COTTONTAIL RABBIT RANGES

AND MORTALITY

IN EASTERN KANSAS

A Thesis

Submitted to

the Division of Biological Sciences

Emporia Kansas State College, Emporia, Kansas

In partial fulfillment

of the requirements for the Degree

Master of Science

---

by

Charles C. Watt

August, 1975

Approved for Major Department

Approved for Graduate Council

ACKNOWLEDGEMENTS

The author is indebted to Richard Hatfield and Tom Hutton, without whose assistance most of the data herein reported would not have been gathered. Also, I am indebted to Dr. Dwight Spencer, my major advisor, and his fellow graduate committee members, Dr. Robert Clarke and Dr. John Ransom.

Dr. Spencer and William Peabody provided aid and advice concerning various aspects of the research throughout the study. I wish to thank Miss Janet Spencer for the typing of the manuscript.

This study was financed by the Kansas Forestry, Fish and Game Commission. This financial support was sincerely appreciated.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
Description of Study Area	3
METHODS AND MATERIALS	8
RESULTS AND DISCUSSION	16
Trapping Success and Population Estimates	16
Equipment Performance	23
Effects of Handling and Transmitter Collar on Cottontail Movements	26
Cottontail Home Ranges	29
Ranges as Determined by the Minimum Area Method	30
Ranges as Determined by the Modified Minimum Area Method	36
Trap Determined Ranges Compared to Radiotelemetry Determined Ranges	40
Home Range Shape	47
Home Range Models	50
Circular Home Range Model	58
Elliptical Home Range Model	60
Home Range Estimators	63
Cottontail Movements	68
Territoriality	77
Mortality	83
SUMMARY	92
LITERATURE CITED	95
APPENDICES	101
Appendix A	101
Appendix B	103
Appendix C	120

LIST OF TABLES

Table | Page

I. Genera of major plant types found in the study area....... 7

II. Trapping record for period 5 August 1974 to 20 May 1975... 16

III. Monthly population estimates, total number of animals captured per month and percentage of estimated population captured on the RNHR study area................ 22

IV. Radio-transmitter performance............................. 24

V. Home range areas as determined by the Minimum Area Method for the 16 radio-tagged rabbits.................... 31

VI. Home range areas reported in the literature for adult cottontails.. 34

VII. Home ranges of 16 radio-tracked cottontails determined by the Modified Minimum Area Method compared to home range values determined by the MAM........................ 37

VIII. Home ranges as calculated by the MAM using all data points, radio location points only and trapping location points only.................................... 40

IX. Lengths of long and short axes of home ranges and length-width ratios of radio-tracked rabbit ranges........ 49

X. Cumulative percentage of data points within recapture radii for male and female rabbits......................... 56

XI. Standard range radius, standard area of activity, and home range areas determined by the MAM, for all radio-tracked rabbits.. 59

XII. Home range areas for five confidence ellipses calculated using the Koeppl et al. (1974) model, for four rabbits.... 61

XIII. Home range areas as estimated by McNab's (1963) equation, the equation derived from the data collected during the present study and the MAM, for rabbits with adequately sampled home ranges...................................... 65

XIV. Home range area as estimated using the equation derived from linear regression analysis of mean travel distance between successive capture data and the MAM, for rabbits with adequately sampled home ranges and captured more than once.. 67

Table (Cont'd) Page

XV. Mean minimum daily travel distance (MMDTD) in yards for 16 radio-tracked rabbits.............................. 69

XVI. Mean distance between successive captures for 14 rabbits captured three or more times...................... 71

XVII. Form reuse ratio for 16 radio-tracked rabbits............. 73

XVIII. Per cent of home range overlap by contemporary rabbits.... 81

XIX. Date of discovery of remains, rabbit number, transmitter type if animal was instrumented, description of remains and probable cause of death for 21 rabbit mortalities known to have occurred on the study area.................. 85

LIST OF FIGURES

Figure Page

1. Major cover types on the study area...................... 4

2. Initial trapping locations and sexes of 54 rabbits captured during this study.............................. 19

3. Chase trails for eight chases of rabbit R-271............ 45

4. Frequency distribution of recapture radii for all male and female rabbits................................ 55

5. Frequency distribution of recapture radii for female rabbits inhabiting the area below Gladfelter pond and the Church site area..................................... 57

6. Fifty, 75, 90, 95 and 99 per cent confidence ellipses for the data points of four rabbits calculated using the Koeppl et al. (1974) model and the home range as determined by the MAM.................................. 62

INTRODUCTION

In Kansas, many sportsmen, landowners and Fish and Game Commission personnel have expressed concern about the "disappearance" of cottontail rabbits in the fall (Peabody, pers. comm.). A number of factors may be responsible for this apparent decline in population levels between summer and fall. Changes in cottontail behavior and habitat usage patterns, that affect observability and harvest of cottontails, may cause an apparent decline in population levels when, in reality, none has occurred (Sheffer, 1972). It is also possible that an actual population decline caused by increased predation during this period of high cottontail density, disease or some other factor, or combination of factors, may be occurring during this period.

To the wildlife manager, a knowledge of habitat usage patterns, home range areas and movement patterns of specific cottontail populations can all assist in the evaluation of habitat and possibly indicate which factors are responsible for population fluctuations. Better understanding of an animal's movements may also allow such problems as predator and disease control, food and cover production and manipulation, and censusing to be more intelligently approached (Doebel and McGinnes, 1974).

The cottontail rabbit, *Sylvilagus floridanus* (J. A. Allen), a major game animal of the eastern United States, has been the subject of a number of movement and mortality studies based primarily on capture-recapture records (Dalke and Sime, 1938; Schwartz, 1941; Haugen, 1942; Janes, 1959; Lord, 1963; Hanson *et al.*, 1959; Chapman and Trethewey, 1972; Trent and Rongstad, 1974).

The movement studies mentioned above are mostly based on capture-recapture data gathered on tagged animals. The major advantage to studies of this type is that a number of activities (reproduction, weight changes and longevity) other than movement can be monitored simultaneously for many individuals (Van Vleck, 1969). The advantage of capture-recapture studies is outweighed by 1) the interference in normal animal activity that trapping necessitates; 2) the bias that is inherent in movements indicated by this method for trap shy or trap prone animals; and 3) the impossibility of trapping the animal at all points within its range (Van Vleck, 1969).

With the advent of radio-nuclide tagging studies of small mammals and radio-transmitter tagging studies of larger mammals within the past 10 to 20 years, many of the disadvantages inherent in capture-recapture studies have been eliminated. Radio-tracking studies allow for detailed recording of an animal's movements without the necessity of recapturing the animal a large number of times and interfering with its normal activities. Recent advances in radio-tracking equipment allow the investigator to determine causes of mortality and mortality rates for radio-tagged animals through the use of designs that alert the investigator immediately after mortality has occurred (Stoddart, 1970). This equipment now makes it possible for an investigator to gather a large amount of data in great detail over extended periods of time on animals that are subject to a minimum of investigator interference. In most cases, this detailed information can be gathered in no other way.

To determine what factors cause or contribute to the apparent decline in the cottontail population in eastern Kansas, a study using radio-tagged rabbits was initiated on the Ross Natural History Reservation (RNHR) in Lyon County, Kansas, in August, 1974. Information on cottontail home range areas, population levels and mortality was gathered using capture-recapture methods and radio-tracking, so that base values for these parameters could be established for the study area. Effectiveness of radio-tracking equipment for gathering this type of information was also tested (Hutton, pers. comm.). Data gathered during this annual study, coupled with data gathered in the next few years on the same study area, should greatly assist in establishing whether or not a rabbit population decline occurs during the late summer and early fall. That information can then be used to correct the situation through the application of suitable management techniques, or show that the problem is merely illusory.

Description of Study Area

This study was conducted on approximately 100 acres of the Ross Natural History Reservation, in northwest Lyon County, Kansas. A detailed description of the location of the area, as well as a description of the geology, terrain features and major vegetational types, may be found in Hartman (1960).

Figure 1 is a map of the study area showing the major vegetational types found there and the two sites of rabbit concentration referred to later in the text. The grid system around the map was designed for use in accurately determining the location of any point within the study area. It was used primarily in conjunction with home range maps (Appendix B).

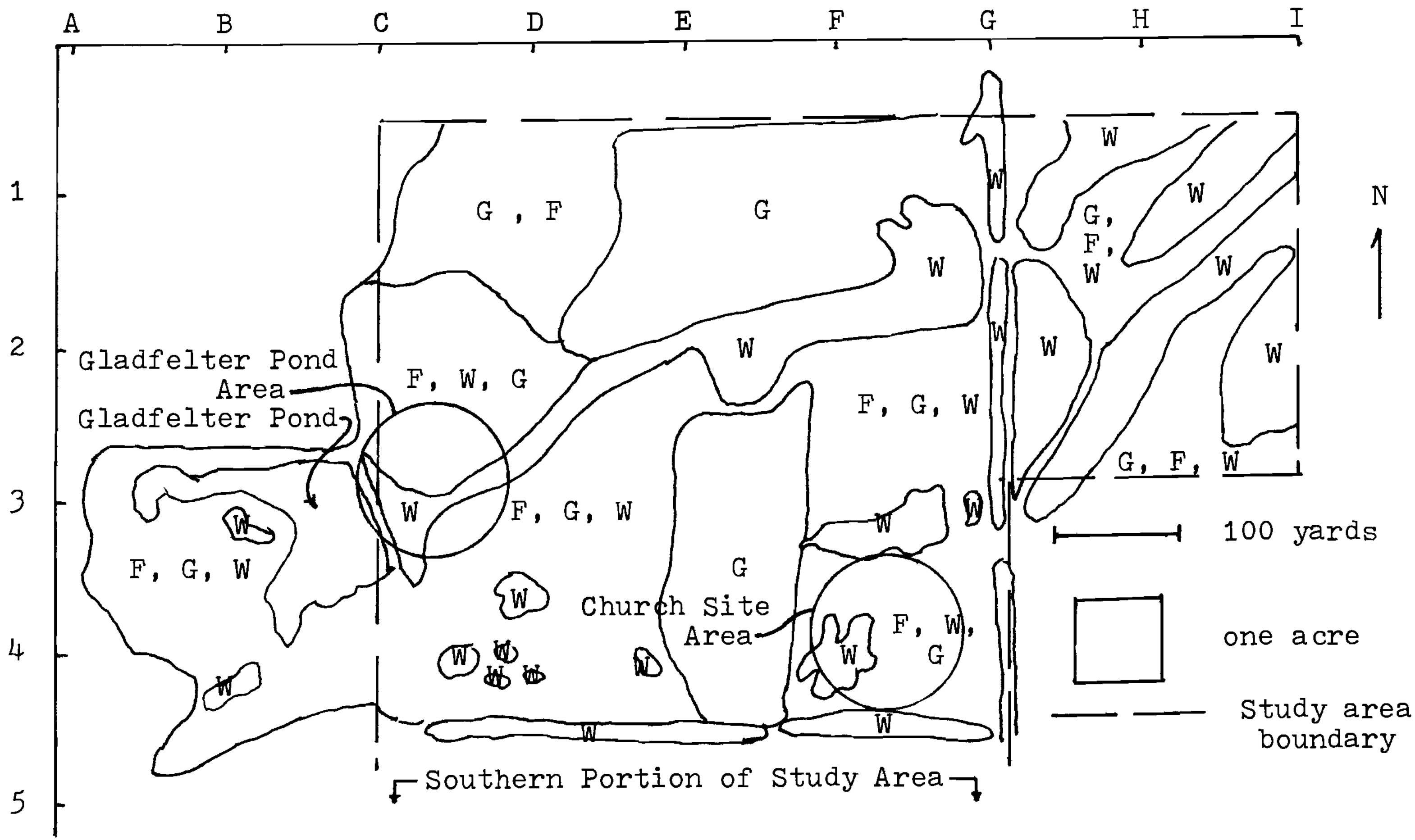


Fig. 1. Major cover types on the study area. W = woody vegetation, Int. W = intermittent woody, F = forbs and G = grasses.

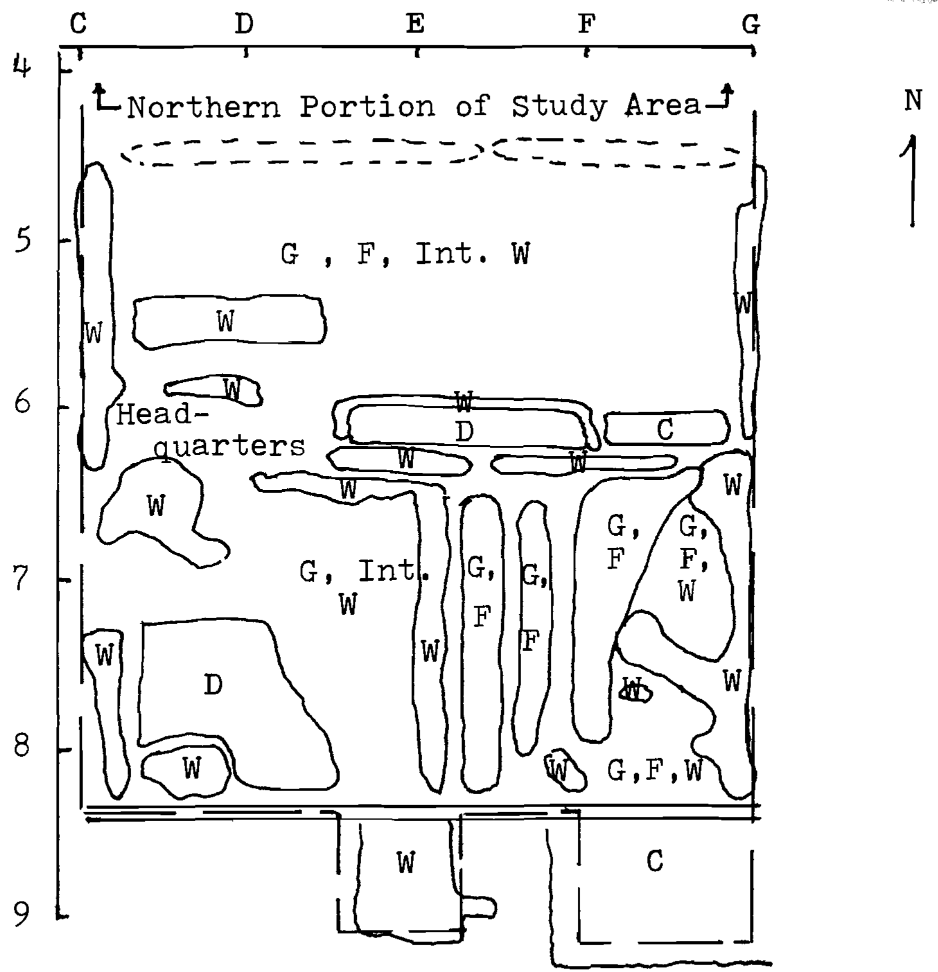

C
D
E
F
G
4
5
6
7
8
9
Northern Portion of Study Area
N
G , F, Int. W
Head-
quarters
G, Int.
W
D
C
G,
F
G,
F,
W
G,F,W

Fig. 1. (Cont'd)

Plants comprising the major vegetational types are listed in Table I.

In general, the cover was sufficiently dense and tall across the study area to serve as good rabbit cover (Schwartz and Schwartz, 1959). Only in the areas E-3,4 and D,E,F-1 was good cover sparse, consisting primarily of grasses. Areas D,E,F-5 and D-7,8 were not particularly good areas for cover.

Table I. Genera of major plant types found on the study area. * = common on study area. For a more detailed description of the flora of the study area see Wilson (1963).

Grasses *	
Andropogon	
Aristida	
Bouteloua	
Bromus	
Elymus	
Panicum	
Setaria	
Sorghastrum	
Sporobolus	
Forbs	
* Ambrosia	Hibiscus
* Asclepias	* Lespedeza
* Aster	Liatrus
* Baptisia	Mirabilis
Cassia	Monarda
Cirsium	* Oenothera
Desmanthus	* Opuntia
* Erigeron	* Salvia
Euphorbia	* Solidago
* Eupatorium	Verbena
Gutierrezia	Verbascum
* Helianthus	
Woody Vegetation	
Acer	Morus
Celastrus	Populus
Celtis	* Prunus
* Cornus	* Rosa
Fraxinus	* Rhus
Gleditsia	Salix
Juglans	* Symphoricarpos
* Juniperus	Ulmus
* Maclura	

MATERIALS AND METHODS

Rabbits were collected on the Ross Natural History Reservation study area using two types of live traps. A closed, rectangular, single door, wooden box trap (Forsythe, 1974) was used in most cases. These traps were either baited, usually with apple, or unbaited and placed in locations that appeared to be good rabbit habitat, generally along boundaries between cover and open areas, with the trap's entrance facing toward the open area. Single door, wire, Tomahawk live traps were used less frequently. They were placed on "runs" and were, generally, left unbaited. Traps were open continuously from August, 1974, to May, 1975.

Traps were checked each day between 0700 and 1100. Sex was determined using criteria described by Petrides (1951). The sex, weight, relative age (juvenile or adult) based on weight, general condition, reproductive status and the presence of ectoparasites were recorded for each captured animal.

Blood samples were taken from most of the captured rabbits. Approximately three ml of blood was obtained by slitting a blood vessel in the ear of the rabbit. Best results were obtained when the rabbit was held upside down and the ear had been prepared for bleeding by flicking the ear, in order to increase blood flow in the ear, making the blood vessels more prominent. After bleeding, cotton was placed on the cut to stop blood flow. Blood obtained from each cottontail was refrigerated until it could be taken to the EKSC microbiology area where tests were run to determine whether or not the animal had contracted tularemia.

Rabbits were ear-tagged using #898 Tab End, Size 3 National Wing Bands manufactured by the National Band and Tag Company, Newport, Kentucky. In addition to that marking method, certain rabbits were marked experimentally with plastic loop fish tags and others were marked with numbered black plastic collars. Plastic loop fish tags did not prove to be a reliable marking method. In almost every case, they were torn from the rabbits ear, probably by brush or by the animal's grooming activities.

The black plastic collars were used after testing indicated that coyotes fed collared cottontails did not destroy the collar. Therefore, positive identification of rabbit remains could be made, even in cases where only fur and bone remained.

When transmitters were available cottontail rabbits weighing over 600 grams were fitted with radio-transmitters supplied by Sidney Markusen, Cloquet, Minnesota, or Wildlife Materials, Inc. (WMI), Carbondale, Illinois. Markusen supplied a total of 10 transmitters of two types. Both types consisted of an adjustable collar on which was mounted a transmitter package, a battery or batteries, and a whip antenna. Electrical tape was used to attach the transmitter and batteries to the collar and also to act as waterproofing. Five of the transmitters were continuous signal, mercury cell powered units (two cells) mounted on leather small pet collars and weighed between 63 and 70 grams. Tests of these collars on penned rabbits indicated that the leather collar could not be drawn snugly around a rabbit's neck. The test rabbit was able to gnaw through the collar and electrical tape when the collar was drawn as tightly as possible. It was evident that the transmitter would have failed if left on the rabbit for any length of time. The whip antenna on the collar was also subject to damage by gnawing.

It was also believed that the 63 to 70 gram package weight was excessive. In order to decrease the weight of the package one of the mercury cells was removed. It was felt that this would not substantially reduce the life or range of the transmitter package. Not only did the removal of one cell lower the weight of the package so that it did not overly encumber the animal, but it also allowed the collar to be fitted more snugly around the animal's neck. The collar's fit was further improved by removing the buckle and rivets on the small pet collar and fastening the collar by means of metal snaps or split rivets. These modifications brought the weight of the transmitter package down to between 39 and 43 grams and allowed the collar to be secured snugly around the animal's neck. In order to reduce the probability of antenna damage by gnawing rabbits, the whip antenna was taped around the collar so as to form a loop around the animal's neck. This modification was successful in minimizing damage to the antenna without adversely affecting transmitter range or signal.

The other five transmitters produced by Markusen were designed to indicate whether the animal was living or dead (mortality collars). This was accomplished by adding a thermistor to the transmitter circuitry which caused the transmitter's signal to change from a pulsing to a continuous signal when the animal's body temperature dropped below 75 F. The use of single lithium batteries and plastic collars helped to reduce the weight of the collar (33 grams) and made a good fit possible so that no major modifications were necessary.

One collar was obtained from Wildlife Materials, Inc. (WMI). This collar was a pulsed signal, mercury cell powered (one cell) unit with a whip antenna mounted on a hard thermoplastic collar. It weighed 28 grams. The whip antenna was held in place along the animal's back by means of a small spring so as not to be subject to damage. The collar was initially too large and was returned to WMI for adjustment.

After Markusen collars had been in service on animals for a short time, it was found that the electrical tape used for waterproofing was inadequate. For this reason, transmitter leads and battery poles were potted using Luxe-cure #60 Superfine Quick Repair self-hardening resin manufactured by the Luxit Acrylic Manufacturing Company, K. C., Missouri. Tape was then applied over the potted transmitter leads and battery.

Each transmitter had a distinct frequency between 150.815 and 151.20 MHz and had an estimated life span of 90 days (mercury cells) or 120 days (lithium cells).

The following procedure was employed when fitting a radio-transmitter to a rabbit: 1) The battery lead was soldered to the transmitter lead, thus activating the collar; 2) The transmitter was tested by setting the channel selector on a receiver to the appropriate channel and determining whether or not the transmitter was operating properly, that is, transmitting; 3) The battery-transmitter connection and battery poles were potted; 4) The potted connection and battery poles were taped; 5) The collar was fitted to the animal's neck and tightened; 6) The antenna was then taped in a loop along the collar.

After the above procedures were completed the animal was returned to his place of capture and released. This initial capture location and any recapture locations were recorded on a map of the study area (Appendix A).

Daytime resting locations of instrumented rabbits were determined by using a portable 24-channel, VHF tracking receiver designed by Sidney L. Markusen and a handheld two element yagi, directional antenna. Instrumented rabbits were located once a day between 0700 and 1100. Receiver ranges varied from 150 to 500+ yards, depending on transmitter type (lithium or mercury powered, Markusen or WMI), antenna configuration (loop or whip), intervening terrain features and weather factors. A rabbit's location could generally be determined within five to 10 yards. Rabbit locations were recorded on a map of the study area.

Rabbits instrumented with non-mortality collars were checked to determine whether or not they were still living. If there had been a marked change in location since the last check, the animal was generally assumed to be alive. If no movement had occurred since the day before, the tracker either listened for indications of movement (warbling of the transmitter signal) or attempted to flush the rabbit until the transmitter signal indicated movement or the animal was sighted. If at all possible the animal was not flushed.

When mortality occurred in either instrumented or non-instrumented rabbits a search of the immediate area was made for identifying ear tags or the transmitter collar, examination was made of the area for signs indicating the cause of death, and the rabbit's remains were examined for indications of the cause of death. This information was recorded and photographs of the mortality site were taken when equipment was available.

When transmitters failed or showed signs of imminent failure, ts were made to trap the instrumented rabbit and recover the collar. apping was unsuccessful the animal was recovered by hunting and the r recovered. In a number of cases recovery was impossible.

Home ranges were determined using the Minimum Area Method (MAM) r, 1947), the Modified Minimum Area Method (MMAM) (Harvey and Barbour,), standard area of activity (Brussard, et al., 1974) and an elliptical range model devised by Koeppl et al. (1975). In the cases of the nd MMAM, locational data points were connected as indicated in the rature and the area enclosed was measured using a compensating polar imeter. Home ranges as determined by MAM were used to test which the animals had ranges that had been adequately sampled. Home ranges etermined by the MAM were plotted after each five locational data ts and accumulated (Odum and Kuenzler, 1955). The accumulated home ge was plotted on an X-Y coordinate after each five locational data nts. If the observation-area curve indicated that the addition of ther locational data points would not cause a marked increase in ge area, the range was considered to have been adequately sampled.

Analysis of the locational data points by the Koeppl et al. (1975) el required that the locational data points for each animal be igned an x and y value. To fulfill this requirement, a map of the dy area was gridded into one centimeter squares so as to form the first quadrant of an X-Y coordinate system. The locational data points for each rabbit were then assigned discrete x and y values.

