow in with the sod cover. Squirrels have been observed to feed on the leaves, but not the flowers. Astragalus flexuosus and Astragalus goniatus grow in patches; therefore a squirrel which happens to have a patch of Astragalus growing in its home range will have a higher percentage of its diet Astragalus. The other members of the Fabaceae that are found in flickertail colonies have not been observed to be used as food.

Observations indicate that the members of the families of Polygalaceae, Malvaceae, Aprocyanceae, Asclepidaceae, Boraginaceae, Convolvulaceae, Labiatae, Plantaginaceae, and Caprifoliaceae are not used for feeding.

Some of these families are quite common, but the squirrels select other plants for consumption. Wolfberry, Symphoricarpos occidentalis, is found in all four study areas; however, it is very abundant at Blanchard. Since the squirrels do not eat Wolfberry, and its seeds can easily germinate on the mounds of the ground squirrels, it is commonly found growing up through the burrow mounds. When the Wolfberry makes it difficult for the squirrels to see while standing in front of their burrows they will build a new burrow system.

In the Asteraceae only two species, Taraxacum officinale Common Dadelion and Lactuca serriola Prickly Lettuce are eaten. The squirrels eat only the leaves of Prickly Lettuce. They bite the leaves off the plant at the base of the petiole and eat the leaves starting from the point that was nearest the plant and proceeding outward. Thus the spines are pointed away from the mouth and can be masticated before being swallowed.

Squirrels will eat various parts of the Common Dandelion at different times. They usually eat only one part at a time. Flickertails have been observed to eat only stems, cutting off the stem from the flower and the base of the plant. At other times the squirrels will eat only flowers, cutting them off the stem and holding the flower in their forepaws while feeding. Sometimes the squirrels have been observed to feed only on the dandelion leaves. One

squirrel was observed putting the mature seeds into her cheek pouch and taking the seeds down the burrow, where they may have been used as nest material.

Water was available to the squirrels in three forms: free water, dew, and food. The dew on prairie grasses has been shown by Weaver (1954) to be several tons per acre. The squirrels feed on dew-soaked grass early in the morning. This water seems to help meet the water needs of the squirrels. Most colonies of Richardson's ground squirrels in the eastern part of North Dakota have open water nearby. However, on only one occasion was a squirrel observed to drink free water during the entire study. The vegetation eaten by the squirrels is high in water content.

Vertebrate Associates

Only one amphibian, Ambystoma tigrinum diaboli (Gray Tiger Salamander) is known to have any ecological relationship with the ground squirrels. Gray Tiger Salamanders are found in abundance on or near colonies after a rain. They could also be captured in standing water at the edges of the colonies. Tiger Salamanders appear to use the flickertail burrows as retreats and perhaps as hibernacula. Mummified remains of Ambystoma tigrinum were found twice in the mound dirt which had been brought up by squirrels from already-existing burrow systems.

No interaction between ground squirrels and reptiles was observed.

During the summer of 1965 a pair of Pied-billed Grebes, Podilymbus podiceps made a nest on the nearby Rush River. The nest was located in reeds approximately 30 meters from the nearest flickertail burrow. On June 2, 1965, a lone grebe was swimming in the river very near the colony when it gave a loud, long, rolling call. Immediately most of the squirrels that were out of their burrows went into high or low high intensity alert. Usually not all the squirrels would respond, but some always did.

A pair of Mallards, Anas platyrhynchos, nested along the edge of the river just across from the colony. The Mallards and several Blue-winged Teal, Anas discors, would often fly very low over the feeding squirrels, and this would precipitate an alarm response. The Blue-winged Teal were observed feeding within 10 meters of feeding flickertails.

The Marsh Hawk, Circus cyaneus, is the only raptor observed near squirrel colonies. Once a Marsh Hawk was observed to swoop down on a squirrel, but it was not known if this attack was successful. On several occasions Marsh Hawks were observed near colonies, flying back and forth quite low to the ground. Only if the hawk was approximately 50 meters from the squirrels would they demonstrate any kind of alarm posture. A Marsh Hawk flying high over the colony would not precipitate any kind of noticeable response.

The Killdeer, Charadrius vociferus, would frequently run along the edges of the colony. The call of the Killdeer

would sometimes cause an alarm posture.

Both the Yellow and Red Shafted Flickers, Colaptes auratus and Colaptes cafer, were observed feeding in the colonies; no noticeable reaction was apparent.