Locational data were then processed and analyzed using a FORTRAN IV computer program supplied by N. A. Slade, Museum of Natural History, University of Kansas, Lawrence, Ks. 66045. The computer program calculated the center of activity, equations of the first and second axis, area of the 95 per cent confidence ellipse, coordinates for the 50, 75, 90, 95 and 99 per cent confidence ellipses for the scatter of points and measures of skewness and kurtosis with their associated t-values, in addition to other statistics, for each rabbit's set of data points. Only those ranges that meet the tests of adequacy described by Koeppl _et al_. (1975) are presented. The area enclosed by the confidence ellipses was measured using a compensating polar planimeter.

The minimum daily travel distance is defined as the straight line distance between locational data points for consecutive days. Recaptures, for the purpose of calculating recapture radii are any locational data points, both those gathered by radio-tracking and those gathered by trapping. Recapture radii are defined as the distance from the center of activity to a locational data point.

For the analysis of minimum daily travel distance, recapture radii, distances between consecutive trap captures, distances between centers of activity and the establishment of home range axes, locational data points were plotted on paper and appropriate measurements were taken.

Home range axes were determined in the following manner: 1) the long axis of the range was considered to be a line segment passing through the calculated center of activity and parallel to an imaginary line connecting the two points of detection farthest apart; 2) a line segment perpendicular to the long axis and passing through the center of activity was the short axis. Lengths of the axes were determined by drawing a line segment through the point most distant from the center of activity along the axis, perpendicular to the axis. The distance between this point on the one arm of the axis and the similarly derived point on the other arm of the same axis was considered the length of the axis.

Distances between center of activities and per cent of range overlap (Getz, 1961) were used as measures of territoriality.

Mean minimum travel distance per day for the first five days was compared with the mean minimum daily travel distance for the total time that the animal was monitored as a measure of the effect of the collar and handling on animal movement.

Population estimates were made using the MLE method (Edwards and Eberhardt, 1967) in conjunction with a modified cottontail life table developed by Lord (1963) and a subjective appraisal of the ability of the study area to support rabbits in conjunction with densities as determined by trapping.

Statistical analyses (t-tests, simple linear regressions and correlation) were run on a Monroe 1785 programable calculator. Students t-test at P = 0.05 was used to test for significant differences between sexes and different portions of the study area for various parameters, unless otherwise stated.

RESULTS AND DISCUSSION

Trapping Success and Population Estimates

Trapping was conducted from 5 August 1974 to 20 May 1975. Table II summarizes the trapping record for this period.

Table II. Trapping record for period 5 August 1974 to 20 May 1975. C/100 equals captures per 100 trap nights.

Date	Trap Nights	Total Captures	Recaptures	C/ 100
8/ 5/74- 8/31/74	484	12	1	2.48
9/ 1/74- 9/30/74	527	8	4	1.52
10/ 1/74-10/31/74	323	15	7	4.64
11/ 1/74-11/30/74	829	22	12	2.65
12/ 1/74-12/31/74	775	13	12	1.68
1/ 1/75- 1/31/75	962	2	2	.21
2/ 1/75- 2/28/75	914	20	7	2.19
3/ 1/75- 3/31/75	1228	16	13	1.30
4/ 1/75- 4/30/75	1054	3	1	.28
5/ 1/75- 5/20/75	758	2	2	.26
Total	7853	113	61	
		Mean C/100		1.44

From these data it did not appear that there was a direct relationship between the number of trap nights per month and the number of animals captured. Trap success, as indicated by the number of rabbits captured per 100 trap nights, was greatest during the fall, peaking in October, and lowest in January. A smaller peak was noted in February and March. With the advent of spring (April and May), trap success again dropped to low levels.

A number of studies conducted to determine the factors that affect trap responses of wild cottontails have found a similar pattern of trap success. Bailey (1969) found that trapping success is generally greatest in the fall. At least two factors probably account for trap success at this time. One factor is that at this time of year cottontail population density is comparatively high (Bailey, 1969). It is also at this time that a large proportion of the population is within the age group (4-5 months) that is most susceptible to capture (Bailey, 1969). Huber (1962), Chapman and Trethewey (1972) and Eberhardt et al. (1963) also found that juveniles were more readily trapped than adults. Bailey (1969) also found that rabbits in all age and sex classes, for some unknown reason, became especially trappable during this time.

Chapman and Trethewey (1972), studying introduced cottontails in Oregon, found trap success to be greatest in January and February. After peaking in January, trap success declined rapidly, reaching a low in May, June and July. Trap success during October, November and December was two to three times greater than trap success during the summer. These results agree with those found in the current study. Forsythe (1974), collected rabbits for a parasite study on the RNHR and from other locations in Lyon County, and he found trap success to be especially low during the summer.

The peak in trap success in February and March found in the current study may be accounted for, in part, by the increased activity that accompanies the onset of the breeding season. All males captured after the middle of February had scrotal testes indicating that the breeding season had begun. Newman (1959), studying the factors that affect winter roadside counts of cottontails, concluded that February and March represent a period of increased movement in the cottontail, due in part to mating activity and in part to weather factors during this period. Lord (1961) found roadside activity to be greatest in March and April, which is in general agreement with the findings of Newman (1959). Chapman and Trethewey (1972) found a similar increase in trap success at the beginning of the breeding season. Bailey (1969) noted peak trap success occurred in November, followed by a rapid decline in trap success to a low in February and early March. Since Bailey used additional captures per trapping period as a measure of trap success, his results are not directly comparable to those found in the current study.

No attempt was made to correlate weather or other factors with trap success.

A total of 54 rabbits were captured on the study area (Fig. 2). Two major concentrations of rabbits occurred as indicated by initial trapping locations. One concentration was located below the dam of Gladfelter pond and the other was located in an Osage Orange hedgerow to the east of the Headquarters (Fig. 2).

Of the 54 rabbits captured, 28 were females, 25 were males and one was not sexed. Of those sexed, the sex ratio was 1:1.12 in favor of the females. Schwartz (1941), among others, noted that there was a decided sex difference in the susceptibility of rabbits to trapping. Males displayed a consistent tendency to stay out of traps (Schwartz, 1941). Bailey (1969) and Huber (1962) both concluded that females were more

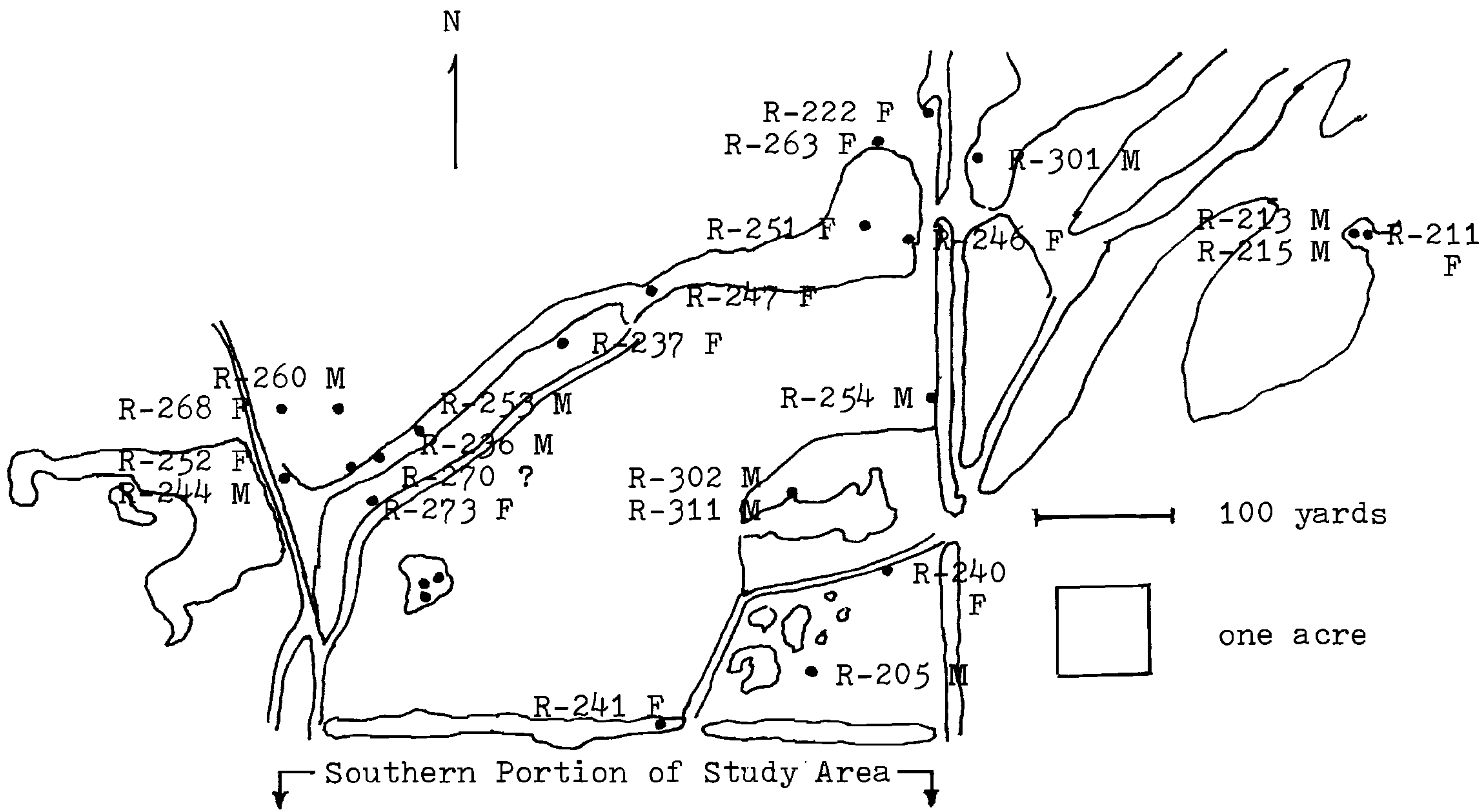


Fig. 2. Initial trapping locations and sexes of 54 rabbits captured during this study.

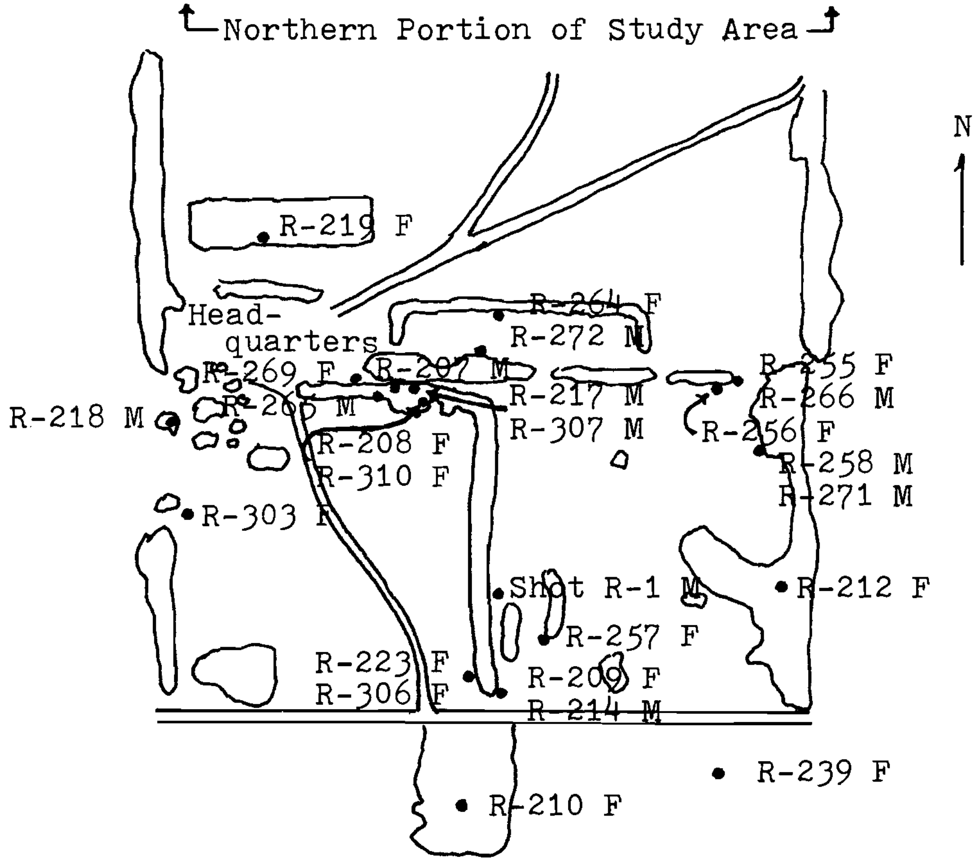

Northern Portion of Study Area
N
R-219 F
Head-
quarters
R-264 F
R-272 M
R-269 F
R-207 M
R-265 M
R-218 M
R-217 M
R-307 M
R-255 F
R-266 M
R-256 F
R-258 M
R-271 M
R-208 F
R-310 F
R-303 F
Shot R-1 M
R-212 F
R-257 F
R-223 F
R-306 F
R-209 F
R-214 M
R-239 F
R-210 F

Fig. 2. (Cont'd)

trappable than males. For this reason, it was difficult to determine whether the sex ratio of 1:1.12 represented the real situation or was due to differences in trap susceptibility. Sex ratios for cottontails gathered in the wild by methods other than trapping indicated that they do not differ significantly from 1:1 (Wainwright, 1969).

Individual rabbits were captured from one to 11 times. Thirty rabbits were captured only once, 11 were captured twice, five were captured three times, two were captured four times, one was captured five times, three were captured six times, one was captured seven times and one was captured 11 times. The mean number of captures per rabbit was 2.15. Sixty-three per cent of the animals caught more than once were females and 69.2 percent of the animals caught more than twice were also females.

With the capture-recapture data gathered during this study in hand, it is possible to derive some estimate of the total population on the study area. Using the MLE (Maximum Likelihood Estimates) derived for cottontails by Edwards and Eberhardt (1967), the August 1974 population on the approximately 100 acres of the study area was estimated to be 96.3 rabbits.

Coupling the estimate of 96.3 rabbits with Lord's (1963) modified life table for cottontails in Illinois gave an estimate of approximately 132 rabbits on the study area in May, the time at which Lord assumed the cottontail population was at its maximum. Table III summarizes the population trend as indicated by the use of the MLE estimate to set a population level for August, which was then fitted into Lord's modified life table to give monthly population estimates.

Table III. Monthly population estimates, total number of animals captured per month and percentage of estimated population captured on the RNHR study area.

Month	Population Estimate	Total Captures	Per cent of Population Captured
May	131.9	--	----
June	120.1	--	----
July	105.6	--	----
August	96.3	12	12.5
September	84.4	8	9.4
October	64.6	15	23.2
November	48.4	22	45.1
December	39.6	13	32.8
January	34.3	2	5.8
February	29.0	20	70.0
March	85.0	16	18.8
April	105.7	3	2.8
May	118.2	2	1.7

If the MLE estimate was relatively accurate, 56.1 per cent of the rabbits on the Reservation at the beginning of the study in August were tagged during the study. In Edwards and Eberhardt's study (1967) discussion of the MLE method, they mentioned the tendency of this method to over estimate the zero capture class and thus lead to a population estimate greater than the true population level. In their study the MLE estimate of the population was 21 per cent higher than the true population level. In all probability then, the true population level on the study area in August was somewhat lower than that estimated by the MLE and, in reality, more than 56.1 per cent of the rabbits on the area were handled.

Another possible estimate of population size on the study area was based on a subjective appraisal of the habitat that was classifiable as good rabbit habitat, based primarily on the quality of the cover over the area. Approximately 70 acres were judged to be good rabbit habitat. The highest rabbit density per 10 acre grid section across the study area occurred in the grid section containing the area below Gladfelter pond. In that area there was a density of 1.2 rabbits per acre as indicated by trapping. If this density was found in all the good rabbit habitat on the study area, an estimate of 84 rabbits was calculated. If this density prevailed over the whole study area a population of 120 rabbits was calculated. In all probability, the population on the study area was somewhere between 84 and 96 rabbits in August, 1974. These estimates would put the population densities for the good rabbit habitat at from 1.2 to 1.4 rabbits per acre and the densities for the whole study area at between .84 and .96 rabbits per acre. Using these population estimates, from 56.1 to 64.2 per cent of the rabbits present on the study area in August were handled during the study.

Equipment Performance

Of the 11 transmitters used during the study, five were not recovered after failure, four failed and were recovered and eventually repaired and two did not fail (Table IV). Generally, if a transmitter functioned for the first week, the life of the collar would approach at

Table IV. Radio-transmitter performance, including days of operation and comments on the fate of each collar. BT refers to battery type (M = mercury, L = lithium).

Collar Number	Weight (g)	Days of Operation	BT	Comments
M-1709	38.0	64	M	Not recovered after failure.
M-1710	43.0	5	M	Not recovered after failure.
M-1711	39.2	12	M	First battery.
		+ 26		Second battery; not recovered after failure.
		38		
M-1712	39.2	89	M	First battery.
		+ 4		Second battery; failed, returned to Markusen; repaired and returned after seven months.
		93		
M-1713	36.7	23	M	Failed, returned to Markusen; repaired and returned after one month.
		58	L	Failed, returned to Markusen; repaired and returned after four months.
M-1727	38.0	5	L	Failed, battery problem; returned to Markusen; repaired and returned after six months.
M-1728	----	110	L	Removed after mortality and allowed to fail in lab.
M-1729	----	39	L	Thermistor circuitry problem; returned to Markusen; repaired and returned after after five months.
M-1730	32.5	104	L	Not recovered after failure.
M-1731	----	6	L	Not recovered after failure; collar lost.
WMI	28.0	54	M	First battery; not on rabbit; no failure.
		54 +	M	Second battery; removed from rabbit, no failure.

least three weeks. Three of the transmitters that failed did so within a week of being attached to an animal. The mean operating life of a transmitter on a single battery, including those that lasted less than a week was 46.6 days (N=14). Those transmitters powered by mercury cells had an average operating life of 41.4 days (N=8) or 53.7 (N=6) days if transmitters that failed within a week are not included in the sample. Lithium powered transmitters had an average operating life of 53.7 days (N=6) or 77.8 days (N=4) if transmitters that failed within a week are not included in the sample. It appears that after the first week, during which time both types of collars are prone to failure, lithium cell powered units will give a longer operating life than mercury cell powered units though mercury cell powered units may operate for as long a period as lithium cell powered units.

Most of the failures involved battery problems and were probably due to shorting of the battery by moisture penetrating the waterproofing material. In all probability, part of the problem is due to inadequate waterproofing. Another major factor may be manipulation of the transmitter collar by the collared animal. From observations of penned, collared animals it was evident that the collared cottontails make some attempt to remove the collar from around the neck. Such manipulations during the several days after the animal is released may account for the collar failures during the first week. Collars that survive for the longer periods either survive manipulation until the cottontail becomes accustomed to the collar or are constructed more sturdily than those that do not survive.

Mercury powered units gave no sign of impending failure. A few of the lithium powered units indicated their impending failure by a change in signal from the pulsed live signal to the continuous dead signal, in spite of the fact that the animal was still living. It appeared that even under the best conditions that some collars are going to be lost due to the inability of the investigator to recover animals at will.

In only one case did a transmitter collar become detached from an animal. A search of the area that this animal was known to frequent was made with the assistance of National Guard personnel using mine detectors. The collar was not found. In all probability, the collar was lost due to failure of the blade fastener on the plastic collar. It was deemed unlikely that the rabbit could have removed the collar while it was intact.

Adequate waterproofing, proper fitting of the collar so that manipulations by the rabbit will have minimal effect and the examination of connections to insure they are secure, should help to eliminate failures caused by animal manipulations and environmental factors, which are evidently responsible for most failures.

Effects of Handling and Transmitter Collar on Cottontail Movements

Little information is available on the effects capture and tagging have on movements of animals used in home range studies. It is generally assumed that handling and tagging have little effect on the animals movements. Kaye (1961), studying the movements of radio-isotope tagged *Reithrodontomys*, found that movements of mice for up to several hours after their release from live traps were suggestive of meandering, possibly indicating that the animals were confused, frightened or hungry. From these observations he concluded that live trapping induces abnormal behavioral responses in harvest mice after release. To what extent this is true for other mammals is not known.

From observations of cottontail rabbits that were collared while in pens, it appeared that animals will attempt to remove the collar using their forepaws and hindfeet. It is not known how long an animal spends trying to remove the collar or to what degree it modifies the animal's behavior. It is not known whether an animal ever becomes accustomed to the transmitter collar. The weight of the collar, its placement and fit, all probably affect an animal's response to the collar and whether or not the animal becomes accustomed to the collar. Before any firm conclusions can be made as to what effect the collar has on animal movements and behavior, more detailed observation and study will be necessary.

One possible measure of the effect of the transmitter collar and handling on a cottontail's movements may be derived from a comparison of movements of a radio-tagged cottontail for several days after release with movements over the whole period that the cottontail was monitored. Student's t-test was used to compare the mean minimum daily travel distance for the first five days after release with the mean minimum daily travel distance for the total period of time that the animal was monitored. It was assumed that the cottontail eventually becomes accustomed to the collar, after which time his movements are little affected. There is no good evidence to either support or refute this assumption. The validity of the assumption can only be judged after more information has been gathered as to the effect of collars on cottontail behavior and movements.

Of the 11 animals tested in this manner, only three (R-205, R-241 and R-246) showed a significant difference between mean minimum daily travel distance during the first five days and mean minimum daily travel distance for the total period monitored. In each case the mean minimum daily travel distance was greater during the initial five day period than for the total monitoring period. In the case of R-241, the excursion into open country in a direction opposite the direction that would have taken the animal to its home range, was probably due to disorientation after release. R-205's fairly long term excursion into an area along the south edge of the study area far from its home range began a few days after his initial capture. In the case of R-246, the significant difference between the two classes of mean minimum travel distances was due primarily to the long distance traveled during the first night after release. This long movement is in all probability due to the animal being captured initially on the extreme perimeter of its range. Return to its normal resting area accounts for the long distance involved in the first night's movement. In the cases of R-205 and R-241, then, differences in mean minimum daily travel distances may possibly be reactions to handling or the transmitter collar. It is possible that some factors may account for the differences. It should also be noted that mean minimum travel distance compares the distance between daily resting locations or between trapping locations and daily resting locations, a distance that may not accurately reflect the true extent of the animal's movement. For that reason these data may be of limited use as an indicator of the effect of the collar and handling on cottontail movement.

If this comparison was valid and reflects the effect that handling and placing a collar on a cottontail has on its movements, then it would appear that most rabbit movement was not significantly affected by handling or radio-tagging.

Cottontail Home Ranges

Home range is defined by Burt (1943) as "that area traversed by the animal in the normal activities of food gathering, mating and caring for the young." According to him "occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range." The home range concept has become a cornerstone of animal behavioral and movement studies.

The home range concept has fostered interest over the years and has also generated the production of a large number of methods to measure home ranges (Brown, 1956). Many of these methods were developed for use with trapping data and are not readily adaptable to home range studies using radio-tracking data. Some, such as the Modified Minimum Area Method (Harvey and Barbour, 1965) were designed for use with data gathered by radio-tracking or radio-nuclide tagging studies.

With the advent of computer technology and an emphasis on modeling, several of the more mathematically inclined biologists have developed home range models designed primarily to make home range data more readily comparable and subject to statistical treatment (Calhoun and Casby, 1958; White, 1964; Jennrich and Turner, 1969; Koeppl et al., 1975).

A number of the methods mentioned above will be used to calculate home ranges of radio-tracked animals studied on the Ross Natural History Reservation.

Ranges as determined by the Minimum Area Method (Mohr, 1947)

The Minimum Area Method (MAM) is one of the most commonly used methods of home range determination. This is due to its simplicity and frequency of use. Table V summarizes home range areas as determined by the MAM for 16 rabbits monitored during the study.

Before the MAM can be applied to a set of locational data points, certain subjective judgements must be made as to which points will be used in the range determination. According to Burt's (1943) definition of home range, investigatory sallies or movements of an exploratory nature obviously outside the home range proper are not to be included in estimates of the home range area. Though this seems reasonable, at times it is difficult to determine which points should be rejected.

In the cases of rabbits R-205, R-241 and R-246, there was some question about whether or not some points should be considered as excursions (Appendix B). Values for the ranges of R-205 and R-241, when all points are included, were substantially larger than the range values calculated when these points are rejected (Table V).

In each case, the decision to reject certain points or retain them was based on a subjective analysis of the evidence. In the case of R-241, the point in question was undoubtedly an excursion. The animal was discovered in this area only once, on the day following her release, indicating that upon release the animal may have been disoriented and moved in a direction away from her home range. She found cover under a multiflora rose hedge and was located there the day following release. After the first day, she returned to her home range.

Table V. Home range areas as determined by the Minimum Area Method for the 16 radio-tracked rabbits. N = number of locational data points.

Rabbit Number	Sex	N	Range (acres)	Qualifications
** R-205	M	54	8.09	Total range
			3.59	Home range, no excursion
R-236	M	13	4.12	Pond excluded
** R-237	F	39	2.83	------------------------
R-240	F	9	1.46	------------------------
** R-241	F	89	7.67	Total range
			5.69	Home range, no excursion
R-245	F	8	2.59	------------------------
** R-246	F	51	2.50	------------------------
R-247	F	11	2.85	------------------------
** R-252	F	27	2.16	------------------------
R-260	M	36	2.03	------------------------
** R-263	F	51	.71	------------------------
R-265	M	19	.60	------------------------
** R-268	F	21	1.81	------------------------
** R-271	M	58	4.55	------------------------
R-272	M	5	.36	------------------------
** R-273	F	41	1.31	------------------------

** Rabbits that were determined to have ranges that had been adequately sampled.

The range of R-205 was more difficult to delineate. What was obviously an excursion, in that only a few points (6) are involved and a long distance separates them from the area of concentration, occurred several days after the animal was released. From 18 December 1974 to 1 January 1975, with only one exception, the animal remained within the excursion range, though only seven locations were determined during this period. After this period, the animal concentrated its activities within the church site area and never returned to the excursion area even though it survived until 17 February 1975. Tentatively, these six points were considered as a long term excursion, possibly due to the animal's initial reaction to the transmitter or some unknown factors. It seemed apparent that the animal was able to find food and cover during the period that it remained in the excursion area and that to call this excursion an investigatory foray would be over simplification.

The points in question in the range of R-246 was trap captures of the animal made before it was radio-tagged. After radio-tagging the animal was never again found in this portion of its range. The fact that these trap captures occurred at widely separated times, and in one case the animal was trapped in the same trap twice, would seem to indicate that though this area is distant from the area where the animal was normally found resting, it was evidently within the range of R-246's forays. For this reason, the three locations were considered to be legitimate parts of this animal's home range.

Two authors (Harvey and Barbour, 1965; Quadagno, 1968), have attempted to devise methods to more objectively determine which points represent investigatory forays. In both cases, decisions involved the more or less arbitrary assignment of a distance from some reference point beyond which a point is considered a sally. Quadagno (1968) avoided this problem by coining the term "total range" which he used to describe a polygon connecting all the outside locational data points regardless of their position in relation to an area of concentration. To determine the home range as normally defined, Quadagno (1968) suggested that any point located two times farther than the calculated average distance from a center of activity was an occasional sally. If, however, an animal was found twice at a location that would be considered an occasional sally by the above criterion that point was considered to be a part of the regularly traversed area and included as a part of the home range. This rule seemed to be generally applicable but should probably be used in conjunction with a subjective appraisal of the situation.

Nine rabbits' ranges were judged to have been adequately sampled. Mean home range area for all rabbits having adequately sampled ranges was 2.79 acres. Mean home range for males having adequately sampled ranges was 4.07 $\pm$ .68 acres (N=2). Mean home range for females having adequately sampled ranges was 2.43 $\pm$ 1.60 acres (N=7). The difference between the sexes was not significant.

In most cottontail home range studies conducted in the past, MAM was used to determine the home range area. Table VI summarizes the home range areas reported in the literature for adult cottontails.

In most cases, home range areas calculated for rabbits in the current study were smaller than those reported in the literature. There are a number of factors that account for the differences.

Table VI. Home range areas reported in the literature for adult cottontail rabbits. All home ranges are annual unless otherwise noted.

References	Method	Mean Home Range Areas (acres) Males	Females
Dalke *	Trapping	8.3	2.9
Allen *	Trapping	3.6	2.2 **
Schwartz (1941)	Trapping	1.4	1.2
Haugen (1942)	Trapping	---	14.0 **
Atzenhoefer and Martin *	Trapping	16.4	13.3
Bruna *	Trapping	13.3	4.3
Janes (1959)	Trapping, Tracking	8.9	7.8
Lord (1963)	Trapping	2.3	2.3
Trent and Rongstad (1974)	Radio-Tracking	8.6	3.4
Current study	Radio-Tracking	4.1	2.4

* Cited in Trent and Rongstad (1974).
** Winter ranges.

A major factor contributing to variation of home range sizes reported in the literature is the variety of methods that have been used to measure them (Janes, 1959; Trent and Rongstad, 1974). Not only have the studies differed in the method of data collection (trapping, tracking or radio-tracking), but also in methods of analysis. The manner in which locational data are analyzed may make a considerable difference in the reported range value.

Home range values reported by Janes (1959) are an example of how the method of range determination can affect reported range value. Janes, using his composite method, calculated mean home range areas for adequately sampled female ranges to be 7.8 acres and for males to be 8.9 acres. The composite method based home range determination on trapping data points and also tracking. Janes also calculated home ranges using MAM. Home range values for males (2.00 acres) and females (2.54 acres) were considerably smaller than those determined by the composite method. Depending on the method of analysis used, different conclusions about how an animal's sex affects its home range size were reached.

Other factors contributing to differences in reported home range areas for cottontails are differences in the abundance of food and cover on the various areas studied (Trent and Rongstad, 1974). Marked differences in cover and food abundance are undoubtedly reflected in an animal's home range size and could account for much of the variation in reported home range areas. Home range size also may be affected by population densities on the area studied because densities are at least partially affected by the quality of the study area cover and abundance of food (Trent and Rongstad, 1974).

Radio-tracking studies show promise as a means of discovering factors that affect the shape and area of the home range. Further radio-tracking studies of cottontail home ranges should help fill the void that presently exists in the available knowledge on accurately determined home range areas.

Ranges as determined by the Modified Minimum Area Method

Harvey and Barbour (1965) suggested that their Modified Minimum Area Method (MMAM) of home range determination was an improvement over the MAM because 1) they felt that in all probability the MAM was giving home range estimates that were too large, including areas from which no indications of the animals presence had been collected (Appendix B); 2) all points are included within the MMAM determined range; and 3) the MMAM gives an objective tool for the determination of which points are sallies outside the home range.

Range areas as determined by the Modified Minimum Area Method (MMAM) were from 18.8 to 92.5 per cent (mean = 43.0 per cent, N=9) of the ranges determined by MAM for rabbits having adequately sampled home ranges (Table VII). Mean ranges for males was 2.86 $\pm$ .66 acres (N=2) and .98 $\pm$ .93 (N=7) for females. Male ranges were significantly larger than female ranges. This conclusion differs from the one drawn from a comparison of range areas as calculated by the MAM. Since these two methods of range determinations are in all probability measuring two different things, the fact that one indicates a sex difference between range areas and the other does not is not surprising. Examination of some theoretical implications inherent in these methods and speculation as to what they measure should help explain why these methods yield such different results.

A number of investigators have found that home range area, as determined by the MAM, often contains areas within it with which the animal is not familiar, that is, areas in which the animal was never located (Odum and Kuenzler, 1955; Harvey and Barbour, 1965). For this

Table VII. Home ranges of 16 radio-tracked cottontails determined by the Modified Minimum Area Method compared to home range values determined by the MAM.

Rabbit Number	Sex	Range MAM (acres)	Range MMAM (acres)	MMAM/ MAM
** R-205	M	3.59	3.32	.925
R-236	M	4.12	1.87	.454
** R-237	F	2.83	1.00	.353
R-240	F	1.46	.05	.034
** R-241	F	5.69	2.97	.522
R-245	F	2.59	.04	.015
** R-246	F	2.50	.73	.292
R-251	F	2.85	.18	.063
** R-252	F	2.16	.62	.287
R-260	M	2.03	.51	.251
** R-263	F	.71	.16	.225
R-265	M	.60	----	----
** R-268	F	1.81	.34	.188
** R-271	M	4.55	2.39	.525
R-272	M	.36	----	----
** R-273	F	1.31	.73	.557

** Rabbits that were determined to have ranges that had been adequately sampled.

reason, Odum and Kuenzler (1955) coined the terms "maximum territory", which is the equivalent of Quadagno's (1968) "total range" and is in many cases equal to the home range as determined by the MAM, and also "utilized territory" which is some portion of the maximum territory. The portion of the maximum territory this utilized territory, or area of utilization, includes is dependent on distribution of habitat features within the maximum territory, location of feeding sites, nesting sites and usage patterns (Odum and Kuenzler, 1955). From an ecological-management standpoint, the area of utilization is probably more important than the maximum territory although unfortunately it is also more difficult to estimate than the maximum territory.

Area of utilization not only varies with habitat features and distribution of feeding and nesting sites, but is also affected by innate behavior patterns. Certain animals tend to establish and follow a relatively simple system of trails, rather than spreading their activities over a large area (Young *et al*., 1950). Animals such as pocket gophers, field mice and rats use only a small part of their range as determined by methods such as the MAM, because they use trails through an area and not random locations within the range (Davis *et al*., 1948). In these animals terrain configuration and trail patterns have an effect on the calculated range area. In animals that confine their movements to trails, real measures of range are meaningless and generally linear measures of home range are used (Davis *et al*., 1948: Young *et al*., 1950; Davis, 1953).

Area of utilization has also been found to vary from day to day. Analysis of the movements of a raccoon monitored at one minute intervals as it moved about on the Cedar Creek Natural History Area indicated that the animal covered only a portion of its home range each day. It took approximately four days for this animal to cover most of its range (Tester and Siniff, 1965).

According to Janes (1959), cottontail rabbits do not generally use pathways or runways while foraging. Neither do they range across the home range area at random. As can be seen by examining the locational data points collected for each rabbit in this study, certain areas were used more frequently and intensly than others (Appendix B). Janes (1959) also reported that the area of utilization for cottontails varied from day to day. He found that foraging cottontails utilized 10 to 20 per cent of their home range areas in one evening.

The differing results that the two methods of home range determination yield are easily explained when one examines the parameters that each attempts to measure. MAM attempts to measure the total area of a rabbit's range; MMAM is a method designed to estimate the area of utilization. Significant differences between male and female ranges, as indicated by the MMAM, indicate that although there is no significant difference between maximum ranges of male and female cottontails, there is a significant difference in the area of utilization depending on the rabbit's sex.

Before concrete conclusions can be made regarding effectiveness of the MMAM in measuring an animal's area of utilization, radio-tracking information for animals during their activity periods and over extended periods of time must be available. Only through analyses of such detailed movement data can the validity of this method be checked and suggestions be made for its improvement.

Trap Determined Ranges Compared to Radiotelemetry Determined Ranges

In the preceding description of range calculations, both radio locational data points and trapping points were used in determining home range. When data point types are used separately and home range is calculated using only one type, home ranges are generally smaller (Table VIII).

Table VIII. Home ranges as calculated by the MAM using all data points, radio location points only and trapping location points only. N = number of trap locations used in trapping range determination.

Rabbit Number	Range (All Points)	Range in Acres (Radio-locations)	Trapping Range Area (Acres)	N
R-205	3.59	3.59	----	2
R-236	4.12	4.03	----	1
R-237	2.83	1.02	1.71	7
R-240	1.46	.34	1.14	4
R-241	5.69	5.32	.51	3
R-245	2.59	.31	1.58	5
R-246	2.50	.71	1.07	6
R-251	2.85	.71	.62	3
R-252	2.16	1.78	.29	4
R-260	2.03	1.54	.67	3
R-263	.71	.51	----	1
R-265	.60	.45	----	1
R-268	1.81	1.51	.47	6
R-271	4.55	4.30	----	1
R-272	.36	.36	----	1
R-273	1.31	1.02	1.12	11

In almost all cases range, as determined by MAM using radio location points only or daily resting locations only, is smaller than range calculated when all data points are used. This difference is due to the fact that 64.4 per cent of the data on trapping location points were located on the perimeter of the range so that their exclusion from the calculation leads to a smaller home range area.

Ranges calculated when only trapping locations are used are for the most part smaller than ranges calculated using all data points. This discrepancy is primarily due to the small number of capture points usually available to form the range polygon. There appears to be no minimum number of capture points that will insure that the home range is adequately sampled. In the cases of R-240 and R-273, four and 11 capture points, respectively, were necessary to approach the home range determined when all data points were used.

In several cases ranges calculated using only trapping data points are larger than ranges calculated from only radio locational data points. This is because animals were most frequently trapped on the perimeter of their ranges, in many cases outside of the area in which they were found resting during the day.

Differences between trapping location range areas and radio location range areas point up the difference between what the two types of data points represent. Radio location points represent daily resting locations while the trapping locations are undoubtedly the result of capture while the animal was foraging, in many cases at locations outside of the area which would be indicated as its home range if only daytime resting locations were used to determine home range. Trap locations were indications of the extent of nighttime movements of the monitored cottontails and apparently indicate that in many cases daytime resting locations do not adequately represent an animal's total range.

During this study, only one rabbit (R-241) was monitored to any extent during its evening activity period. A total of 16 radio locations were obtained during five nights of observation in late November and early December. Home range area of the nighttime locations as determined by the MAM was 4.60 acres (.49 acres by the MMAM). Home range for all points (night and day radio locations and trapping locations), not including the obvious excursion, was 8.22 acres. This is considerably larger than the range of 5.69 acres calculated when daytime resting locations and trapping locations are used. Since data were gathered only on this one individual it is not known how well daytime resting locations represent ranges of other rabbits or home ranges in general. Data gathered on this one individual seem to indicate that daytime resting locations used exclusively will result in the animal's range being greatly underestimated.

Trent and Rongstad (1974) used daytime resting locations to plot home range areas of Wisconsin rabbits and concluded that home ranges based on daily resting locations showed no important differences when compared with ranges determined from locations gathered during nighttime monitoring. They based their conclusions on the reliability of daily resting locations being representative of the home range on the following: 1) on only one occassion did they recapture a rabbit in a trap not within its home range as determined by resting locations; 2) monitoring the animals at night and determining their home range using only nighttime locations indicated no important differences between the home ranges calculated using daytime resting locations and home ranges calculated using nighttime locations; 3) three rabbits chased by beagles remained within their range as determined by daily resting locations; and 4) home ranges calculated using resting locations were similar to those found in the literature.

In this study rabbits were regularly recaptured outside their home ranges as determined by daily resting locations only. There appeared to be important differences in home ranges based on nighttime locations and home ranges based on daytime resting locations. Although most locations recorded for R-241 were within the home range indicated by trapping and daytime resting locations, a number of locations were in areas where the animal had never been located resting or trapped. After examining illustrations in Trent and Rongstad's (1974) article, it also appears that what this author would consider as "important differences" in home range area and location also occurred in their study.

Use of beagle chases as a method of range determination for rabbits was described by Toll et al. (1960). They felt that this method of range determination had much promise and cited the following reasons: 1) ranges determined by this method agreed closely with those determined by capture-recapture methods; and 2) successive chases of the same animal encompassed similar areas and is evidence of the validity of this method.

In Janes' (1959) study rabbits were tracked and pursued and it was found that it was not easy to drive a cottontail out of its home range. He concluded that the resulting chase trails were usually circular and covered 70 to 90 per cent of the rabbit's home range. Davis et al., (1948) speculated that the major function of a definable home range may be protection from predators resulting from the animal's intimate acquaintance with its home range. If this knowledge of local surroundings is of significance in protection then evolutionary selection of individuals which have an innate disposition to remain in a home range is possible (Davis et al., 1948). Such an innate disposition may account for the difficulty Janes (1959) had in driving cottontails from their home range. If such an innate disposition to remain within its home range was found in cottontails, then the beagle chase method should be at least an indicator of home range size and location.

In the present study one rabbit (R-271) was chased by the investigators and her trail was recorded. She was trailed on eight occasions (Fig. 3). In each of the chases she moved through some areas where she had not been located resting. If these chases were indicative of the animal's range, radio location and trapping ranges appreciably underestimated the true home range.

It appears that the rabbit's penchant for running in a circle within its home range was either not evident in the animal monitored in this manner or that radio-tracking determined range considerably underestimates the true range. Which of these options is correct can only be resolved by subjecting more animals to chases and determining whether this animal's response was abnormal, or it was an indication of a normal rabbit response to being chased.

A number of factors affect movements of a cottontail when it is pursued. Undoubtedly the pursuer's approach path would have some effect on the direction in which the rabbit would move as would the presence of other barriers, both physical and behavioral. If the animal is on the perimeter of its home range it is possible that the chase could force the animal out of its range and thus negate the effectiveness of this method in measuring the home range. It appears that this happened a

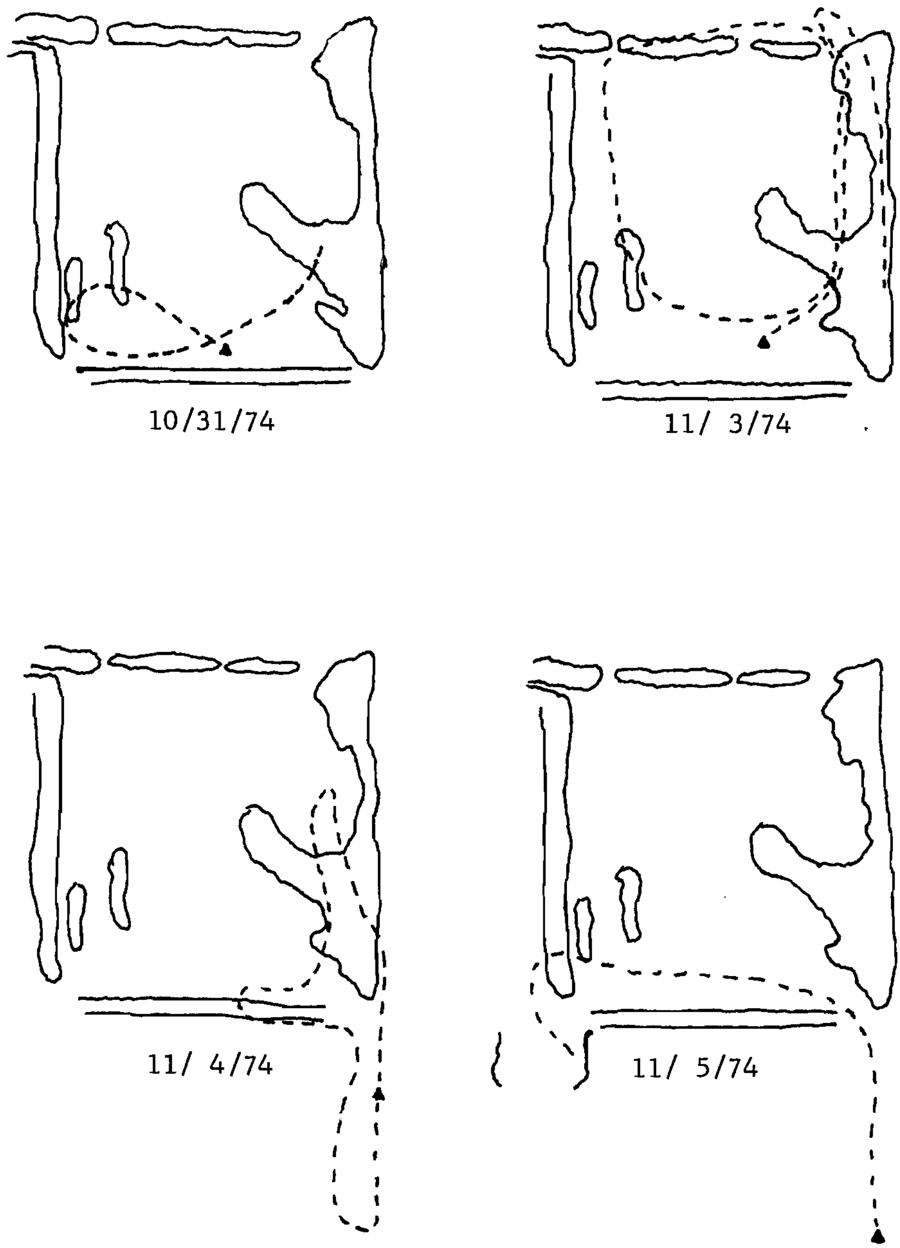
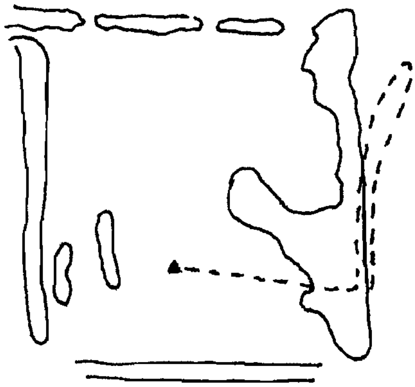
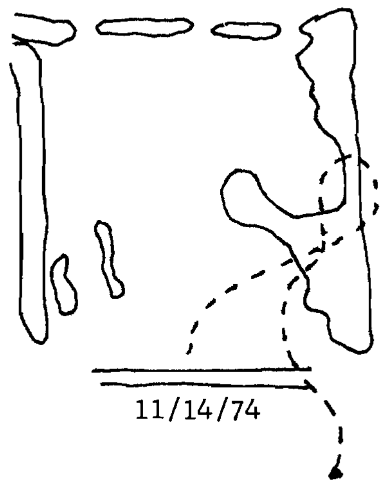


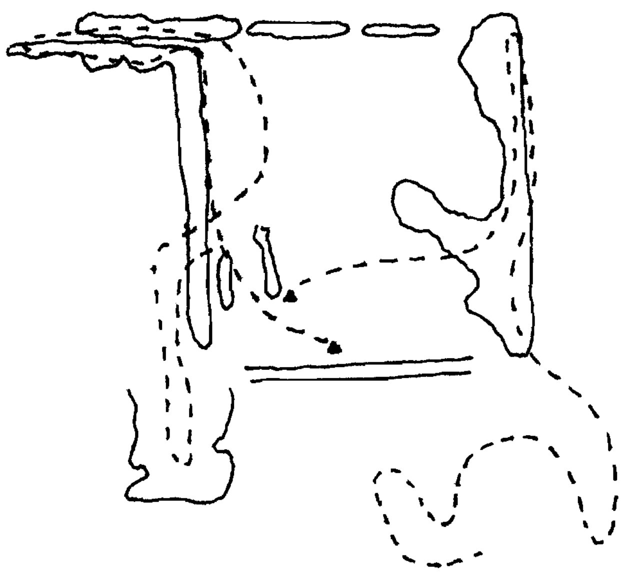
Fig. 3. Chase trails for eight chases of rabbit R-271. ▲ represents start of chase.



11/7/74



11/14/74



11/15/74

Fig. 3. (Cont'd)

number of times with R-271.

In all probability, the rabbit, once forced out of its range, will attempt to return. To consider this loop that the animal may have made just to return to the perimeter of its home range to be representative of the animal's range would seem to me to be ill advised when one considers all the variables that may affect the animal's response to pursuit and the resulting path of movement. Only after more chases have been made on a large number of animals can the validity of chase methods for range determinations be judged.

After examining the points presented by Trent and Rongstad (1974) as evidence supporting the effectiveness of daily resting locations as indicators of range size and how they apply to data gathered during the current study, it appears that daily resting locations are inadequate as indicators of the animal's home range area. To get home range areas that are truly representative of the animal's range, daytime resting locations must be used in conjunction with trapping locations and/or nighttime locations. Gathering information on nighttime movements is particularly important for animals such as the cottontail that are primarily active during the early evening, night and the early morning.

Home Range Shape

Blair (1942) speculated that some factors within the biotic community must be determinants of shape and extent of an animal's home range. What these factors may be is not known. Such factors as the local distribution of plants that serve as food and cover, interrelationships between conspecifics and relationships between other species have been suggested as determinants of shape and extent of range (Blair, 1942).

It has been generally assumed that a circular home range is indicative of an optimum and homogeneous habitat. Allen (1939) stated that in cases where food, water and other requirements are close at hand, home ranges are likely to be small and compact. Janes (1959) reported that cottontail home ranges are roughly circular in uniform habitat.

Stumpf and Mohr (1962) examined the literature and found that linear home ranges have been reported for many animal species. They theorized that linear home ranges may reflect habitat preferences in areas with heterogeneous cover, the influence of barriers to movement from one area to another, or the unsuitability of physical and biotic conditions in the area in which the animal lives, the less satisfactory the conditions the longer and narrower the range. Mohr (1965) felt that in all probability polygamous species, in which males and females maintain separate home ranges, would find it extremely difficult to maintain circular home ranges.