A pair of Brown Thrashers, Toxostoma rufum, nested in the Mapleton colony the first two years of the study. They made their nest in a trash heap in quadrate A 1. On June 10, 1965, female 11 and several of her young approached the dump where the thrashers had built the nest. The male thrasher immediately flew at the squirrels, flapping its wings and calling. The adult female squirrel then moved away from the nest about 5 meters. The young squirrels did not retreat as did their mother. The male thrasher then attacked one of the squirrels and the squirrel reared back on its haunches, showing its incisors and holding its front paws up at either side of its mouth. The tail of the ground squirrel was brushed out. --The squirrel retreated.

The prairie vole, Microtus ochrogaster, and the deer mouse, Peromyscus maniculatus, were trapped in considerable numbers on the surrounding prairie during most of the three study years. However, no prairie vole and only one deer mouse were ever captured in a ground squirrel colony. These mice seem to avoid the parts of the prairie occupied by flickertails.

The greatest predator on flickertails at the present time I believe to be the domestic cat, Felis domesticus. On

several occasions cats were observed to capture squirrels. The cats always took squirrels from the edge of the colony, not from the middle. The second most successful predator was the Striped Skunk, Mephitis mephitis; it was very common. On June 29, 1965, about 300 meters from the edge of the colony, a skunk was observed coming down a dirt road carrying a small mammal in its mouth; it appeared to be a young flickertail. I chased the skunk and retreived its prey. It was a small female squirrel weighing about 250 grams. It was not ear-tagged or marked with dye. On two other occasions Striped Skunks were observed chasing flickertails. It seems probable that they are able to catch young squirrels. The badger, Taxidea taxus, is also an important predator.

CHAPTER VI

DISCUSSION

Animals that live in northern climates have three ways to cope with the extremely low winter temperatures. The animals may migrate, as do ducks, they may adapt to the cold, as do foxes, or they may hibernate, as do flickertails. The flickertail's hibernation cavity is located from 4 to 6 feet below the surface of the ground. At this depth the temperature does not go below 32° F. The adult Richardson's ground squirrels gradually enter hibernation around August 1, whereas the young squirrels hibernate about September 1. Flickertails emerge in the spring approximately April 1 and thus spend 8 months of the year in hibernation, and four months out. Gunderson (1961) estimated that a flickertail in South Dakota spends about 90 per cent of its time in the burrow. This estimate seems reasonable for the flickertails in eastern North Dakota. In four months of diurnal activity the squirrels must compress an entire year's worth of activity. During this time they must mate, raise young, remake their burrow systems, and acquire enough food so that the proper amount of energy may be stored as fat to last the

winter. In order to make the best use of the small amount of time available, two adaptations are apparent.

The gestation of flickertails is 18 days (Denniston, 1957) as compared with 28 days for Citellus tridecemlineatus (Bridgwater, 1966). This adaptation permits the abbreviation of the yearly reproductive cycle time. In a Texas population of Citellus tridecemlineatus the young appeared above the ground over a 3 month period (McCarley, 1966), whereas the flickertails were observed for the first time above ground over only a 4 day period. The condensed emergence time of the flickertails is probably due to the shorter period of suitable weather for above-ground activity, which would place a selective pressure for properly timed births and emergence times.

The young ground squirrels are born in the burrow. They are born without hair and with their eyes completely closed. These findings do not agree with Brown and Roy (1943) who stated "the young are born covered with fur and within a few days after birth the young are able to fend for themselves." It was at least a month after birth that the young squirrels could feed on vegetable material. Brown and Roy evidently confused emergence with birth.

Three different types of burrow entrances can be recognized. A type 7 burrow has a mound, a type 2 burrow is funnel shaped without a mound and the type 3 burrow is without a mound and goes approximately straight down from the surface

and is very much like that of Citellus tridecemlineatus (McCarley, 1966). Gunderson (1961) suggested that a type 3 burrow is made by young squirrels and that it leads directly from the surface to the nest cavity. He also states that the dirt from this burrow is pushed back into the winter burrow tunnel. No squirrel was ever observed digging a type three burrow. How Gunderson arrived at his conclusion is not clear. Gunderson measured the dirt in an exceptionally large mound and found it weighed 400 pounds and contained approximately 5 cubic feet of earth. Brown and Roy (1943) considered that flickertails in Southern Alberta to have two different types of burrows: summer burrows and winter burrows. The summer burrows were reported to be short and the winter burrows longer. This distinction between the burrows used in the summer and those used in the winter seems somewhat artificial. The same entrance serves during both seasons and only various parts of the tunnels are used. Most adult flickertails have one burrow system. This system may have as many as 10 openings, as much as 27 feet of tunnels (Gunderson, 1961). Gunderson (1961) stated that food availability was a factor in selection of the burrow site, but almost all potential habitat had an abundance of plant material acceptable to flickertails, so it does not seem that this would be a factor in the selection of burrow sites. The burrows are placed away from any trees which accumulate snow which slows down the thawing process in the spring.