One measure of range shape is the length-width ratio of the range axes (Table IX).

The mean length-width ratio of all adequately sampled ranges was 1:2.56 (N=9). Mean length-width ratio for males with adequately sampled ranges was 1:3.69 ± 1.41 (N=2); mean length-width ratio for females with adequately sampled ranges was 1:2.24 ± .53 (N=7). The ratio for males was significantly larger than the ratio for females. Only after more data are gathered, will it be possible to determine whether this significant difference is real or due to the small sample size.

Table IX. Lengths of long and short axes of home ranges and length-width ratios of radio-tracked rabbit ranges.

Rabbit Number	Short Axis (yards)	Long Axis (yards)	Ratio
** R-205 *	68.8	322.3	1:4.68
R-236	124.7	382.4	1:3.07
** R-237	98.5	255.1	1:2.59
R-240	84.7	171.4	1:2.02
** R-241 *	138.6	374.7	1:2.70
R-245	133.4	201.2	1:1.51
** R-246	84.2	235.1	1:2.79
R-251	104.7	268.4	1:2.56
** R-252	104.2	165.8	1:1.59
R-260	93.4	194.0	1:2.07
** R-263	59.5	92.9	1:1.56
R-265	40.0	102.7	1:2.56
** R-268	75.5	190.9	1:2.53
** R-271	124.2	334.7	1:2.69
R-272	41.1	79.0	1:1.93
** R-273	78.5	149.9	1:1.91

* Excursion points not included in measurement.
** Adequately sampled ranges.

Stumpf and Mohr (1965) calculated length-width ratios based on data collected by Dalke and calculated the range length-width ratio for male cottontails to be 1:2.4 and 1:2.5 for females. Similar calculations based on data gathered by Allen (1939) yielded a ratio of 1:2.6 (Stumpf and Mohr, 1965). Both of these ratios agree in general with those calculated for rabbits in this study. The major difference between their ratios and those calculated in the current study is due to differences in the ratios for the two sexes derived from Dalke's data and ratios for males and females found in this study. Dalke's data show little difference between the two sexes range shapes while in this study a significant difference was noted. Part of the difference is due to the fact that the two ratio pairs are not directly comparable. Dalke's home range data were obtained using the capture-recapture method of range determination and may not be directly comparable with ranges determined by radio-tracking and trapping. More importantly, only 90 per cent of Dalke's observations were used in the length-width ratio determination (Stumpf and Mohr, 1962). Additional data collection using radio-tracking techniques and a similar method of range length and width determination may answer the question of whether there is a sex difference in range shape.

Examination of the orientation of the home range axes seems to indicate that barriers, such as streams, "edge", and vegetation distribution directly affect orientation of range axes. This is particularly evident in the rabbit ranges located below Gladfelter Pond (R-236, R-252, R-260, R-273, R-268, Appendix B).

Each of the factors mentioned by Stumpf and Mohr (1962) probably play some part in determining why cottontails maintain linear ranges. Especially important on the Ross Natural History study area are habitat heterogeneity and the presence of barriers to cottontail movement.

Home Range Models

Van Winkle (1975), in his summary of the several home range models, classified the models as being one of two types. One type, the univariate models, has been used by a number of authors (Hayne, 1949; White, 1964; Brussard _et al_., 1974; Doebel and McGinnes, 1974). All models of this type assume a circular home range shape and a normal distribution of data points around the center of activity. These models imply that the only rabbit position information that is important is the distance from a capture point to the center of activity and that direction is not important. Although these assumptions may be true in areas with homogeneous environments, it is doubtful that they are applicable to the present study area.

More recently, bivariate models have been proposed that are not based on the assumption of circularity of home range shape (Jennrich and Turner, 1969; Van Winkle et al., 1973; Koeppl et al., 1975). They do require that position points conform to the bivariate normal distribution and a number of other constraints. As in the case of the univariate models, these conditions are difficult to meet in other than homogeneous habitats (Van Winkle, 1975). To date, only one model has been devised to analyze the distributions of locations that do not conform to the normal distribution and that is applicable to movements in heterogeneous habitats (Van Winkle et al., 1972). Unfortunately this model applies only to the relatively specialized case of animals inhabiting an ecotone.

Because of the numerous assumptions that must be met before a model can be confidently used, models are of limited use in delineating an animal's home range. When models can be applied to data they do assist in making inferences concerning an animal's relative familiarity with any point within its range. In most cases, the simpler methods of analysis (MAM and MMAM) are adequate.

The basic statistic common to both univariate and bivariate models is the center of activity. Hayne (1949) operationally defined this term as the geometric center of a set of capture points. Calculation of this statistic simplifies locational data by reducing it to a single point (Koeppl et al., 1975).

The significance of this point, as far as the animal is concerned, may be negligible in cases where the animal prowls the perimeter of his range and never approaches the calculated center of activity, or the point may coincide with the animal's nesting site and thus have significance. Ables (1969) coined the term "biological center of activity" to describe an area of high use as indicated by the clumping of locational data points.

Smith *et al*. (1973) suggested that in many cases an animal's calculated center of activity does not coincide with an area that is biologically significant and as a result this may have survival value. They reasoned that locating nesting sites and other biologically significant points on the periphery of the range would make it more difficult for predators to use information from direct or indirect observations to precisely predict the location of the nest site and this may increase an animal's chances for survival.

Figures contained in Appendix B show home ranges of radio-tracked rabbits and the location of the center of activity in relation to the other locational data points. In most cases, the center of activity is not located near any of the animal's biological centers of activity.

Analysis of the frequency distribution of locational data points around the center of activity (activity radii) has been used by Davenport (1964), Ables (1959) and Tester and Siniff (1965) as a method for determining if a home range has limits. This method of analysis may also be used for comparative purposes, comparing how individuals inhabiting different areas and the two sexes utilize the area surrounding the center of activity.

Odum and Kuenzler (1955) and Tester and Siniff (1965) concluded that barriers to movement, either physical or behavioral, would result in limitations on recapture radii and lead to kurtosis in a frequency distribution histogram of the radii. Odum and Kuenzler (1955) suggested that a test for kurtosis would be a good method for determining whether an animal occupied an area with a definite boundary. Ables (1969) also suggested that negative skewness (skewness to the right), which is indicative of data points concentrated near the periphery of the range, may be used as an indicator of the presence of boundaries.

Though these statistical analyses are helpful in determining whether or not a range has limits, Ables (1969) found that ranges with limits occurred without being detected by either method. In every case, Ables (1969) felt that a subjective appraisal of the situation could be used to determine the presence of range limits. He felt that the presence of a range shape, <u>per se</u>, other than a circle, suggested that a range had limits and could be used to reliably indicate the presence of range limits.

Frequency distribution histograms of recapture radii for all radio-tracked cottontails are included in Appendix C.

Each of these histograms show one of five combinations of skewness and kurtosis. The distribution of recapture radii for rabbits R-205, R-236, R-245, R-251 and R-252 are all leptokurtotic and skewed to the right. Distribution of activity radii for rabbits R-237, R-240, R-241 and R-246 are all leptokurtotic and skewed to the left. Distribution of activity radii for rabbits R-263 and R-265 are skewed to the left and show no kurtosis. Distribution of activity radii for rabbits R-268, R-272 and R-273 are skewed slightly to the left and show no kurtosis. Distribution of recapture radii for R-271 shows little skewness or kurtosis.

Only in the cases of R-263 and R-265 do distribution of recapture radii indicate the possibility that the range is circular. In all other cases, the frequency distributions deviate from what would be expected if the range was circular. In a number of cases, the range boundary appears to be indistinct, for example, in the case of R-241. This tailing off of the recapture radii distribution may be indicative of the situation or due in part to the inclusion of some locational data points that were considered excursion points (R-205) in the analysis. Even in cases where tailing is found, relatively few points are found in the tail, indicating that the periphery of the range has been approached. In almost all cases the ranges appear to have a definite shape other than circular, which also indicates that the ranges have limits.

Comparison of the frequency distributions of recapture radii for males and females indicated that activity was distributed differently around the center of activity depending on sex (Fig. 4). Females were much more likely to be found near the center of activity than males. The distribution of recapture radii for females was closer to that of a circular range than for males. In contrast, male recapture radii were more evenly distributed among the distance classes up to 100 yards. Further evidence of sex differences in home range usage come from the examination of the cumulative percentages of recapture radii for males and females for each distance class (Table X).

Eighty-six plus per cent of the female locational data points fell within 75 yards of the center of activity. A similar percentage of the

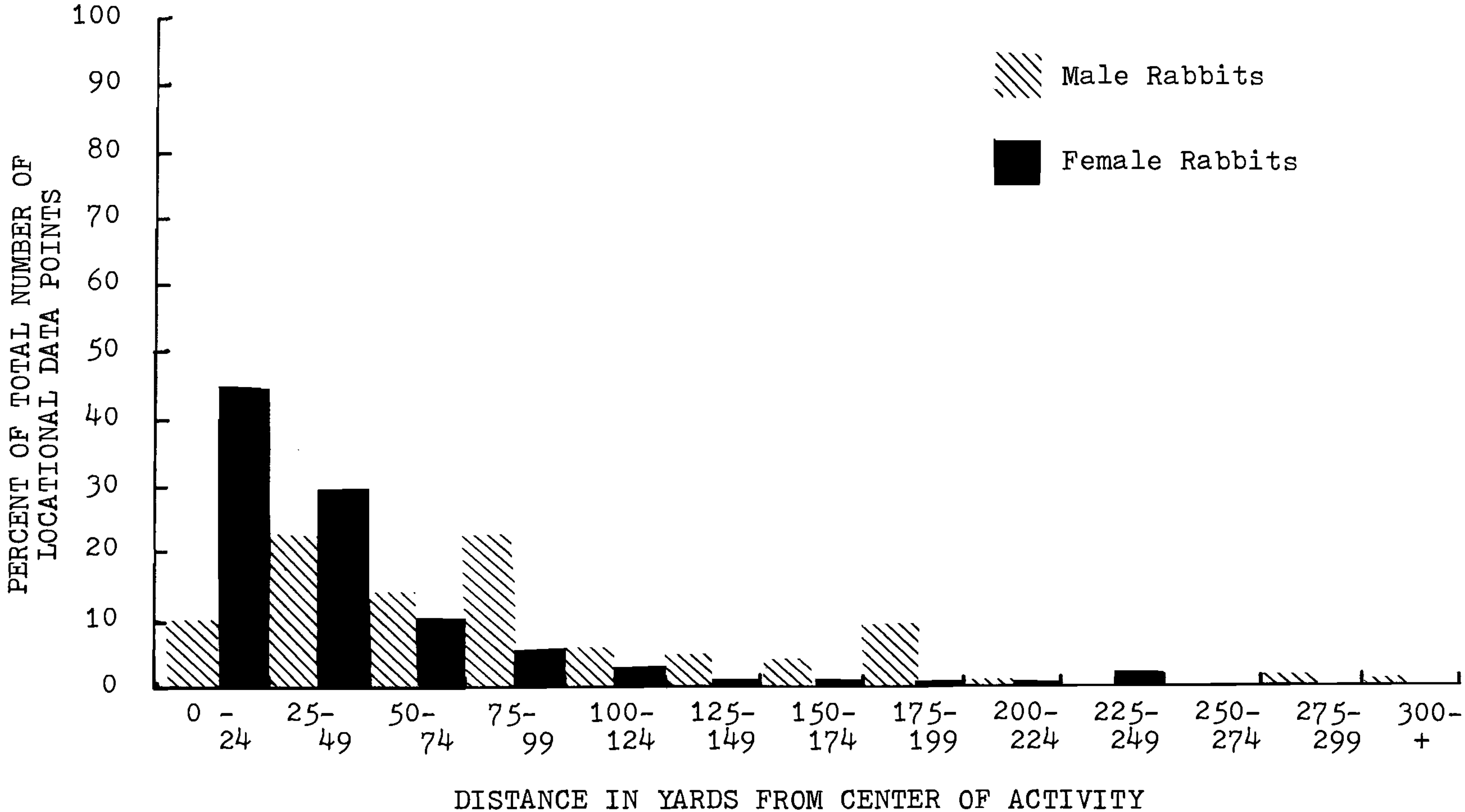


Fig. 4. Frequency distribution of recapture radii for males and females.

Table X. Cumulative percentage of data points within recapture radii for male and female rabbits.

Distance Class (yards)	Cumulative Percentage of Data Points Within Recapture Radii	
	Males	Females
0- 24	10.2	45.8
25- 49	33.3	75.6
50- 74	47.3	86.3
75- 99	71.0	92.4
100-124	77.0	95.6
125-149	82.4	97.0
150-174	86.2	97.9
175-199	95.9	98.2
200-224	97.0	98.5

recapture points fell within 175 yards of the center of activity for males. It appeared from these data and the frequency histogram data, that males range farther from the calculated center of activity than females and that they make more intensive use of areas farther from the center of activity than females. This would seem to agree with the conclusion that home ranges of males were on the average larger than those of females, though the differences in range size was not significant.

Comparison of the distribution of recapture radii for female rabbits inhabiting the area below Gladfelter pond and those inhabiting the church site area indicates that females in the church site area showed a greater tendency to concentrate their activity near their center of activities, though they were active to some degree to distances of 250 yards from the center of activity (Fig. 5). In contrast, female rabbits inhabiting the area below Gladfelter pond were less active in the immediate area surrounding the center of activity, but were not active at distances more than 125 yards from the center of activity.

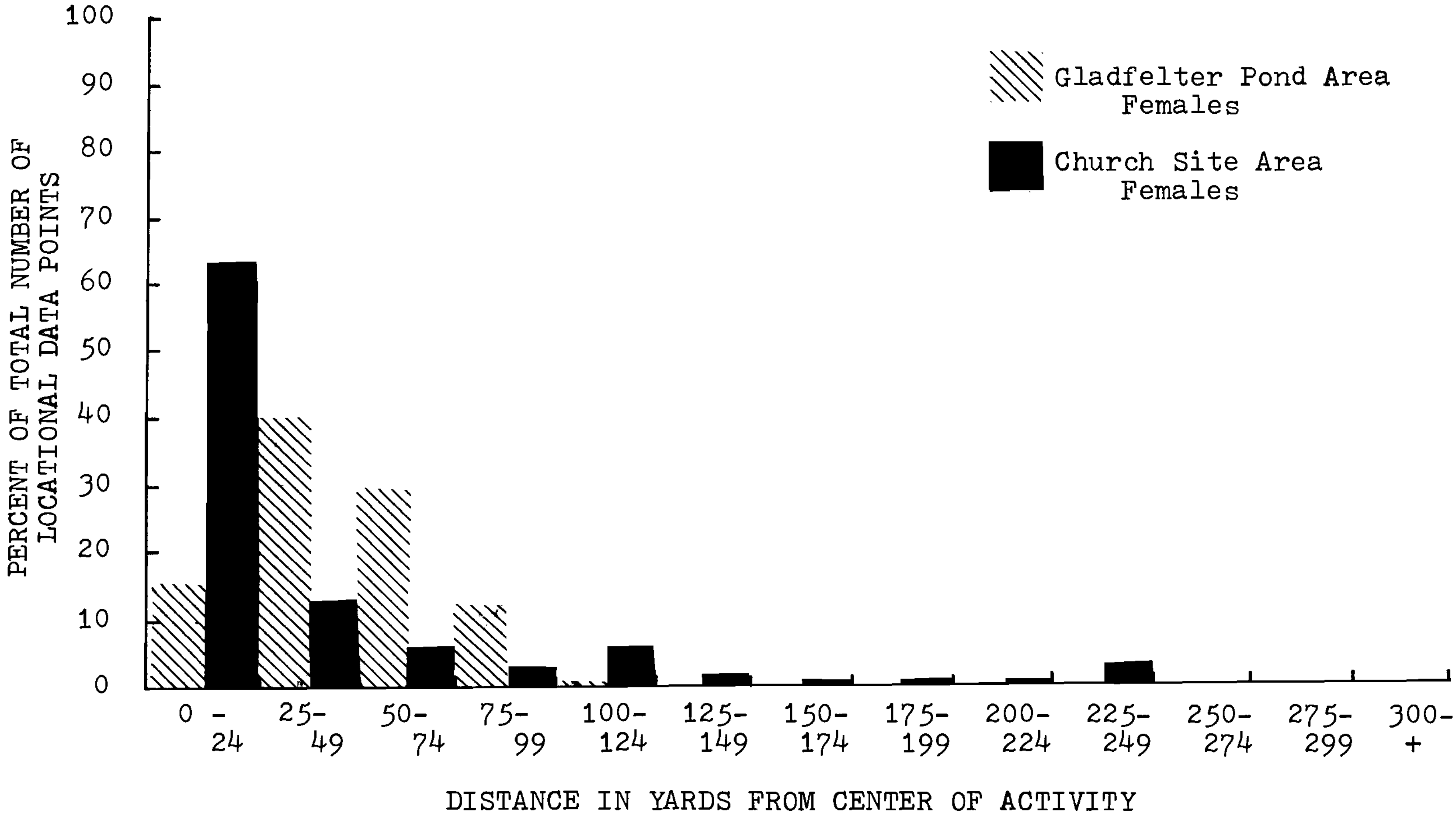


Fig. 5. Frequency distribution of recapture radii for female rabbits inhabiting the area below Gladfelter pond and the Church site area.

In both areas more than 80 per cent of the data points are found within 75 yards of the center of activity.

If it can be assumed that recapture radii would be shorter in areas of good habitat than in areas of poor habitat, then it would appear that there is little difference between the two areas. In all probability, differences that appear when the histograms are compared can be attributed to differences in terrain features between the two areas rather than habitat inadequacies that necessitate movements over a larger area in order for the animals to survive. The area below Gladfelter pond is surrounded by barriers to movement, in the form of a stream course on the south side and a drainage draw that limits the extent of good cover on the north side. Fewer barriers to movement are evident in the church site area. The presence or lack of barriers may also account for the fact that a comparison of the home range areas of rabbits from these two sites indicate a significant difference between the two.

Circular Home Range Model

The standard area of activity, an estimate of home range area devised by Brussard _et al_. (1974), was used to illustrate how circular home range estimates compare with the other methods of determining home ranges (Table XI). There appears to be no pattern to the differences between the MAM home range areas and the standard areas of activity. Some ranges calculated by the standard area of activity method are larger than ranges calculated by the MAM, others are smaller. In a number of cases there is surprisingly close agreement, in most part due to chance and in a few cases due to the fact that some of the home ranges approach circularity.

Table XI. Standard range radius, standard area of activity and home range areas determined by the MAM, for all radio-tracked rabbits.

Rabbit Number	Standard Range Radius (yards)	Standard Area of Activity (acres)	Home Range Area (MAM) (acres)
R-205	172.15	19.24	3.59
R-236	125.93	10.29	4.12
R-237	59.43	2.29	2.83
R-240	62.82	2.56	1.46
R-241	70.37	3.21	5.69
R-245	75.29	3.68	2.59
R-246	47.90	1.49	2.50
R-251	88.22	5.05	2.85
R-252	57.33	2.13	2.16
R-260	53.68	1.87	2.03
R-263	22.57	.33	.71
R-265	33.03	.71	.60
R-268	52.40	1.78	1.81
R-272	39.50	1.01	.36
R-273	49.81	1.61	1.31

Mean standard area of activity for all rabbits with adequately sampled ranges (N=9) was 4.19 acres. Mean standard area of activity for males was 12.43 $\pm$ 9.64 acres (N=2); mean standard area for females was 1.83 $\pm$ .88 acres (N=7). The difference between the standard areas of activity for males and females was significant.

Elliptical Home Range Model

The elliptical home range model devised by Koeppl _et al_. (1975) was used to analyze the locational data points collected for each rabbit.

Of the 16 animals for which data were available, only four were suitable for analysis using the model. Data for the other 12 animals were judged inadequate either because of few data or because distribution of data points did not conform to the bivariate normal distribution.

The area of the 95 per cent confidence ellipses was from two to three times larger than the areas calculated by the MAM (Table XII; Fig. 6). In all cases the area of the 75 per cent confidence ellipse was close to the MAM calculated range value.

Koeppl _et al_. (1975) believed that this model provides a reliable measure of home range size if the locational data follow a bivariate normal distribution. Their use of confidence ellipses or probability ellipses make it possible to determine quickly the probability of an animal being found at any location within its range.

The model suffers from the same problem that affects the MAM. Both methods include areas with which the animal is, in all probability, not familiar. The elliptical model contains even more area with which the animal is unfamiliar than the MAM calculated range and thus probably greatly overestimates the animal's range. Only further data collection

Table XII. Home range areas for five confidence ellipses calculated using the Koeppl *et al*. (1974) model for rabbits R-260, R-268, R-271 and R-273.

	Confidence Ellipses		
Rabbit Number	Per cent	Area (acres)	MAM (acres)
R-260	50	.96	
	75	1.85	2.03
	90	2.99	
	95	4.23	
	99	6.55	
R-268	50	.94	
	75	2.14	1.81
	90	3.61	
	95	4.94	
	99	8.31	
R-271	50	2.09	
	75	4.23	4.55
	90	6.91	
	95	9.34	
	99	14.26	
R-273	50	.79	
	75	1.52	1.31
	90	2.46	
	95	3.46	
	99	5.38	

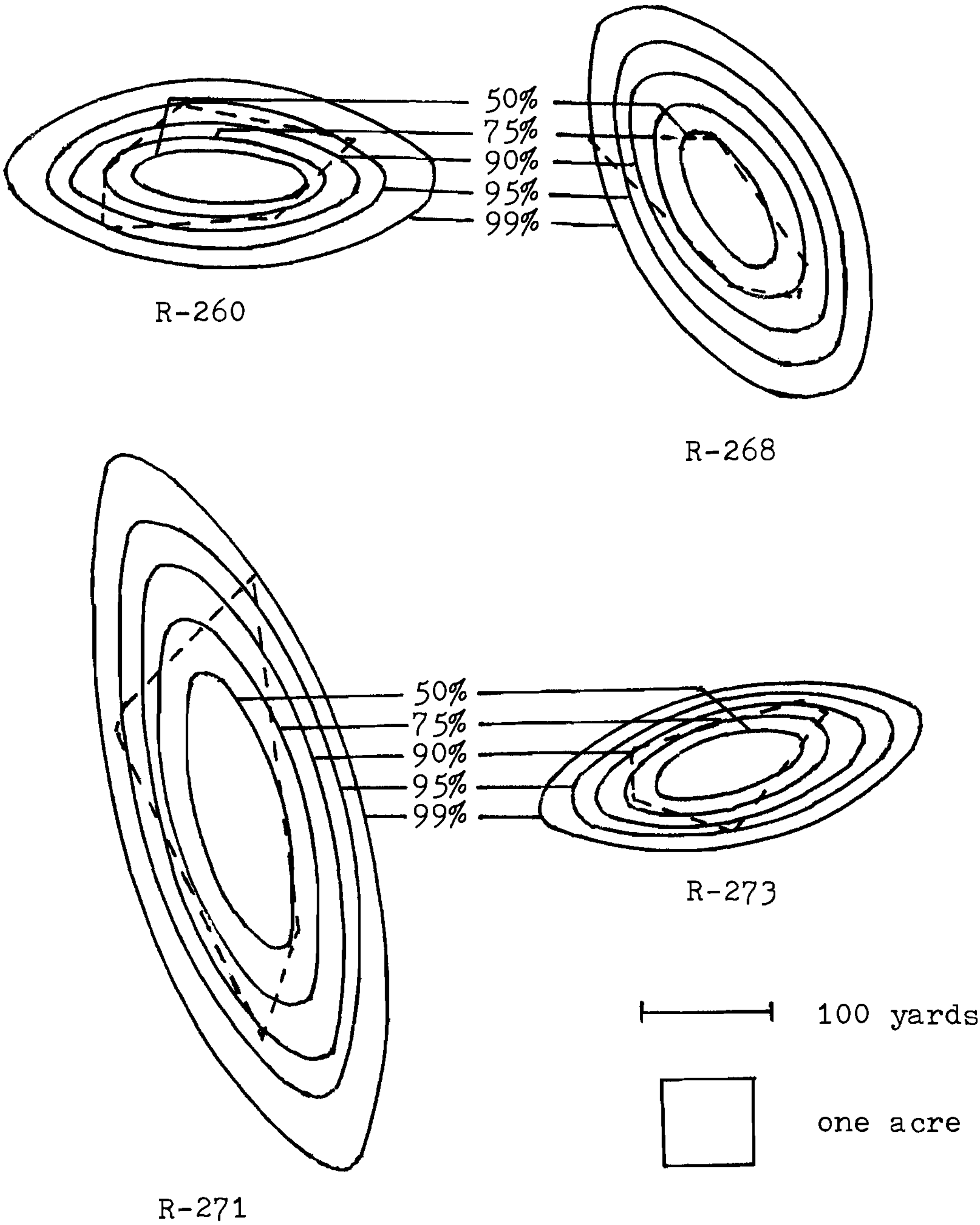


Fig. 6. Fifty, 75, 90, 95 and 99 per cent confidence ellipses for the data points of four rabbits calculated using the Koeppl et al. (1974) model and the home range as determined by the MAM (dashed lines).

and analysis using this method will determine whether it is a useful method of range determination. At present, it appears that the simpler methods of range determination (MAM and MMAM) yield more useable information than these more complex models. Further attempts to develop models that are applicable to real situations may change this situation.

Home Range Estimators

Since it is rarely possible to determine the ranges of large numbers of animals using radio-tracking techniques, as these techniques involve considerable cost and expenditure of time, estimators of home range area derived from range values for radio-tracked animals which allow range determinations from much less or readily obtainable data would be useful.

Two such methods have been suggested in the literature. McNab (1963) suggested that animal size greatly affects the home range of an animal in that 1) the animal's size affects the size of the area that it can move over and 2) a large animal will have greater energy requirements than a smaller animal, which would necessitate movement over a larger area to gather food unless food was present in superabundance. McNab (1963) examined the literature and found that there appeared to be a relationship between an animal's mass and its home range area. He further refined his analysis by dividing the mammals into two feeding types, hunters and croppers, for which he derived separate equations reflecting the relationship between the animal's weight and home range area (McNab, 1963). He placed rabbits in the cropper class, for which he derived the equation $R_c = 3.02\ W^{0.69}$, where R_c equals range in acres and W equals the animal's weight in kilograms, as the home range area estimator.

Home range areas calculated using this equation (Table XIII) do not differ significantly from those calculated by the MAM, though the equation is not capable of differentiating differences between individuals within the species, as it was derived using animals of different species to show that bioenergetic and body size play a part in determining range size through a whole range of animal sizes.

To improve upon McNab's (1963) equation, a simple linear regression analysis was run using weight and range data for those animals whose ranges had been adequately sampled. The resulting equation was $R = 1.93\ W^{4.00}$, where R equals the area of the home range in acres and W equals the animal's weight in kilograms. The calculated correlation coefficient was + .47.

The equation derived from the data gathered during this study agree more closely with reality (as indicated by the ranges calculated by the MAM), however, values calculated using the equation also differ decidedly from the MAM values (Table XIII). Mean home range area for the sample based on the MAM was 2.79 ± 1.59 acres. Mean home range area for the same animals based on McNab's equation was $3.12 \pm .16$ acres. The mean home range area for this sample using the equation derived from the data gathered during this study was $2.41 \pm .71$ acres. Home ranges calculated by either estimator do not differ significantly from the mean home range as determined by the MAM.

Obviously, the notion that an animal's range is determined by its feeding requirements is simplistic. This is statistically indicated by the low correlation coefficient value calculated for the linear relationship

Table XIII. Home range areas in acres as estimated by McNab's (1963) equation, the equation derived from the data collected during the present study, and the MAM, for rabbits with adequately sampled home ranges.

	Home Range Estimates (acres)		
Rabbit Number	McNab Equation	Equation Based on Current Data	MAM
R-205	3.05	2.06	3.59
R-237	3.12	2.33	2.83
R-241	3.32	3.34	5.69
R-246	3.29	3.16	2.50
R-252	3.03	1.97	2.16
R-263	3.02	1.95	.71
R-268	3.36	3.56	1.81
R-271	3.15	2.46	4.55
R-273	2.86	1.40	1.31

between animal weight and home range area. It is well known that habitat differences affect the degree to which an animal must wander in search of food (Emlen, 1973). Movements are also the result of social and behavioral factors which have little to do with the animal's size or bioenergetics (Emlen, 1973). Environmental factors such as barriers and weather and social and behavioral factors also act as limits to movement. None of these factors are considered in McNab's (1963) analysis. For this reason, the equations derived to estimate an animal's range based on body weight are of little value except as rough estimates of home range areas, until their underlying premise, that is, that an animal's food requirements are the major factor determining home range size, has been proven. For the present, this has not been adequately demonstrated. It may be possible, after gathering home range data on more animals to refine this equation so that it more accurately represents reality. If animals are grouped by sex and habitat area it may be possible to reduce the part that behavioral and habitat differences influence the equation, allowing the basic premise to be more clearly examined and its validity determined.

The other method for estimating home range areas from data more easily acquired than radio-tracking data involves using the mean distance between successive captures as an index of home range size (Wolfe, 1968). Wolfe found that the average difference between successive captures was positively correlated with home range area as calculated by the MAM. He concluded that by calculating the mean distance between successive captures for a relatively small number of recaptures for each animal, that the animals could be ranked as to home range size with a considerable degree of accuracy (Wolfe, 1968).

Taking this idea one step further, a simple linear regression analysis was run using mean distance between successive capture data and home range data for those animals whose ranges had been adequately sampled. The equation derived from this analysis was $R = .13\ D^{0.67}$, where R equals the range in acres and D equals the mean distance between successive captures in yards. Home range area was positively correlated with mean distance between successive captures ($r = .57$).

Mean home range area calculated for the animals in the sample using the equation derived from data gathered in this study was 2.70 $\pm$ .69 acres (Table XIV). For the same set of animals, mean home range based on the MAM was 2.84 $\pm$ 1.45 acres. Mean home range values for both methods were not significantly different.

Table XIV. Home range area as estimated using the equation derived from linear regression analysis of mean travel distance between successive capture data and the MAM, for rabbits with adequately sampled home ranges and captured more than once.

Rabbit Number	Home Range Area (acres) Estimated	MAM
R-205	2.42	3.59
R-237	3.12	2.83
R-241	3.07	5.69
R-246	3.69	2.16
R-252	2.96	1.31
R-268	1.82	1.81
R-273	1.85	2.50

The correlation coefficient was greater in this case than in the case of the weight-range comparison, though it was still not high. The fact that this method of estimation takes movements by the animal into consideration should make it a better estimator than McNab's (1963) in that habitat differences and social and behavioral factors that might affect range size would undoubtedly affect the animal's movement as indicated by successive trap captures. Further data gathering should help to determine the usefulness of this technique for estimating ranges and whether such factors as trap placement and the number of recaptures considerably affect the result of the analysis.

Cottontail Movements

Three measures of cottontail movement can be applied to the data gathered in the present study. These are: 1) mean minimum travel distance; 2) mean distance between successive captures; and 3) degree of reuse of forms.

Mean minimum daily travel distance (MMDTD) for each radio-tracked rabbit is shown in Table XV.

Mean MMDTD for all radio-tracked animals was 51.2 yards. Mean MMDTD for males was 58.2 $\pm$ 37.2 yards (N=6) and for females was 47.0 $\pm$ 20.8 yards (N=10). Differences between mean MMDTD's for males and females were not significant.

MMDTD may be used as an indicator of habitat differences as it is an indicator of the extent of an animal's movement, albeit one of questionable significance. In poor habitats, in all probability, MMDTD's would be larger than they would be in good habitats, reflecting the fact that the animal in such a habitat would have to move over a greater area to fulfill its needs. Small MMDTD's would also probably be indicative of homogeneous habitats, habitats in which all an animal's needs could be fulfilled in a relatively small area.

Table XV. Mean minimum daily travel distance (MMDTD) in yards for 16 radio-tracked rabbits.

Rabbit Number	Mean Minimum Daily Travel Distance (yards)
R-205	73.9
R-236	126.3
R-237	41.1
R-240	35.9
R-241	30.8
R-245	78.2
R-246	31.7
R-251	76.3
R-252	62.6
R-260	30.8
R-263	21.2
R-265	27.6
R-268	30.2
R-271	44.2
R-272	46.2
R-273	61.7

Comparison of mean MMDTD's between rabbits inhabiting the area below Gladfelter pond and rabbits inhabiting the church site area was made to determine whether there was a significant difference in mean MMDTD values for the two areas. Mean MMDTD for rabbits inhabiting the area below Gladfelter pond was 62.3 $\pm$ 39.1 yards (N=5). Mean MMDTD for rabbits inhabiting the church site area was 54.2 $\pm$ 24.2 yards (N=4). Differences between the two areas were not significant.

Comparison of mean MMDTD's indicates that there are no qualitative differences between the Gladfelter pond area and the church site area.

This conclusion was also reached when the frequency distribution of recapture radii were compared. A significant difference between the areas was noted when home range areas determined by the MAM for ranges that had been adequately sampled were compared. Only further data will be able to indicate which of these conclusions is correct.

Mean distance between successive captures has been used in a number of capture-recapture studies as an indicator of differences in rabbit movements (Janes, 1959; Huber, 1962; Chapman and Trethewey, 1972).

Mean distance between successive captures (MDBSC) was calculated for the 14 rabbits captured three or more times during the present study (Table XVI).

Mean MDBSC was 138.9 yards (N=14) or 107.4 yards (N=13) if R-247 is excluded from the calculation. R-247 was an introduced cottontail and the high value for the MDBSC is in all probability due to the animal's disorientation and attempts by the animal to establish a home range. Further aspects of R-247's behavior will be discussed later.

Mean MDBSC for males was 116.3 $\pm$ 54.8 yards (N=4). Mean MDBSC for females was 103.4 $\pm$ 31.9 yards (N=9). There was no significant difference between the MDBSC for females and that for males.

Mean distances between successive captures calculated in this study were considerably smaller than the 300 yards for males and 228 yards for females reported by Janes (1959) and considerably larger than the distances of 48.5 $\pm$ 30.6 yards for adult males and 43.5 $\pm$ 31.4 yards for adult females reported by Chapman and Trethewey (1972). Mean distances reported by Huber (1962) for rabbits in five acre enclosures of 99.7 yards for all rabbits, 101.6 yards for adult males and 98.8 yards for adult

Table XVI. Mean distance between successive captures for the 14 rabbits captured three or more times.

Rabbit Number	Sex	Mean Distance Between Successive Captures (yards)
R-215	M	61.6
R-237	F	114.9
R-240	F	105.4
R-241	F	112.1
R-243	M	159.1
R-244	M	167.6
R-245	F	114.5
R-246	F	147.7
R-247	F	547.9
R-251	F	126.0
R-252	F	106.4
R-260	M	77.0
R-268	F	51.2
R-273	F	52.5

females and mean distances of 145 yards for all rabbits, 167.1 yards for males and 129.0 yards for females, for rabbits in 40 acre enclosures, agree more closely with the values found in the present study.

Differences between distances between successive captures for females and males were not significant in the present study. This conclusion was supported by the findings of Chapman and Trethewey (1972), but at variance with Huber (1962).

These differences may be due to differences in trapping procedure (Huber and Janes both set traps in a grid across their study areas, while Chapman and Trethewey and I placed traps along the margins of cover in good rabbit habitat), to differences in habitat, to differences in the methods of analysis (Janes used only those distances obtained from animal ranges that had been adequately sampled; Chapman and Trethewey used capture distances from rabbits captured two or more times), and to differences in the studied populations ability to move (Huber's study was conducted in five and 40 acre enclosures). Chapman and Trethewey (1972) also felt that on their study area the interaction of eastern cottontails with brush rabbits may have affected the distance between captures.

The degree to which animals re-use forms may also be compared as an indicator of differences in animal movement patterns and behavior (Table XVII).

Examination of the data presented in Table XVII shows that the reuse ratio approaches one, indicating that the animal was in a different resting location each day that it was monitored, only for those animals that were monitored for a relatively short period of time. When all

Table XVII. Form reuse ratios for 16 radio-tracked rabbits. N equals number of days each rabbit was radio-tracked.

Rabbit Number	N	Form Reuse Ratio Number of Data Points/ Number of Days Monitored
R-205	54	.463
R-236	13	1.000
R-237	39	.410
R-240	9	.899
R-241	89	.258
R-245	8	1.000
R-246	51	.314
R-251	11	.818
R-252	27	.481
R-260	36	.417
R-263	51	.314
R-265	19	.316
R-268	21	.620
R-271	58	.414
R-272	5	.600
R-273	41	.463

animals are considered, the mean reuse ratio value was .549 (N=16). When only those animals captured 19 or more times are considered, the value was .409 (N=11).

Mean reuse ratio value for males was .53 ± .25; for females it was .56 ± .25 (N=10). Differences between the two sexes were not significant.

According to this analysis, both males and females frequently reuse forms. On the average, cottontails were found resting in a form that they have used previously approximately 50 per cent of the time.

Janes (1959) determined that, on the average, cottontails on his study area in Eastern Kansas maintained an average of 3.5 forms. This was a considerably smaller number of forms that was indicated by the number of different daily resting locations found for rabbits in the current study. An average of 18.3 (range: 13-25) daily resting locations were found for rabbits having adequately sampled home ranges. It was possible that some daily resting location points determined for animals in the current study were not forms, but even if this were so, the difference was so great that it, in all probability, was indicative of real differences in the number of forms used by rabbits on the two study areas. Janes (1959) low number of forms per cottontail would mean that the reuse ratio, if it had been calculated, would have been much smaller than that calculated for the current study.

Janes (1959) mentioned that there may be from 20 to 30 resting locations within one animal's home range area since five to seven cottontails may use the same area and that the same resting spot may be used by different cottontails at different times. These observations may account for the greater number of forms per rabbit indicated by the data collected in the current study, but does not account for the small number of forms per rabbit estimated by Janes (1959).

During the present study there were no indications of an animal moving from an established home range to another area. It is possible that monitoring the animals over a longer period of time would have indicated changes that were not evident over the relatively short period of time each animal was monitored. Janes (1959) concluded that cottontails usually establish their home ranges in areas where they were born and usually remained in these areas until they died. Changes from one home range to another were unusual and in Janes' study, he cited only one instance of this occurring. Minor shifts in home range in response to changes in weather and vegetation were common (Janes, 1959).

Trent and Rongstad (1974) also found no indications of major home range shifts in radio-tagged animals that they monitored.

No good evidence of ingress or egress from the study area was noted during the present study, although movements of this type may have occurred. Increased trapping success in February and March may be indicative of movements onto the study area but could just as logically reflect increased susceptibility to capture at this time due to increased activity brought on by the beginning of the breeding season. Before any concrete conclusions can be made about the importance of ingress and egress on the population, more data must be gathered.

Trent and Rongstad (1974) concluded that permanent movements into and away from their study area were not important factors affecting the population of the study area. They also found no evidence of permanent egress from the study area (Trent and Rongstad, 1974). To account for this lack of evidence for dispersal, Trent and Rongstad (1974) theorized that their study may have been conducted in a year of little dispersal due to the phase at which the population cycle of cottontails was. Chapman and Trethewey (1972) similarly reported little movement off their 28.9 acre study area.

Movements of one rabbit that was not radio-tagged are of particular interest in that they shed some light on the possible cause of the noted lack of success in introducing cottontails into new areas, something that was a common management technique a number of years ago but has since fallen into disrepute.

R-247 was captured in the city of Emporia and taken to RNHR and kept in a covered pen until a decision could be made as to what to do with her. On 10 October 1974 the animal escaped from the pen. On 21 February 1975 the animal was recaptured 482.5 yards NE of the pen from which she had escaped. Three days later she was captured 639.5 yards from the last point, only 171.9 yards to the south of the pen from which she had escaped. As can be seen by comparing her MDBSC with other rabbits captured three or more times (Table XVI), her movements were exceptionally long.

These exceptionally long movements over a large area may indicate that the animal had not been able to establish a normal home range during the time that it had been free. This apparent difficulty in establishing a normal home range could account for the fact that it has been concluded that restocked rabbits generally do not survive long enough to have any beneficial effect on the cottontail population of the area being stocked (McDowell, 1955). Obviously, the inability to establish a home range, either due to disorientation or other factors, leading as it would to movements over large areas with which the animal is not familiar, would greatly increase the introduced animals chances of being preyed upon. A study of radio-tagged rabbits introduced into an area with which they are not familiar could shed further light on the mortality rate of introduced animals and their behavior as indicated by their movements.

Territoriality

The question of whether territorial behavior is part of the eastern cottontail's behavioral repertoire is still a subject of controversy. Getz (1961) defined the term "territory" as "that portion of the home range of an individual that is defended from intrusion by other members of the same species of the same sex." It might involve the defense of the whole home range or just a portion of it (Getz, 1961). It is particularly difficult to determine whether such behavior occurs in the wild, as observations of interactions between conspecifics of the same sex are difficult to obtain. Most of the information, regarding the occurrence or absence of territoriality must therefore be based on indirect evidence.

Getz (1961) mentioned five methods of analysis that may be used to obtain indications of territorial behavior. These included: 1) the percentage of exclusive home ranges; 2) the percentage of partially exclusive home ranges; 3) the distances between centers of activity; 4) the distribution of centers of activity; and 5) sexes of the individuals involved in multiple captures. The percentage of range overlap has also been used as an indicator of territoriality (Haugen, 1942; Janes, 1959; Trent and Rongstad, 1974).

Home range overlap is also of interest in studies of wildlife diseases and reproductive behavior. Probably more important than the per cent overlap of home ranges, one with another, in epidemiological studies, studies of reproductive behavior and territoriality is the intensity of use of the overlap area by the two animals whose ranges overlap (Adams and Davis, 1967). It is readily apparent that the use intensity of the two animals in the area of overlap is important in determining the opportunities for contacts between them and for exposure to each others environment (Adams and Davis, 1967). If neither animal uses the area of overlap very much, less chance for contact exists than if the area is used more intensively. Temporal usage patterns of the overlap area may also limit the chances for contact if the two animals do not use the area concurrently (Adams and Davis, 1967). Before any significance can be attached to the fact that two animals ranges overlap, much more detailed information about each animals movements must be available.

Adams and Davis (1967) were able to gather such detailed information by direct visual observation of California ground squirrels. In animals which are less easily observed in the wild, such as cottontails, radio-tracking studies offer a means by which such information may be gathered. Optimum results would be obtained only in cases of almost constant movement recording of a whole population. To obtain these results would require an automatic system similar to that at the Cedar Creek Natural History Area in Minnesota (Tester and Siniff, 1965).

The evidence for cottontail territoriality, gathered for the most part by indirect methods, seems to indicate that cottontails show no territorial behavior. Marsden and Holler (1964), after examining the social behavior of penned cottontails, concluded that territorial behavior was not common in cottontails. On two occasions they noted defense of nest by females. On several occasions dominant males were seen to defend the area around females, but they did this irrespective of the female's location within the pen.

Janes (1959) found that cottontail ranges overlapped indiscriminately on his study area in Eastern Kansas and concluded that cottontails maintained no definable territory.

In a more recent study, using radio-tracking, Trent and Rongstad (1974) found that during the breeding season, each male's home range overlapped one or more other male's home range by at least 50 per cent, while no female overlapped any other radio-tagged female by more than 25 per cent. There was no range overlap among radio-tagged females during the mid-July to mid-September period. From mid-September to mid-January, home ranges of all rabbits overlapped indiscriminately, indicating that territoriality played no part in restricting rabbit movements during this period.

Trent and Rongstad (1974) concluded that though the literature seems to support the idea that female cottontails will protect their nests, the pronounced lack of overlap that they found during the breeding season was in all probability due to the fact that female home ranges tended to shrink during the breeding season. This reduction in range area during the breeding season was due in part to the fact that the female remained near the nest while young were present and in part to the fact that food and cover were more readily available and close at hand at this time. Janes (1959) noted a similar reduction in the range size of pregnant females in his study of Kansas cottontails and cited similar reasons for the range reduction. This reduction in range size by females would probably account for the small percentage of overlap of female ranges, as smaller ranges would be less likely to overlap than larger ranges (Trent and Rongstad, 1974). Trent and Rongstad (1974) came to no final conclusion about the presence or absence of territorial behavior in female cottontails during the breeding season. They suggested that this question might be answered by conducting a radio-tracking study where densities are increased by introductions and the changes that occur in range size and configuration are noted.

In this study, rabbits were monitored only during the late summer, fall, winter and spring. Per cent of range overlap and mean distances between center of activities were used as indicators of territoriality.

Per cent of range overlap was calculated only for rabbits that were contemporary and living in the same general area (no physical barriers to travel separating them). Ranges as determined by the MAM (Mohr, 1947) were used to determine the per cent overlap. Students t-test was used to determine the significance of any differences between classes.

Table XVIII summarizes the information gathered on per cent of range overlap.

Male ranges overlapped female ranges to a significantly greater extent than female ranges overlapped the male ranges. Male ranges overlapped female ranges to a significantly greater extent than the ranges of males overlapped those of other males. There were no significant differences between the percentage of overlap of female ranges with ranges of other females and any of the other classes.

Table XVIII. Per cent of home range overlap by contemporary rabbits.

	N	Per cent Overlap Mean	Per cent Overlap Range
Female-Female	12	23.1 ± 29.5	0.0-51.0
Male-Male	2	22.2 ± 7.8	16.6-27.7
Male-Female	2	51.9 ± 2.1	50.4-53.4
Female-Male	2	21.7 ± 6.6	17.0-26.4

The small sample sizes of the male-male, male-female and female-male classes make definite conclusions subject to confirmation by more data. As can be seen, there are considerable differences in percentage of overlap in all classes. Whether these differences are artifacts of the small sample size is not known. If these statistically significant differences are indications of the real situation, it would appear that there is a tendency for male ranges to overlap the female ranges to a greater extent than those of other males. Whether, this might be some indication of territoriality on the part of males, perhaps due to some dominance hierarchy established in the wild population, is a question open to confirmation or refutation by more data.

That male ranges are on the average larger (though the difference is not significant) than females may account for what appears to be a tendency for male ranges to overlap the ranges of females to a greater extent than female ranges overlap the ranges of males. Again, before any conclusion can be drawn, more data must be gathered.

The question of female territoriality in the non-breeding season can be answered with more conviction. It appears, based on the data gathered during this study, that females do not exhibit territorial behavior during the non-breeding season. This conclusion is supported by data gathered by Janes (1959), Marsden and Holler (1964) and Trent and Rongstad (1974). This conclusion does not agree with the conclusion of Haugen (1942). He concluded, based on the fact that female ranges showed little overlap, while the ranges of males and females and males and males tended to overlap indiscriminately, that females were territorial during the breeding season and into the fall and winter. These conclusions are based on the assumption that the degree of home range overlap is a valid indicator of the degree to which animals come into contact and their responses to such contact, an assumption that is at best questionable.

Comparison of the mean distances from the center of activity of one female to that of another and from one male to that of a female, indicate that there was no significant difference between these distances. The mean distance between male and female centers of activity was 156.0 $\pm$ 16.0 yards (N=2); for females and females, the mean distance was 133.7 $\pm$ 62.5 yards (N=6). That there was no significant difference between the distances separating the center of activities of males-females and female-females would seem to indicate that territoriality was not a factor in the distribution of rabbits during the non-breeding season. This conclusion was in general agreement with that derived from analysis of percentage of overlap data.

Mortality

The study of cottontail mortality and its causes has generally involved collecting data by direct observation, noting the disappearance of cottontails as indicated by the failure to recapture them, and analyzing gut contents and scat of the major cottontail predators. Only recently has radio-telemetry been applied to the study of animal mortality.

Radio-telemetry studies of mortality allow much more accurate determinations of the cause of an animal's death by making the researcher quickly aware that mortality has occurred. It also allows a sample of the population to be examined in detail, which yields data from which conclusions about the effect of mortality on a whole population can be derived.

One of the first applications of radio-telemetry technology to the study of mortality in cottontails was conducted by Mech (1967) on the Cedar Creek Natural History Area in Minnesota. His study was designed to test the feasibility of radio-tracking equipment to study mortality and for that reason sheds little light on the effect that disease, predation and other factors have on the cottontail population. In his study mortality was suspected when an animal failed to move as indicated by no change in the bearings recording the animal's position (Mech, 1967). A field check was then made to determine if mortality had occurred. Trent and Rongstad (1974) used a similar procedure to detect mortality in their study of rabbit ranges and survival rates in Wisconsin.