In connection with the selection of burrow sites I should like to propose that the evolution of the flickertail and the bison, Bison bison, are so closely intermingled that the selection of sites for colonies is still reminiscent of this relationship. Flickertails are found in areas where the native grasses would have been 4 to 6 feet high. Richardson's ground squirrel shows a decided preference for closely grazed grass. The millions of bison on the Great Plains were not limited by the grass, but rather by the availability of water. The buffalo would remain perhaps for considerable time near water grazing the area around a waterhole very closely. These areas would have been ideal for the flickertails to build their colonies, because they prefer closely grazed area. Today, most flickertail colonies are found near water, even though they do not usually drink it. It seems that this site is selected because the buffalo used to maintain these areas suitable for the flickertails.

The daily cycle of the flickertails is much like that of Citellus tridecemlineatus in Texas (McCarley, 1966). The ground squirrels are out late in the day during the spring, out both morning and afternoon in the early summer, and out mostly in the morning during late summer. These activities correspond to the time during the day when the temperature is most favorable.

The maintenance behavior of flickertails has been described. Tinbergen (1952) has pointed out the importance

of accurate descriptions of maintenance behavior. Some patterns of social behavior have been derived from the act systems of maintenance behavior. Most of the maintenance behavior shown by Richardson's ground squirrel is very similar to that of the Uinta ground squirrel (Balph and Stokes, 1963). However the upright coiled posture reported in the Uinta ground squirrel is not seen in the flickertail. This posture is basically the low high alert with a curve in the middle of the spinal column bending the anterior of the squirrel forward. Flickertails bend forward at the level of the pelvic girdle, but not the middle of the spinal column. The postures are much the same as those reported for Citellus lateralis (Gordon, 1943) and Citellus tridecemlineatus (Grubitz, 1963). Grooming behavior is similar to that of Eutamias (Gordon, 1943).

Tail flicking behavior, from which the flickertail gets its name is a frequent action. Balph and Stokes (1963) suggest that tail flicking is an intention movement because in the Uinta ground squirrel it normally precedes a movement. They further postulate that it may help the squirrel identify the movement of another squirrel, and not of some potentially dangerous species.

The identification kiss, a behavior described by King (1955) in Cynomys ludovicianus, is found in flickertails. King stated that the prairie dogs used this behavior to identify certain members of the population. In flickertails

it seems that the function of identification has been lost, for in no instance was an adult squirrel observed to give the kiss to an immature animal and then to give chase; the young squirrel was identified before the kiss took place.

The special pits that are used as defecation sites in California ground squirrel, Citellus beecheyi (Linsdale, 1946), were not observed in Richardson's ground squirrels.

Flickertails are not randomly spaced across the prairie, but are aggregated into colonies. The colonies are made up mostly of adult females and their young with the males some distance from the colony proper. The colonies contain a dominant female, subordinate females, and outcast females. During the three years of the study, the dominant female occupied the central area of the colony and won the majority of agonistic encounters, while the subordinate females lived around the edge of the dominant and would defend an area around their home burrows. The outcast females lived further out from the subordinate females and did not defend their territory against the other squirrels and therefore had to occupy an area on the periphery of the colony.

There appears to be selective pressure in favor of a female squirrel that will vigorously defend her territory and will not trespass on the territory of others. Overly subordinate squirrels are pushed to the outer perimeter of the colony which makes them easy prey for cat, skunks, and

birds. The more dominant individuals tend to travel long distances from their home burrows into unfamiliar territory; if danger threatens they are hard pressed to find safety as quickly as those squirrels who always stay in their known territory. The subordinate females defend their territory, and always are in a position to quickly dart down a burrow. Of the seven squirrels present during both 1965 and 1966 all would fall into the category of those squirrels which defended their territories, but which were not dominant. Of the three squirrels present the first year but not the second, two were dominant, and one was subordinate.

The fact that certain plants are found in the flickertail colonies, does not mean that all of these plants will be eaten, selection of available food takes place. Some species are eaten during certain times in the year and not in others. Bromus inermis and Poa pratensis, both introduced from Europe, were not among the original prairie plants, and both have become major items of diet for flickertails in the areas studied. This represents a major change in food preference over a relatively short period of 80 years or less. Jones (1966) has shown that the habitat of the Sharp-tailed Grouse (Pedioecetes phasianellus columbianus) did not contain two of the most important foods of these birds today, Taraxacum officinale, and Bromus tectorum. In certain areas where complete destruction of the habitat was not experienced the Sharp-tails were able to

make an adaptation to the new food source, though their numbers were reduced (Jones, 1966). Flickertails have evidently been able to adapt to the new plant environment. Just as the grouse were able to sustain themselves with "relatively lower numbers" (Jones, 1966), flickertails usually exist in fewer number than were described by early naturalists such as E. T. Seton.