A further advance in the ability of radio-tracking equipment to detect mortality occurred with the advent of transmitter packages containing motion sensitive mercury switches (Knowlton et al., 1968) and packages containing thermistors (Stoddart, 1970). In the case of motion sensitive transmitters, mortality was surmised when no animal movement occurred for an abnormally long period of time. The thermistor equipped transmitters were designed to alert the investigator that a mortality had occurred by causing a transmitted signal change when the animal's body temperature dropped below a predetermined level. At present, the transmitter package equipped with a thermistor holds the most promise for mortality studies.

During this study mortality information was collected on all animals monitored by radio-tracking and also for any rabbit remains found on the study area (Table XIX).

Of the 21 cases of mortality listed in Table XIX, seven were due to man's activities. Of these seven, two (14 and 15) were due to improper fitting of the collar which caused death by shock and starvation; three (2, 11, and 13) were shot, in two cases (2 and 11) by the researchers in an attempt to recover a collar that was approaching the end of its expected life and in one case (13) by a poacher. Two were trap related mortalities, one (7) due to shock or starvation while trapped and the other (20) caused by predation while the animal was in a wire trap. Thirty-three per cent of the recorded mortalities were due to "unnatural" causes.

Of the remaining mortalities, five were apparently caused by mammalian predators, five died of unknown causes, three were evidently victims of avian predation, and one was a victim of disease.

The major mammalian predators present on the study area are the coyote (Canis latrans), the dog (Canis familiaris), the domestic cat

Table XIX. Date of discovery of remains, rabbit number, transmitter type if the animal was instrumented (Mort. = Mortality collar; Non-mort. = Non-mortality collar), description of remains, including relative age and sex of the dead animal if they were known, and probable cause of death and evidence leading to this conclusion for 21 mortalities known to have occurred on the study area.

	Date of Discovery	Rabbit Number	Instrumented Rabbit	Description of Remains	Cause of Death/Sign
1)	8/ 6/74	-----	------	Adult, ?. Remains intact.	No sign of predation.
2)	8/31/74	-----	------	Juvenile, M.	Shot.
3)	8/31/74	R-265	Non-mort. collar	Juvenile, M. Fur, stomach, hind foot.	Mammalian predator/runny scat.
4)	9/ 7/74	R-254	------	Juvenile, M. Captured by hand, transported to the KSU Diagnostic Lab.	Tularemia/tests run at the lab after animal died.
5)	9/12/74	-----	------	Juvenile, ?. Remains intact. Dead 2-7 days.	No sign of predation.
6)	9/16/74	-----	------	?, ?. Fur, stomach, intestine.	Great Horned Owl feather.
7)	10/ 4/74	R-249	------	Juvenile, M.	Trap mortality.
8)	11/ 2/74	-----	------	?, ?. Fur.	Coyote/tracks.
9)	11/ 7/74	-----	------	?, ?. Fur, blood.	Coyote/scat.
10)	11/13/74	-----	------	?, ?. Fur, blood, bone bits. Apparently rabbit was dug out of rock wall.	Mammalian predator/digging.

Table XIX. Continued

	Date of Discovery	Rabbit Number	Instrumented Rabbit	Description of Remains	Cause of Death/Sign
11)	11/15/74	R-271	Non-Mort. collar	Adult, M.	Shot to recover collar.
12)	11/19/74	R-236	Mort. collar	Adult, M. Animal intact. Found buried under grass; 4 puncture wounds left side, one on the right.	Owl/puncture wounds.
13)	12/ 2/74	R-252	Mort. collar	Adult, M. Found buried under cow chip approx. ¼ mile SE of normal location.	Shot/poached.
14)	12/ 7/74	R-268	Non-mort. collar	Adult, F. Remains intact.	Shock/right lower incisor caught in collar.
15)	12/12/74	R-251	Mort. collar	Adult, F. Remains intact.	Starvation/lower incisor caught in collar; lost 400+ g. in 8 days.
16)	12/16/74	-----	------	?, ?. Fur, blood.	Unknown.
17)	2/27/75	R-205	Mort. collar	Adult, M. Fur, blood.	Coyote/tracks.
18)	3/ 3/75	-----	------	?, ?. Fur.	Unknown.
19)	3/ 5/75	-----	------	?, ?. Fur.	Unknown.
20)	4/12/75	R-239	------	Adult, F. Front legs eaten off, meat stripped from one hind leg.	Trap mortality/mammalian predator.

Table XIX. Continued

	Date of Discovery	Rabbit Number	Instrumented Rabbit	Description of Remains	Cause of Death/Sign
21)	4/22/75	-----	------	Adult, ?. Intact, evidence of some feeding on entrals.	Avian predator/ whitewash of avian excreta.

(Felis catus), the raccoon (Procyon lotor), the badger (Taxidea taxus), the striped skunk (Mephitis mephitis), and the opossum (Didelphis marsupialis). All of these animals are known to feed on the cottontail.

Of these, only the coyote and dog are major predators on adult cottontails. Both coyotes and dogs have been sighted and trapped on the Reservation study area. Tracks of both animals have been seen on numerous occasions across the study area.

If tracks are present at the sight of a mortality, coyotes and dogs are fairly easily differentiated. In many cases, though, no tracks were present at the site. In such cases, examination of the remains may yield clues as to which predator was responsible. Coyote kills have been described by a number of authors in the past (Fitch and Packard, 1955; Tiemeier, 1955; Stoddart, 1970). Fitch and Packard (1955) described a rabbit kill site in the following manner. "Ordinarily little remains of the rabbit except fur strewn over an area of several square feet to several square yards." Usually the rabbit's tail was discarded as were its stomach and intestines if they contained much food. Often the coyote would leave a scat on or near the discarded remains. No similar description of a dog kill is available.

Tentatively, most of the rabbit mortalities ascribed to mammalian predation are probably coyote kills. It is possible that some were dog kills. It is suggested that an attempt to characterize dog kills, to determine if there are sufficient differences in killing "style" to enable more positive identification of the agent of death when only the animal's remains are available, would be useful. Also, radio-tracking of coyotes and domestic dogs on and near the study area should give some indication of the amount of time each canid spends on the area and thus some idea of its contribution to predation.

Mammalian predation accounted for 24 per cent of the total mortalities or 36 per cent of the mortalities caused by natural agents.

Of the five cases of mortality where the cause is not known, analysis of the descriptions of the kill site may indicate a possible causative agent. Three of the mortalities (16, 18 and 19) were indicated only by the presence of hair at the kill site. As mentioned above, such a description is characteristic of coyote kills. In all probability then, these three mortalities were caused by canid predation.

The other two mortalities (1 and 5) are more difficult to interpret. In both cases the animals remains were intact, and there was no evidence that they had been fed on. It is possible that these animals were victims of disease. Both were found dead within a month of R-254, a rabbit that died of tularemia. It is possible that other factors were responsible for their death.

Of the three cases of suspected avian predation (6, 12 and 21), only one (21) shows characteristics similar to those found in literature descriptions of avian predation. Stoddart (1970) found that where jack-rabbit remains had been fed on by raptors or corvids, the carcasses were partially or completely eaten except that portions of the skeleton were left and in all cases, hair was strewn about the site. Without exception, the whitewash of avian excreta was present at the site. In the case of mortality number six the only evidence of avian predation was the presence of a Great Horned Owl feather. Except for the feather, the kill site description appears to be that of a coyote kill.

The other possible avian predator kill (12) seems to indicate that an owl or other avian predator made an unsuccessful attempt to kill an adult rabbit, which was able to get away and burrow under the grass, where it eventually died as a result of the wounds sustained in the encounter. The diagnosis of avian predation as the cause of death was the only plausible way to account for the apparent fatal wounds.

At most, only three of the total mortalities were probably caused by avian predation. This means that 14 per cent of total mortalities, or 21 per cent of mortalities due to natural causes, were a result of avian predation.

One rabbit (4) was captured by hand and was obviously ill at the time . This rabbit was transported to the Kansas State University Veterinary Diagnostic Lab, where it died while under observation. Necropsy of the animal by the lab indicated that the cause of death was tularemia. Though blood samples taken from most animals captured after this were analyzed for the presence of tularemia, no other specimens were found to be suffering from the disease. This is not particularly surprising, when one considers that the disease is usually fatal five days after it is acquired and the fact that a slow moving sedentary animal suffering from an illness will be more difficult to trap than a more active individual. For these reasons and also because it is impossible to be sure that the disease did not contribute to the mortalities that have been attributed to other causes, the extent of the disease on the study area is not known.

Trent and Rongstad (1974) reported 27 mortalities in a sample of 54 rabbits that were radio-tagged. Sixty-three per cent of these mortalities were due to fox predation, seven per cent were caused by weasel predation, 15 per cent were due to avian predation and 15 per cent were due to unknown causes.

In this study, in all probability, 64 per cent of the natural mortalities were the result of mammalian predation, 14 per cent were caused by avian predators, eight per cent were caused by disease and 14 per cent were due to unknown causes. This distribution of mortality causes agrees generally with the distribution of mortality causes found for cottontails in Wisconsin by Trent and Rongstad (1974).

Of the 16 animals radio-tagged, seven died. Three of these died of "natural" causes. Of the other radio-tagged rabbits, four collars malfunctioned leaving the status of the animal unknown and five were known to be alive when the transmitters were removed. The magnitude of normal mortality in this population sample cannot be accurately estimated due to the large number of animals that disappeared, died because of human intervention, or died because of equipment induced injuries.

SUMMARY

1. A study of cottontail rabbit movements, home range areas, population levels and mortality was conducted on Emporia Kansas State College's Ross Natural History Reservation in Northwest Lyon County, Kansas from 5 August 1974 to 20 May 1975. Radio-tracking equipment and trapping were used to gather data.

2. Fifty-four rabbits (28 females, 25 males and one unsexed) were captured during the study period. The sex ratio for sexed rabbits was 1:1.12. Rabbits were captured from 1 to 11 times. The mean number of captures per rabbit was 2.15. Fifty-six per cent of the rabbits were captured only once. Trap success was highest in the fall and next highest at the beginning of the breeding season in late February.

3. The population on the 100 acre study area was estimated to be between 84 and 96 rabbits in August, 1974, indicating that 56.1 per cent of the rabbits inhabiting the study area were captured.

4. Sixteen rabbits were radio-tagged with 11 transmitter collars. Of the 11 transmitters, five were not recovered after transmitter failure, four were recovered after failure and repaired and two did not fail. Lithium cell powered units gave a longer operating life on the average than mercury cell powered units. Transmitter operating lives ranged from five to 110 days (mean-46.6). Transmitter collars and handling appeared to have little measureable effect on cottontail movement.

5. Rabbit home ranges were calculated using four methods: two polygon methods and two modeling methods. The modeling methods were

determined to be generally inadequate for home range determination when compared to the simpler polygon methods.

6. Mean home range areas for nine rabbits with adequately sampled home ranges as determined by the Minimum Area Method was 4.07 acres for males and was not significantly different from that for females.

7. Mean home range areas for the nine rabbits with adequately sampled ranges, as determined by the Modified Minimum Area Method, was 2.86 acres for males and .98 acres for females. Male ranges were significantly larger than female ranges.

8. In all probability differences between ranges calculated by the two polygon methods (the Minimum Area Method and the Modified Minimum Area Method) were due to the fact that the Minimum Area Method was a measure of the maximum home range area, while the Modified Minimum Area Method was a measure of the area of utilization.

9. Ranges determined using only daily resting locations were in all probability inadequate for accurately estimating animal home ranges.

10. Chase ranges, in all probability, were poor estimates of home range area.

11. Cottontail home ranges were generally linear in shape. The average length-width ratio for rabbit ranges with adequately sampled home ranges was 1:2.56.

12. Analysis of recapture radii indicated that almost all rabbit ranges had limits. The distribution of recapture radii about the center of activity indicated that males generally range farther from their centers of activity than females and make more intensive use of areas farther from their centers of activity than females.

13. Analysis of recapture radii distributions was suggested as a method for determining qualitative differences in different habitats.

14. Two home range estimator equations, one based on rabbit weights and one based on mean distance between successive captures were presented.

15. Mean minimum daily travel distances for all radio-tracked rabbits was 51.2 yards; mean distance between successive captures was 107.4 yards.

16. An average of 18.3 daily resting locations were found for rabbits having adequately sampled home ranges. On the average cottontails were found 50 per cent of the time resting in a location that they had previously used.

17. There were no indications of an animal moving from an established home range to another area.

18. No evidence of ingress or egress from the study area was noted.

19. R-246, an introduced rabbit, moved over a large area indicating that it had difficulty establishing a home range. This difficulty may account for the lack of success commonly found in restocking programs.

20. Conclusive evidence of territoriality in cottontails was not found.

21. Twenty-one cases of mortality were noted during the study. Seven mortalities were due to man's activities. Of the natural mortalities, 64 per cent were the result of mammalian predation, 14 per cent were caused by avian predators, eight per cent were caused by disease and 14 per cent were due to unknown causes.

LITERATURE CITED

LITERATURE CITED

Ables, E. D. 1969. Home range studies of red foxes (Vulpes vulpes). J. Mamm. 50(1): 108-120.

Adams, L. and S. D. Davis. 1967. The internal anatomy of home range. J. Mamm. 48(4): 529-536.

Allen, D. L. 1939. Michigan cottontails in winter. J. Wildl. Mgmt. 3(4): 307-332.

Bailey, J. A. 1969. Trap responses of wild cottontails. J. Wildl. Mgmt. 33(1): 48-52.

Blair, W. F. 1942. Size of home range and notes on the life history of the woodland deer mouse and eastern chipmunk in northern Michigan. J. Mamm. 23(1): 27-36.

Brown, L. E. 1956. Movements of some British small mammals. J. Animal Ecol. 25: 54-71.

Brussard, P. F., P. R. Ehrlich and M. C. Singer. 1974. Adult movements and population structure in Euphydryas editha. Evolution 28(3): 408-415.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mamm. 24: 346-352.

Calhoun, J. B. and J. U. Casby. 1958. Calculation of home range and density of small mammals. U. S. Public Health Monograph No. 55: iv + 1-24.

Chapman, J. A. and D. C. Trethewey. 1972. Movements within a population of introduced eastern cottontails. J. Wildl. Mgmt. 36: 155-158.

Dalke, P. D. and P. R. Sime. 1938. Home and seasonal ranges of the eastern cottontail in Connecticut. Trans. Third North Amer. Wildl. Conf.: 659-669.

Davenport, L. B., Jr. 1964. Structure of two Peromyscus polionotus populations in old field ecosystems at AEC Savanah River Plant. J. Mamm. 45(1): 95-113.

Davis, D. E. 1953. Analysis of home range from recapture data. J. Mamm. 34(3): 352-358.

Davis, D. E., J. T. Emlen, Jr., and A. W. Stokes. 1948. Studies on home range in the brown rat. J. Mamm. 29(3): 207-225.

Doebel, J. H. and B. S. McGinnes. 1974. Home range and activity of a grey squirrel population. J. Wildl. Mgmt. 38(4): 860-867.

Eberhardt, L., T. Peterle, and R. Schofield. 1963. Problems in a rabbit population study. Wildl. Monographs No. 10: 1-51.

Edwards, W. R. and L. Eberhardt. 1967. Estimating cottontail abundance from live-trapping data. J. Wildl. Mgmt. 31: 87-96.

Emlen, J. M. 1973. Ecology: An evolutionary approach. Addison-Wesley Publishing Company, Inc., Reading, Mass. 493 p.

Fitch, H. S. and R. L. Packard. 1955. The coyote on a natural area in northeastern Kansas. Trans. Kans. Acad. of Sci. 58(2): 211-222.

Forsythe, S. W. 1974. Parasites of cottontail rabbits in Lyon county, Kansas. Unpub. M. S. thesis, Emporia Kansas State College, Emporia, Ks. 29 p.

Getz, L. L. 1961. Home ranges, territoriality and movement of the meadow vole. J. Mamm. 42: 24-36.

Hanson, J. C., J. A. Bailey and R. J. Siglin. 1969. Activity and use of habitat by radio-tagged cottontails during winter. Trans. Ill. Acad. of Sci. 62(3): 294-302.

Hartman, E. L. 1960. The F. B. and Rena G. Ross Natural History Reservation. Emporia State Research Studies VIII(4): 1-40.

Harvey, M. J. and R. W. Barbour. 1965. Home range of Microtus ochrogaster as determined by a modified minimum area method. J. Mamm. 46(3): 398-402.

Haugen, A. O. 1942. Home range of the cottontail rabbit. Ecology 23(3): 354-367.

Hayne, D. W. 1949. Calculation of size of home range. J. Mamm. 30: 1-18.

Huber, J. J. 1962. Trap response of confined cottontail populations. J. Wildl. Mgmt. 26(2): 177-185.

Janes, D. W. 1959. Home range and movements of the eastern cottontail in Kansas. U. of Kansas Publ. Mus. Nat. History 10(7): 553-572.

Jennrich, R. I. and F. B. Turner. 1969. Measurement of non-circular home range. J. Theoret. Biol. 22: 227-237.

Kaye, S. V. 1961. Movements of harvest mice tagged with Gold-198. J. Mamm. 42(3): 323-337.

Knowlton, F. F., P. E. Martin and J. C. Haug. 1968. A telemetric monitor for determining animal activity. J. Wildl. Mgmt. 32(4): 943-948.

Koeppl, J. W., N. A. Slade, and R. S. Hoffmann. 1975. A bivariate home range model with possible application to ethological data analysis. J. Mamm. 56(1): 81-90.

Lord, R. D., Jr. 1961. Seasonal changes in roadside activity of cottontails. J. Wildl. Mgmt. 25(2): 206-209.

______________. 1963. The cottontail rabbit in Illinois. Illinois Dept. of Cons., Tech. Bull. No. 3: xi + 1-94.

Marsden, H. M. and R. N. Holler. 1964. Social behavior in confined populations of the cottontail and swamp rabbit. Wildl. Monographs No. 13: 1-39.

McDowell, R. D. 1955. Restocking with native cottontails. J. Wildl. Mgmt. 19(1): 61-65.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. Amer. Naturalist 97: 133-140.

Mech, L. D. 1967. Telemetry as a technique in the study of predation. J. Wildl. Mgmt. 31(3): 492-496.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37: 223-249.

__________. 1965. Home area and comparative biomass of the North American red squirrel. Canadian Field Nat. 79: 162-171.

Newman, D. E. 1959. Factors influencing the winter roadside count of cottontails. J. Wildl. Mgmt. 23(3): 290-294.

Odum, E. P. and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk 72: 128-137.

Petrides, G. A. 1951. The determination of sex and age ratios in the cottontail rabbit. Am. Midl. Nat. 46(2): 312-336.

Quadagno, D. M. 1968. Home range size in feral house mice. J. Mamm. 49(1): 149-151.

Schwartz, C. W. 1941. Home range of the cottontail in central Missouri. J. Mamm. 22(4): 386-392.

Schwartz, C. W. and E. R. Schwartz. 1959. The wild mammals of Missouri. The U. of Missouri Press and Missouri Cons. Comm. xvi + 1-341.

Sheffer, D. E. 1972. The cottontail rabbit in Pennsylvania. Pa. Game News, June: 9-11.

Smith, M. H., B. J. Boize and J. B. Gentry. 1973. Validity of center of activity concept. J. Mamm. 54(3): 747-749.

Stoddart, L. C. 1970. A telemetric method for detecting jackrabbit mortality. J. Wildl. Mgmt. 34(3): 501-507.

Stumpf, W. A. and C. O. Mohr. 1962. Linearity of home range of California mice and other animals. J. Wildl. Mgmt. 26: 149-154.

Tester, J. R. and D. B. Siniff. 1965. Aspects of animal movement and home range data obtained by telemetry. Trans. of the 30th North Amer. Wildl. and Nat. Resources Conf.: 379-392.

Tiemeier, O. W. 1955. Winter foods of Kansas coyotes. Trans. Kans. Acad. of Sci. 58(2): 196-207.

Toll, J. E., T. S. Baskett and C. H. Conaway. 1960. Home range, reproduction and foods of the swamp rabbit in Missouri. Am. Midl. Nat. 63(2): 398-412.

Trent, T. T. and O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Mgmt. 38(3): 459-472.

Van Vleck, D. B. 1969. Standardization of Microtus home range calculation. J. Mamm. 50(1): 69-80.

Van Winkle, W. 1975. Comparison of several probabilistic home range models. J. Wildl. Mgmt. 39(1): 118-123.

Van Winkle, W., Jr., D. C. Martin and M. J. Sebetich. 1973. A home range model for animals inhabiting an ecotone. Ecol. 54(1): 205-209.

Wainwright, L. C. 1969. A literature review on cottontail reproduction. Colo. Div. Game, Fish and Parks, Spec. Rept. 19: 1-24.

White, J. E. 1964. An index of the range of activity. Am. Midl. Nat. 71(2): 369-373.

Wilson, J. S. 1963. Flowering plants of the Ross Natural History Reservation, Lyon and Chase Counties, Kansas. Emporia State Research Studies XI(4): 1-91.

Wolfe, J. L. 1968. Average distance between successive captures as a home range index for Peromyscus leucopus. J. Mamm. 49(2): 342-343.

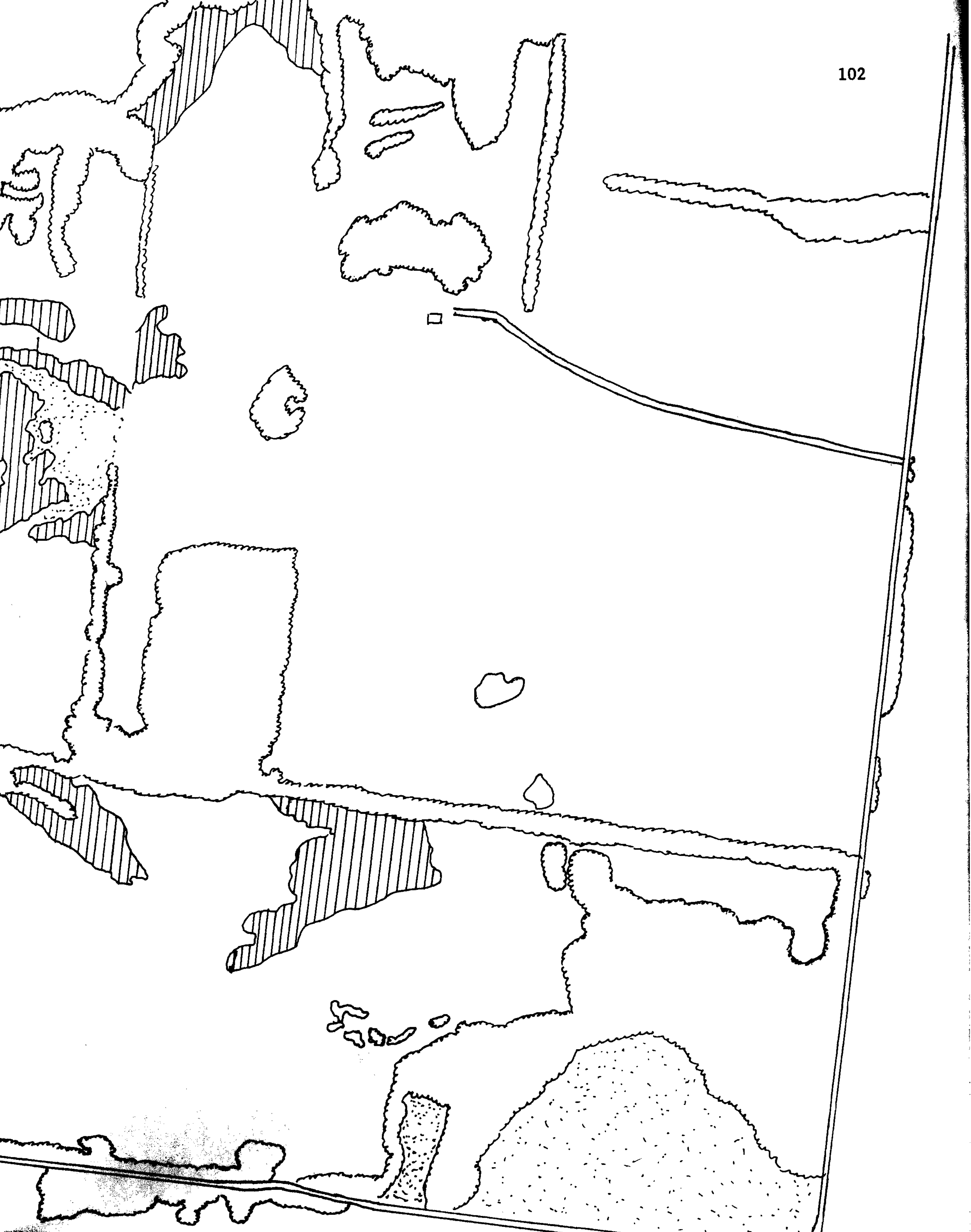
Young, H., R. L. Strecker and J. T. Emlen, Jr. 1950. Localization of activity in two indoor populations of house mice, *Mus musculus*. J. Mamm. 31(4): 403-410.

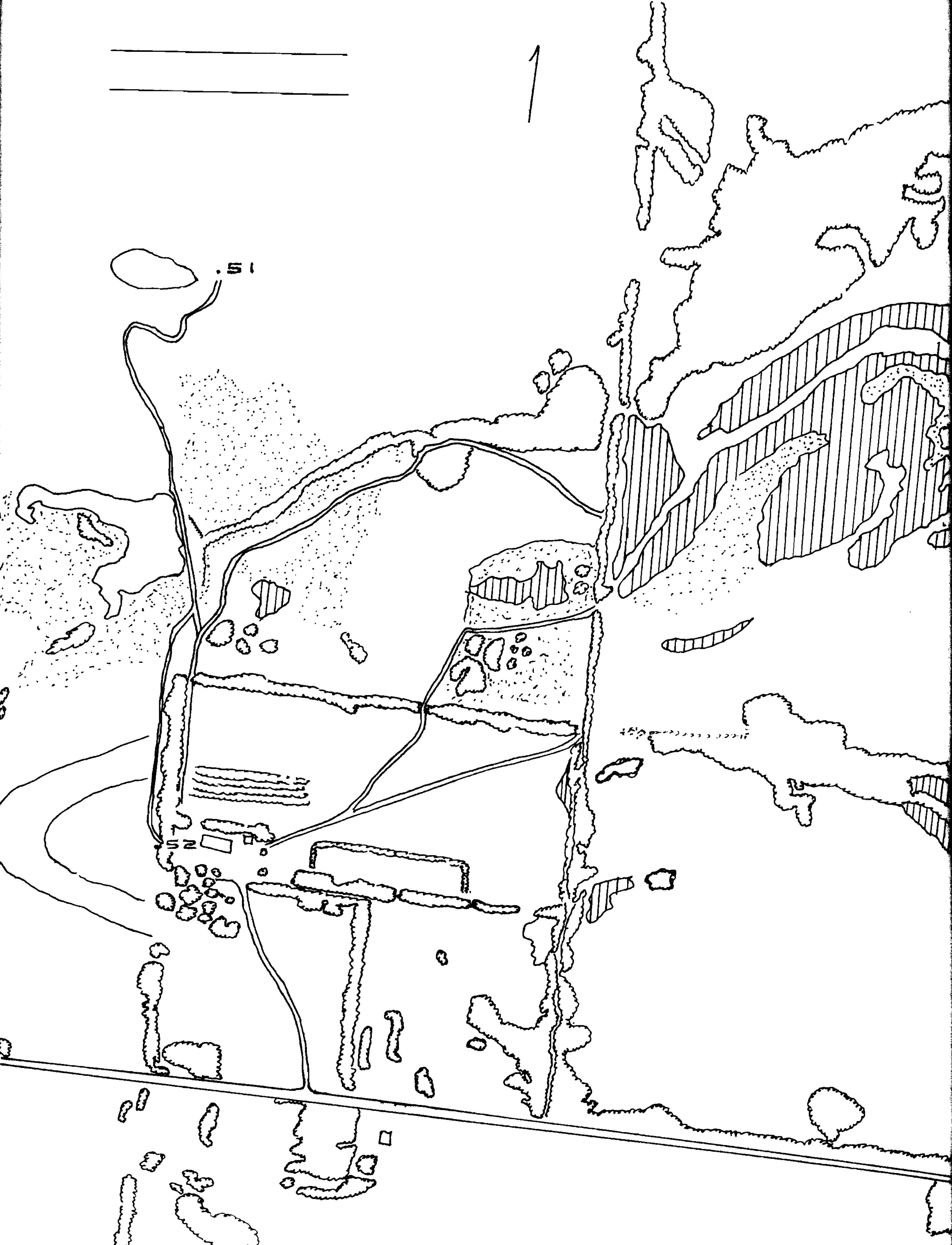
APPENDIX A

Map of Study Area

Used

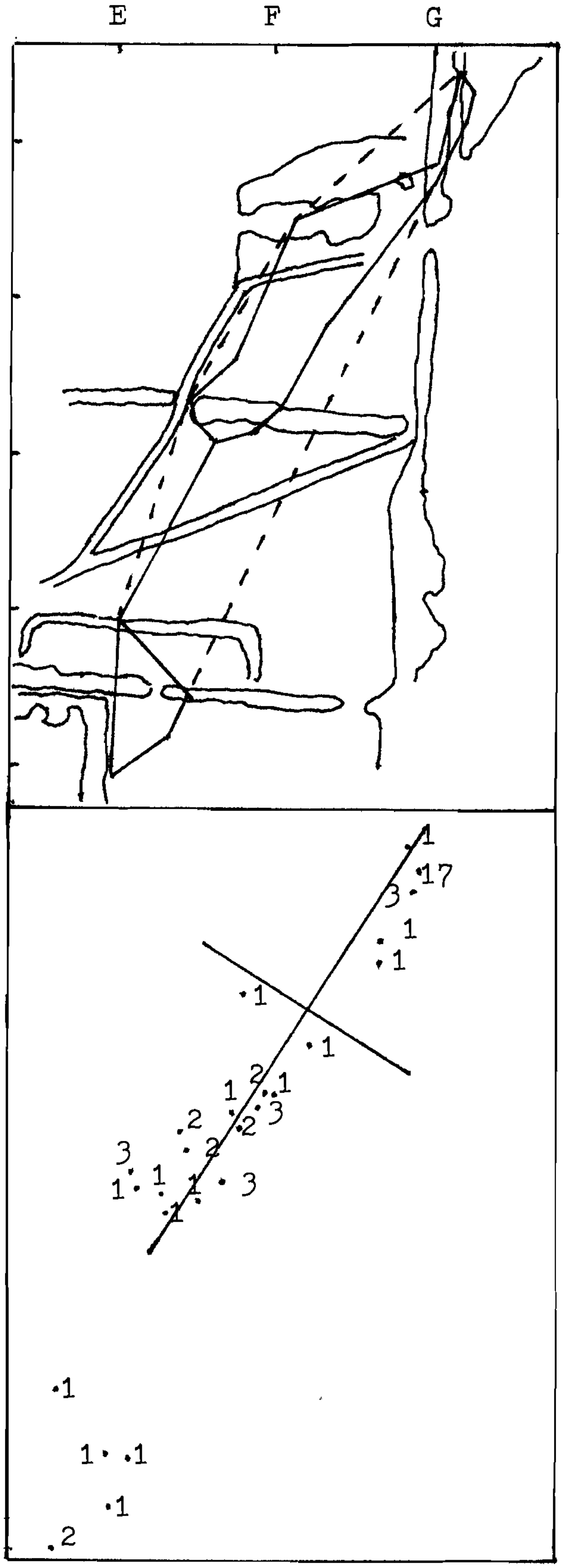
For Recording Locational Data Points




1
.51
.52

APPENDIX B

Maps showing MAM and MMAM determined ranges over a map of the study area and distribution of data points, orientation of axes, and center of activity.



---- MAM
—— MMAM

R-205

Male

Tracked from

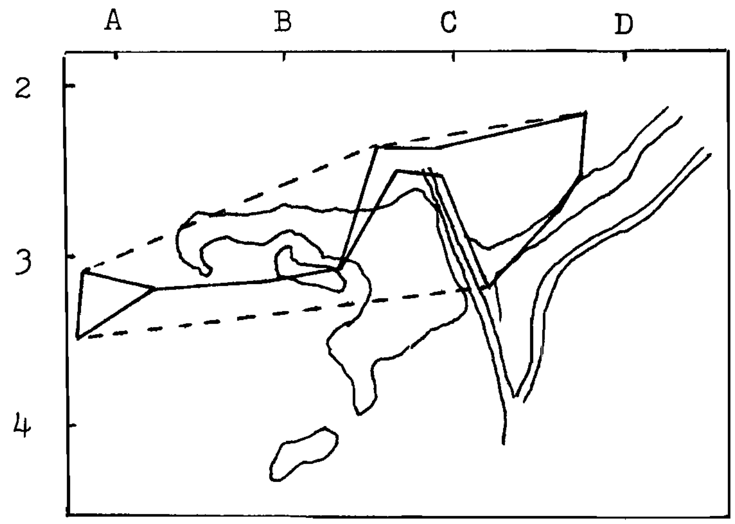
12/16/74

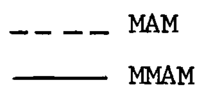
to

2/17/75

one acre

100 yards

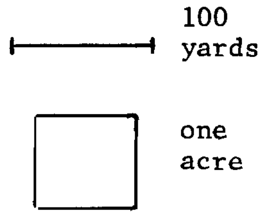


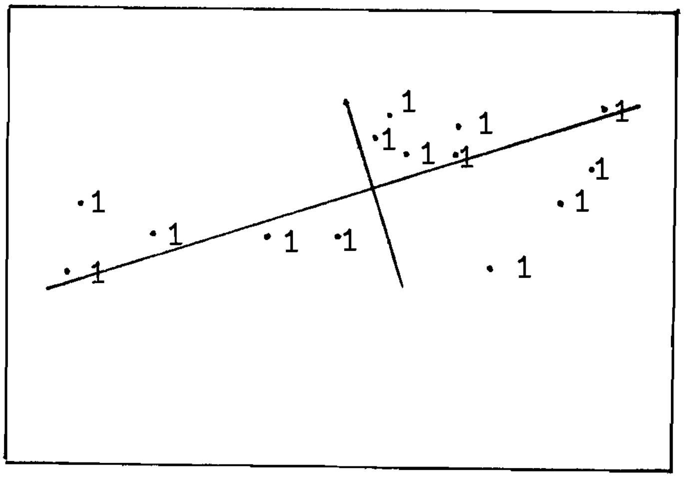


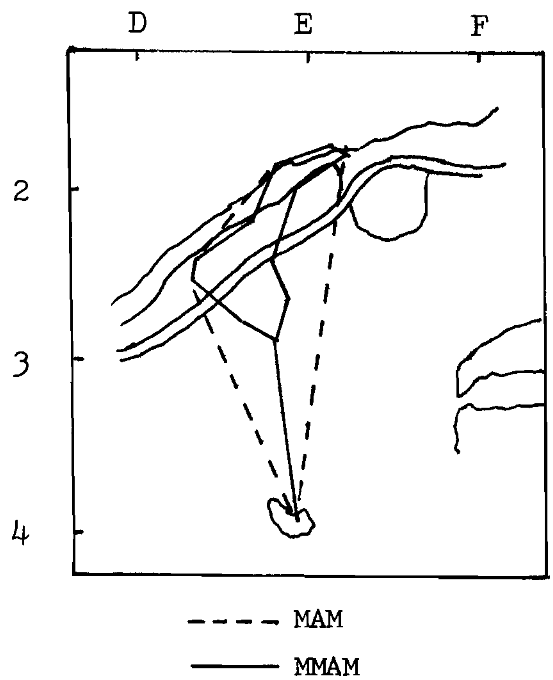
R-236

Male

Tracked from
11/4/74 to 11/19/74



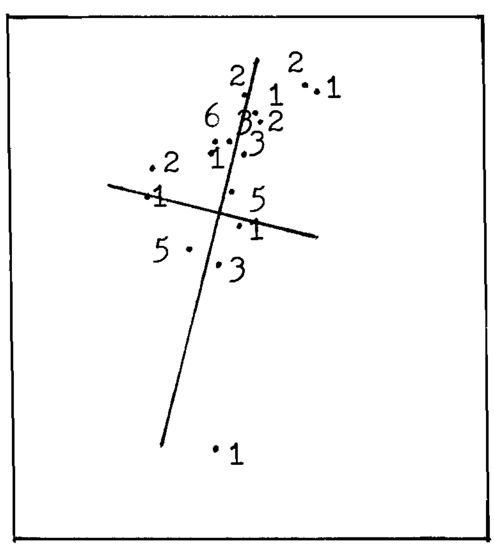


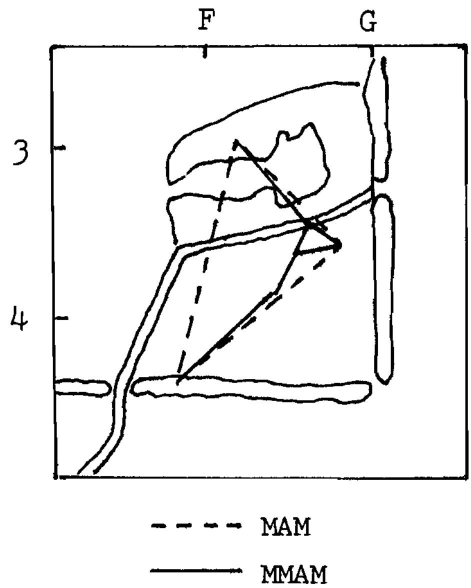


R-237
Female
Tracked from
11/3/74 to 11/23/74
and 12/8/74 to 1/16/75

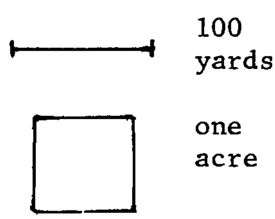
100 yards

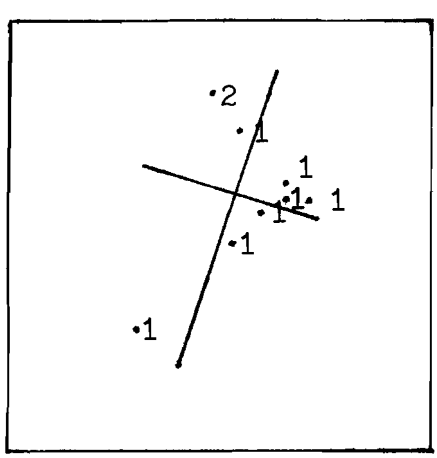
one acre

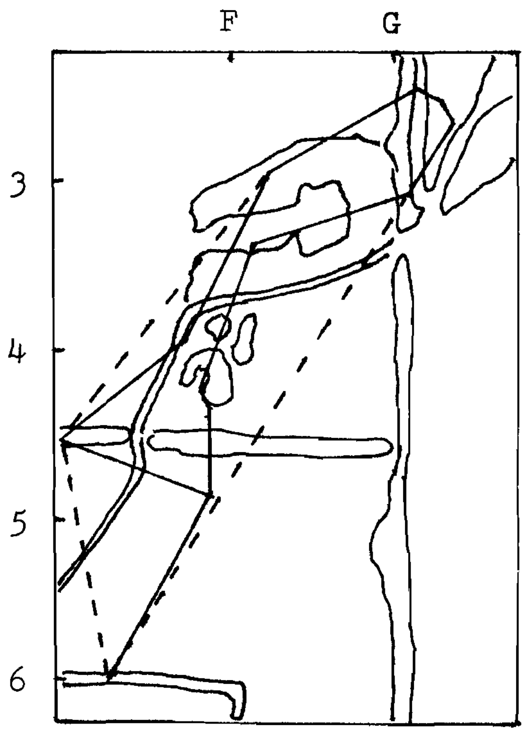




R-240
Female
Tracked from
11/9/74 to 11/16/74





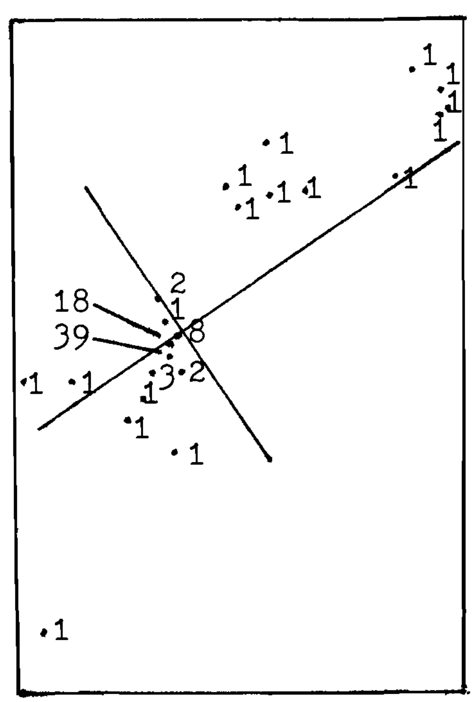


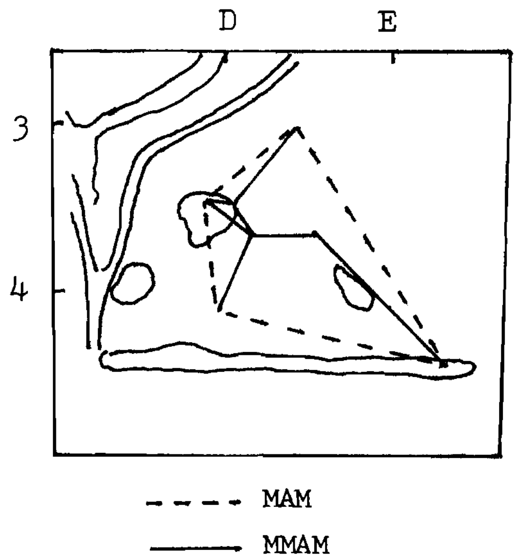
- - - - MAM
——— MMAM

R-241
Female
Tracked from
11/13/74 to 2/24/75

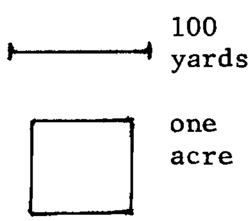
100 yards

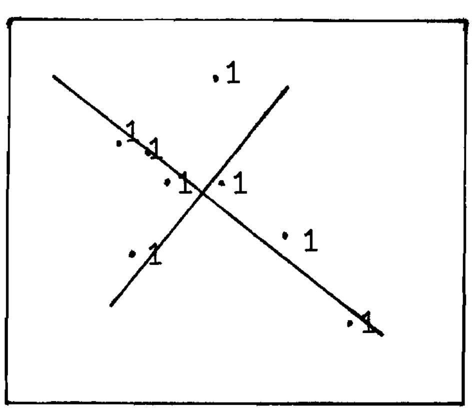
one acre

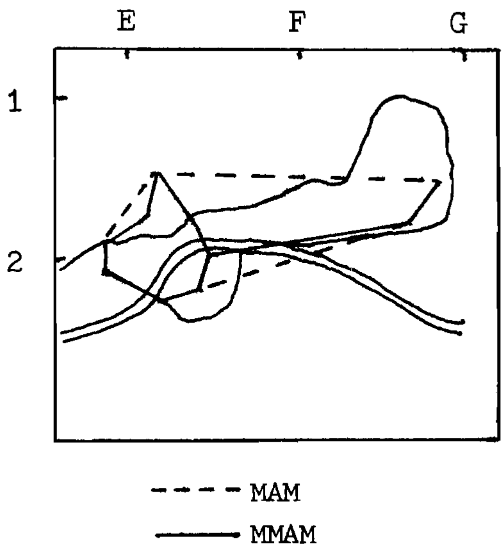




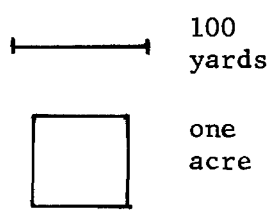
R-245
Female
Tracked from
11/25/74 to 11/29/74

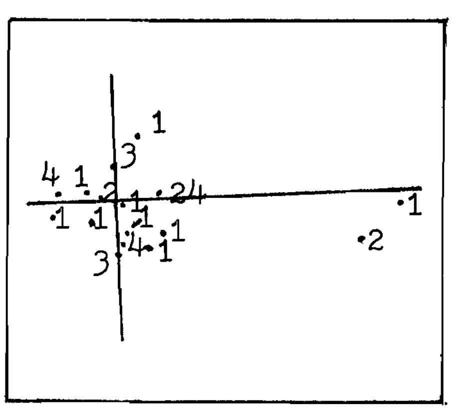


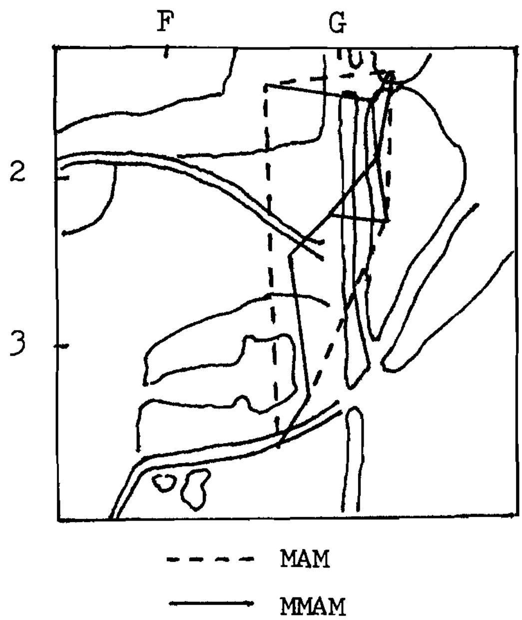




R-246
Female
Tracked from
3/25/75 to 5/19/75



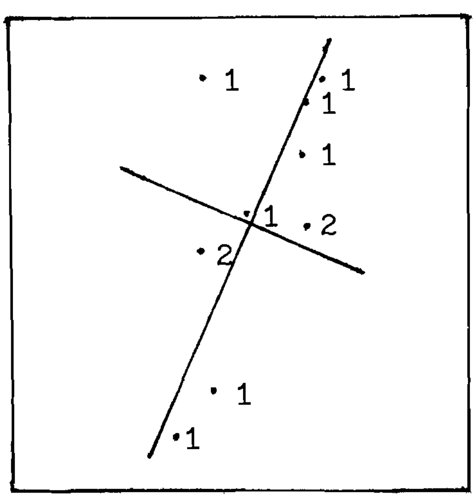


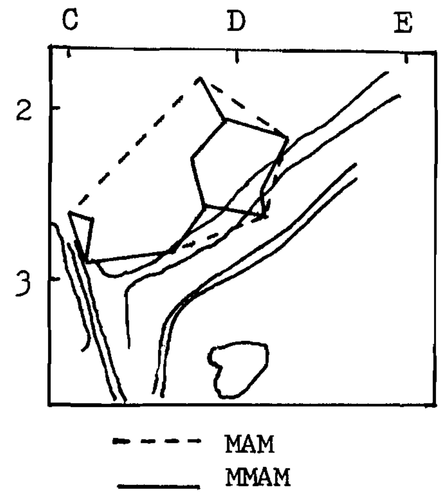


R-251
Female
Tracked from
12/4/74 to 12/12/74

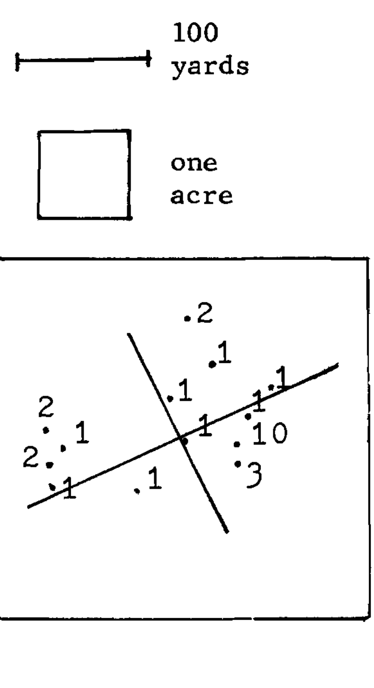
100 yards

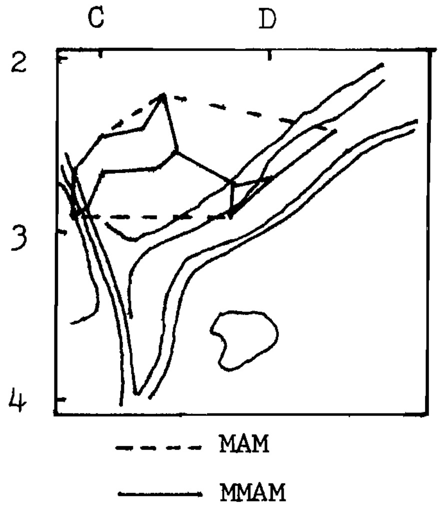
one acre



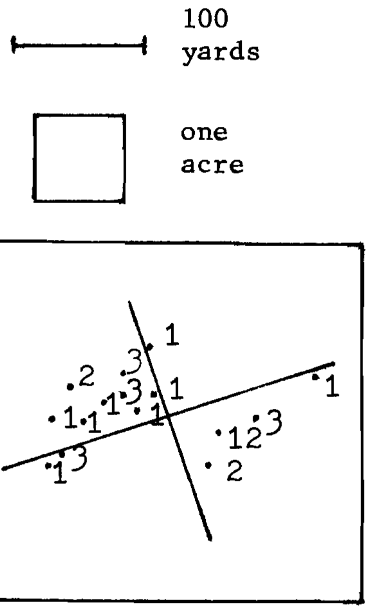


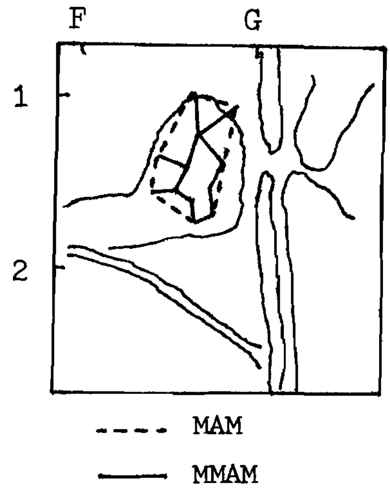
R-252
Female
Tracked from
10/31/75 to 12/2/74