LITERATURE CITED

American Society of Mammalogists, Committee on Nomenclature. 1960. Status of Spermophilus versus Citellus. J. Mamm. 41.

Balph, D. F. and A. W. Stokes. 1963. On the ethology of a population of Uinta ground squirrels. Amer. Mid. Nat. 69: 106-126.

Benninghoff, W. S. 1952. Interaction of vegetation and soil frost phenomena. Arctic 5: 34-44.

Bridgwater, D. D. 1966. Laboratory breeding, early growth and behavior of Citellus tridecemlineatus. Southwestern Nat. 11: 325-338.

Brown, J. H. and G. D. Roy. 1943. The Richardson ground squirrel, Citellus richardsoni Sabine, in southern Alberta: its importance and control. Sci. Agric. 24: 176-197.

Cuvier, F. 1825. Des dents des mammiferes . . ., p. 255.

Denniston, R. 1957. Notes of breeding and size of young in the Richardson's ground squirrel. J. Mamm. 38: 414-416.

Gray, J. 1944. Studies in the mechanics of the tetrapod skeleton. J. Exp. Biol. 20: 88-116.

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

Gunderson, D. 1961. Life history of Richardson's ground squirrel, Citellus richardsoni. M. S. Thesis, South Dakota State Univ., Brookings.

Herschkovitz, P. 1949. Status of names credited to Oken, 1816. J. Mamm. 30: 289-301.

Hinde, R. A. 1958. Behavior and speciation. Biol. Rev. 34: 85-120.

_____. 1959. Food and habitat selection in birds and lower vertebrates. Proc. XV Intern. Congr. Zool. London, 1958: 808-810.

_____. 1961. Behavior. In Marshall, A. J. Ed. Biology and comparative physiology of birds, vol. 2. Academic Press. New York, pp. 373-411.

Hitchcock, A. S. 1951. Manual of the grasses of the United States. U.S. Dept. of Agric. Spec. Publ., 200.

Howell, A. H. 1938. Revision of the North American ground squirrels. U.S. Govt. Print. Off.: Washington, D.C. 256 pp.

Jones, R. E. 1966. Spring, summer, and fall foods of the sharp-tailed grouse in eastern Washington. Condor 68: 536-540.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contr. Lab. Vert. Biol., Univ. Mich. 67: 1-123.

Koford, C. 1958. Prairie dogs, white faces, and blue grama. Wildf. Mono. 3, 78 pp.

Kolstoe, S. O. 1966. The flickertail. North Dakota Outdoors. 28: 46.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Am. Geog. Soc. Spec. Publ., #36, 116 pp.

Linsdale, L. M. 1946. The California ground squirrel. Univ. Calif. Press: Berkeley and Los Angeles. 342 pp.

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

Potter, L. 1956. Yearly soil temperatures in eastern North Dakota. Ecol. 37: 62-70.

Quay, W. B. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angle in rodents. J. Mamm. 46: 23-37.

Ridgeway, R. 1912. Color standard and color nomenclature. A. Hoen and Company, Baltimore, Maryland.

Sabine, J. 1822. Accounts of the marmots of North America hitherto known, with notices and descriptions of three new species. Trans. Linn. Soc. London. 13: 579-591.

Scott, J. P., and J. L. Fuller. 1951. Research on genetics and social behavior. J. Hered. 42: 191-197.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68: 113-151.

Seton, E. T. 1929. Lives of game animals. Vol. IV. Part 1. Doubleday, Doran and Company Inc., Garden City, New York.

Sleggs, G. F. 1926. The cheek pouches of Richardson's ground squirrel, Citellus richardsoni (Sabine). J. Morphol. and Physiol. 41: 581-591.

Soper, D. J. 1926. Richardson's ground squirrel. Nat. Mag. 8: 105-106.

Stevens, A. O. 1963. Handbook of North Dakota plants. Cushing-Mallory Inc. Ann Arbor, Michigan. L.C. 63-14319.

Tinbergen, N. 1952. Social behavior in animals. Metheun, London. 150 pp.

Walker, E. P. 1964. Mammals of the world. The John Hopkins Press, Baltimore, Maryland. Vol. II. 1500 pp.

Weaver, J. E. 1954. North American prairie. Johnson Publishing Co. Lincoln, Nebraska. 348 pp.