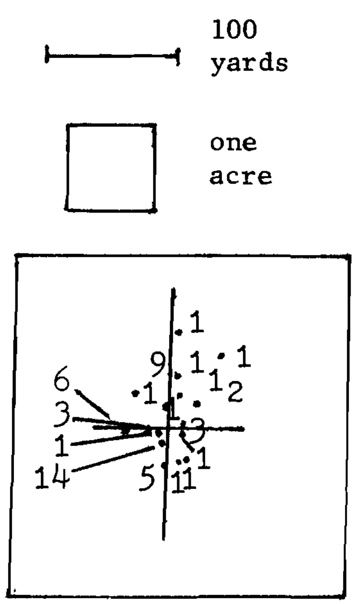


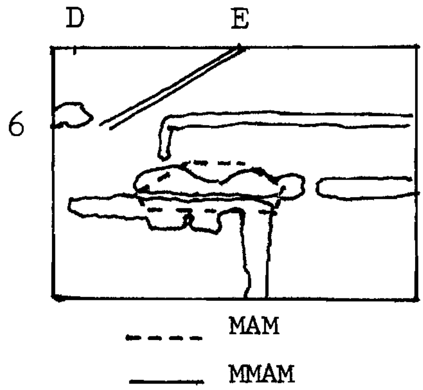
R-260
Male
Tracked from
8/31/74 to 10/7/74



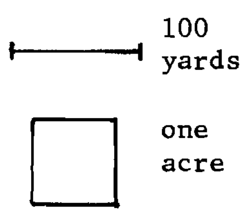


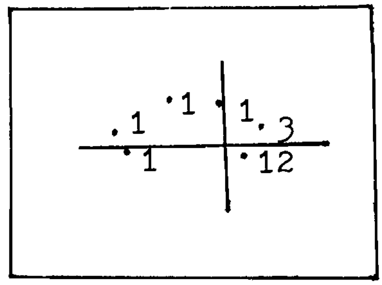
R-263
Female
Tracked from
8/16/74 to 10/7/74

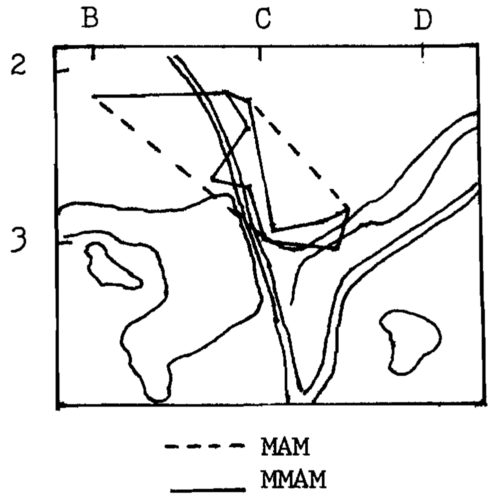




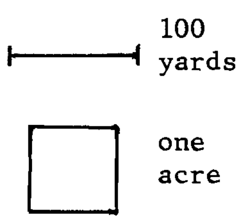
R-265
Male
Tracked from
8/12/74 to 8/31/74

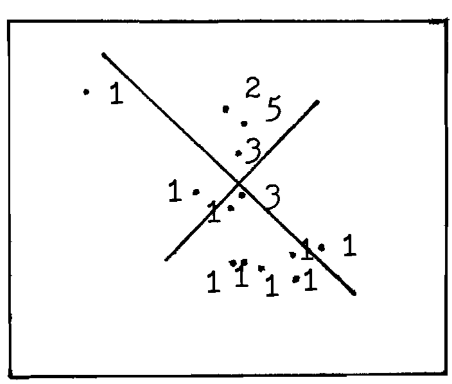


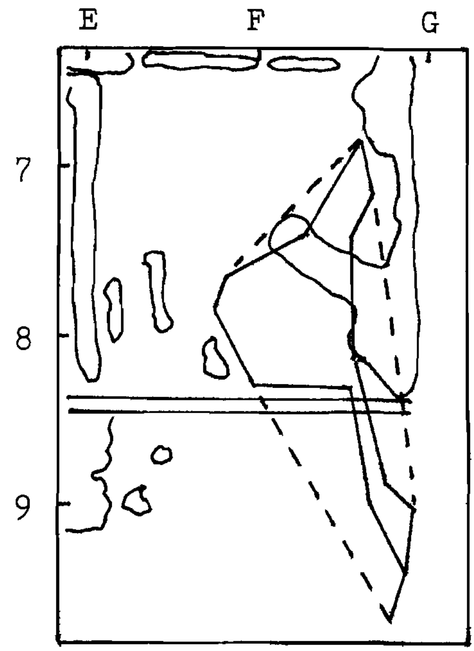




R-268
Female
Tracked from
11/19/74 to 12/7/74







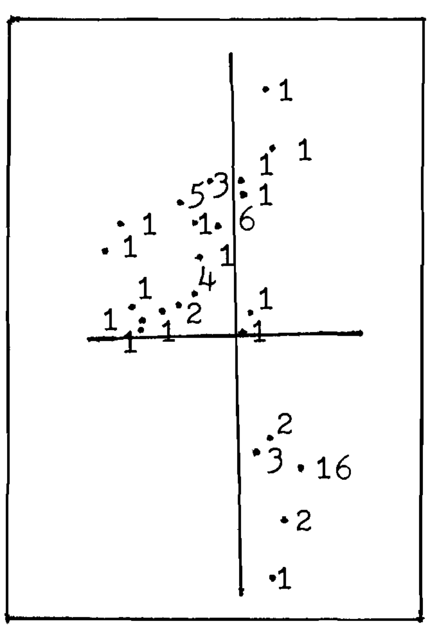
- - - - MAM

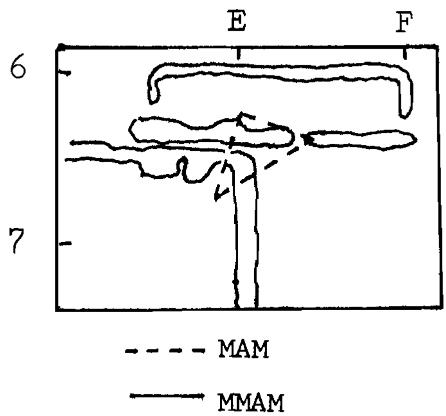
——— MMAM

100 yards

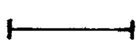
one acre

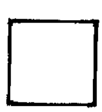
R-271
Male
Tracked from
8/29/74 to 11/15/74

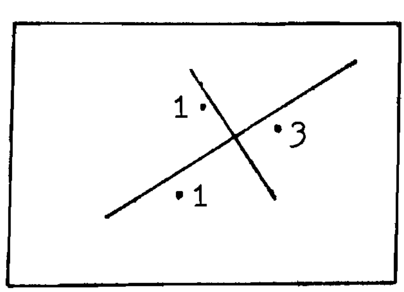


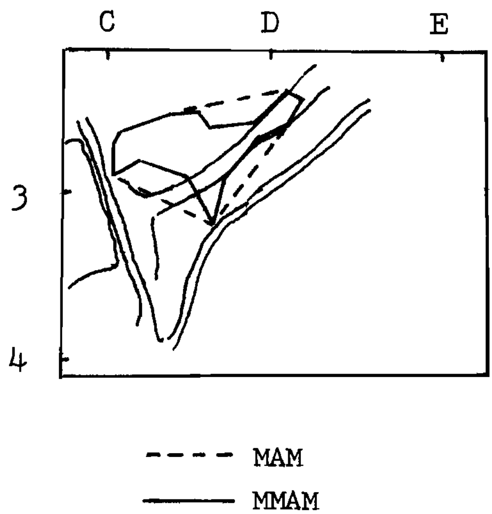


R-272
Male
Tracked from
8/13/74 to 8/20/74

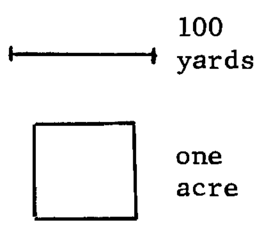


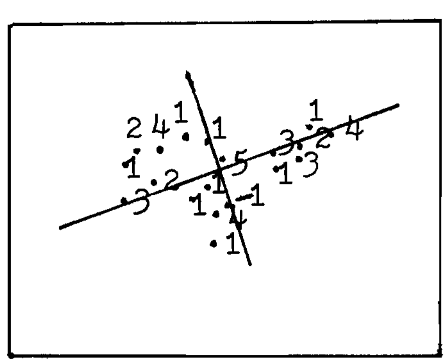






R-273
Female
Tracked from
8/31/74 to 10/20/74
and 11/21/74 to 12/20/74



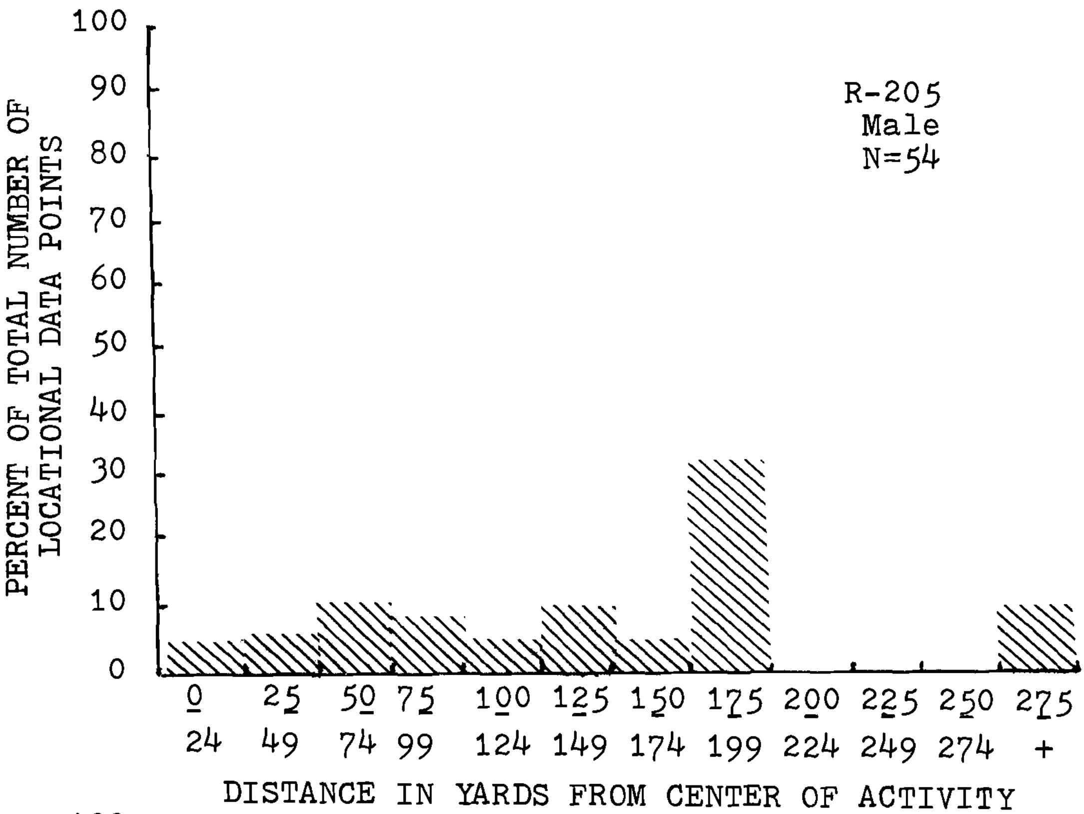


APPENDIX C

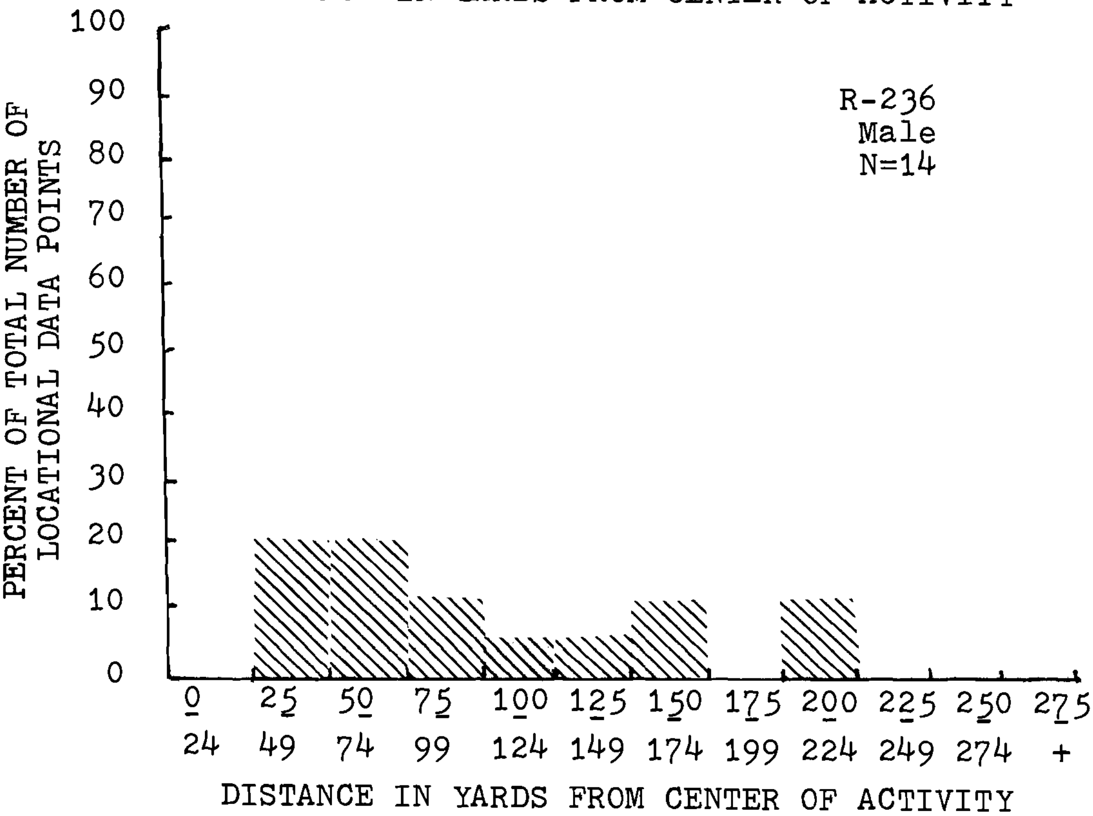
Frequency Distribution Histograms

of

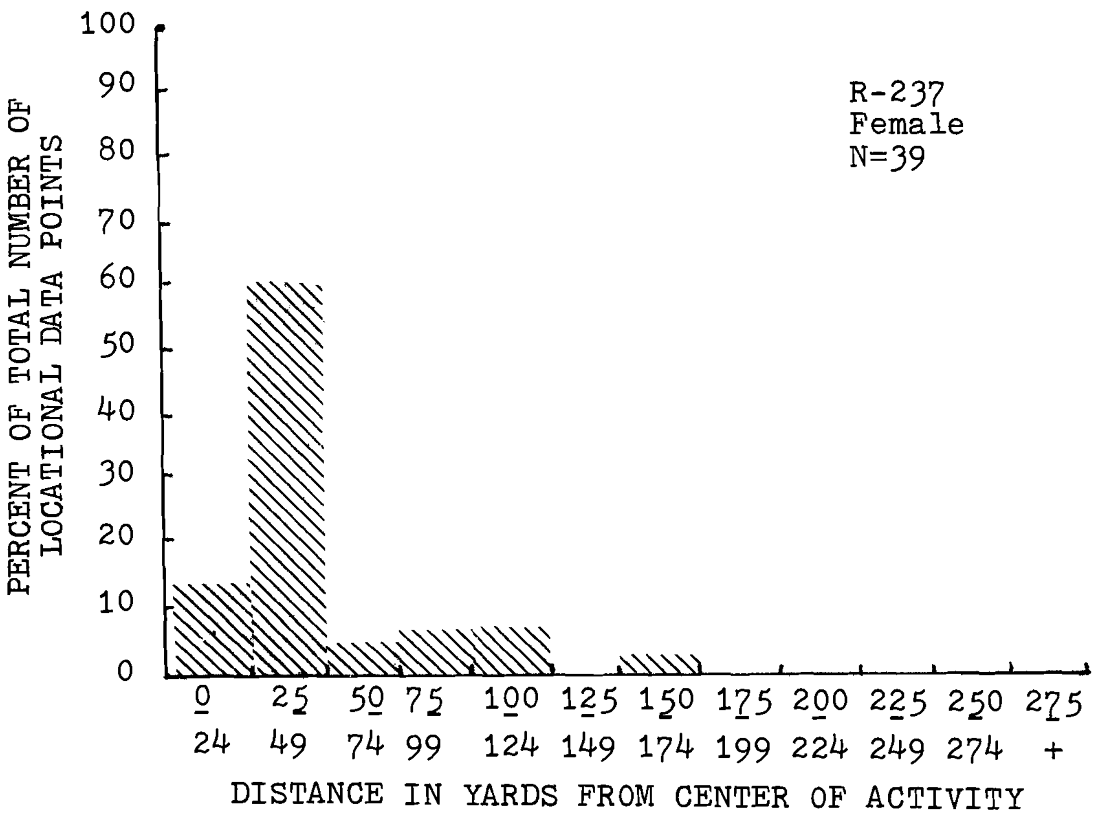
Recapture Radii

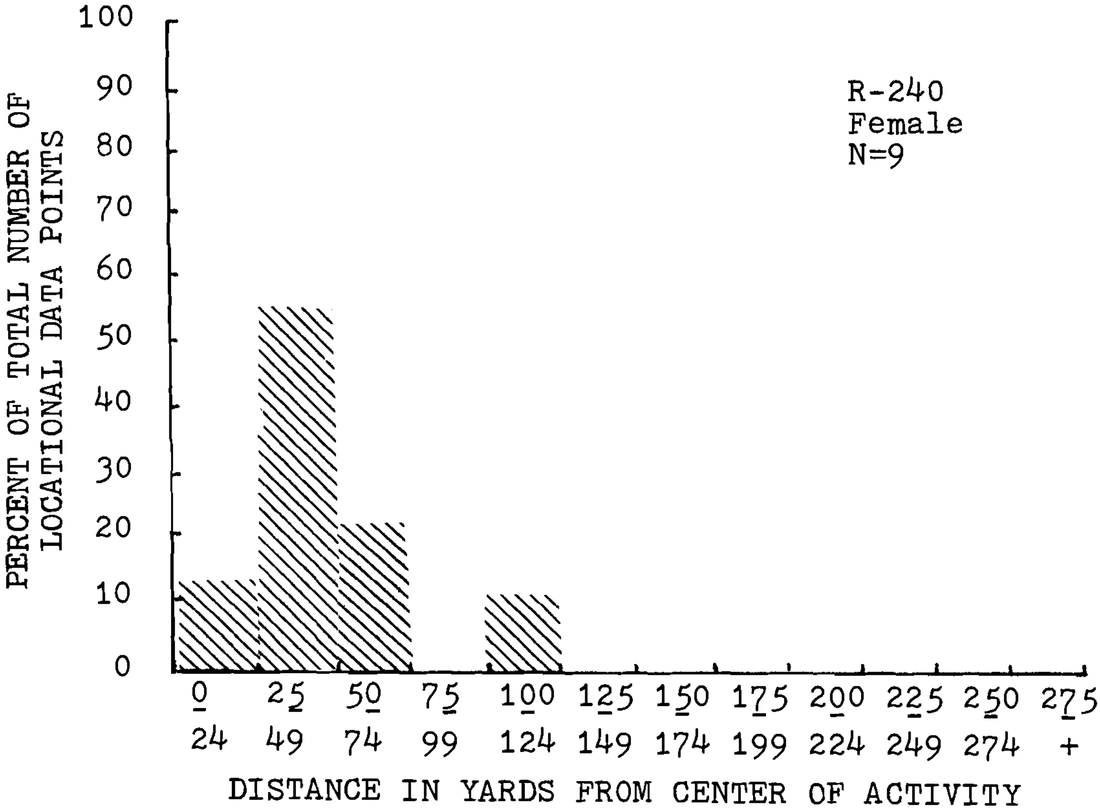


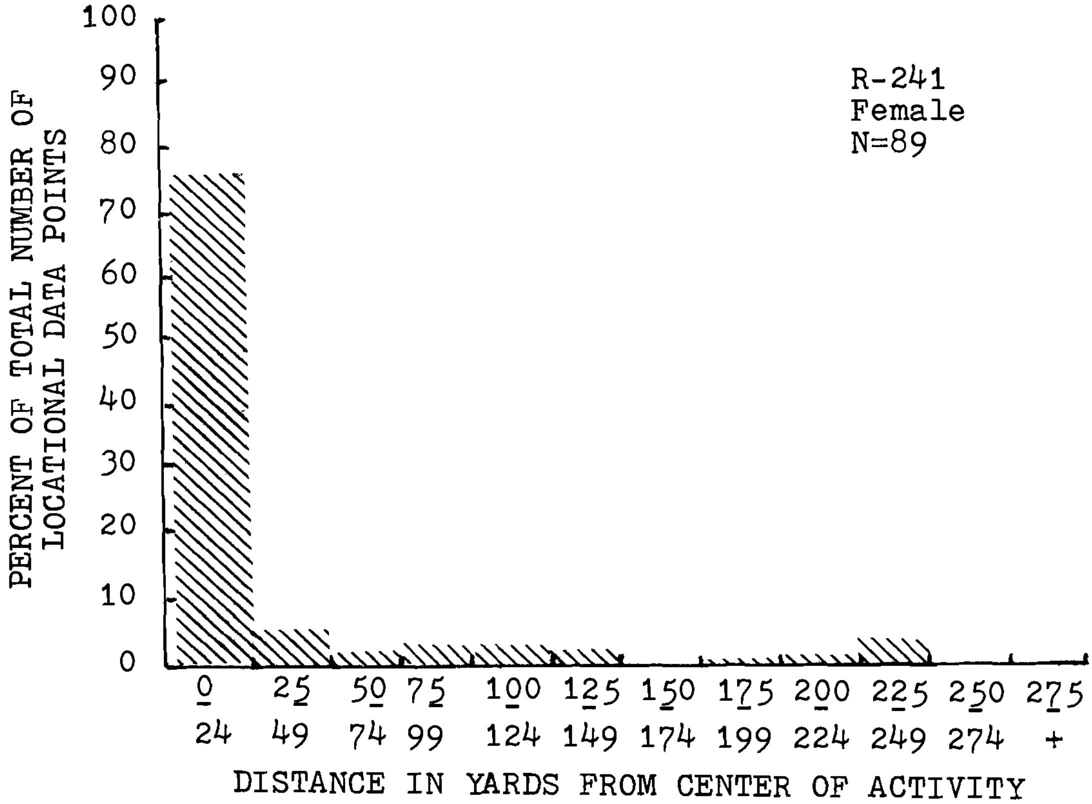
100
90
80
70
60
50
40
30
20
10
0
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
R-205
Male
N=54
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

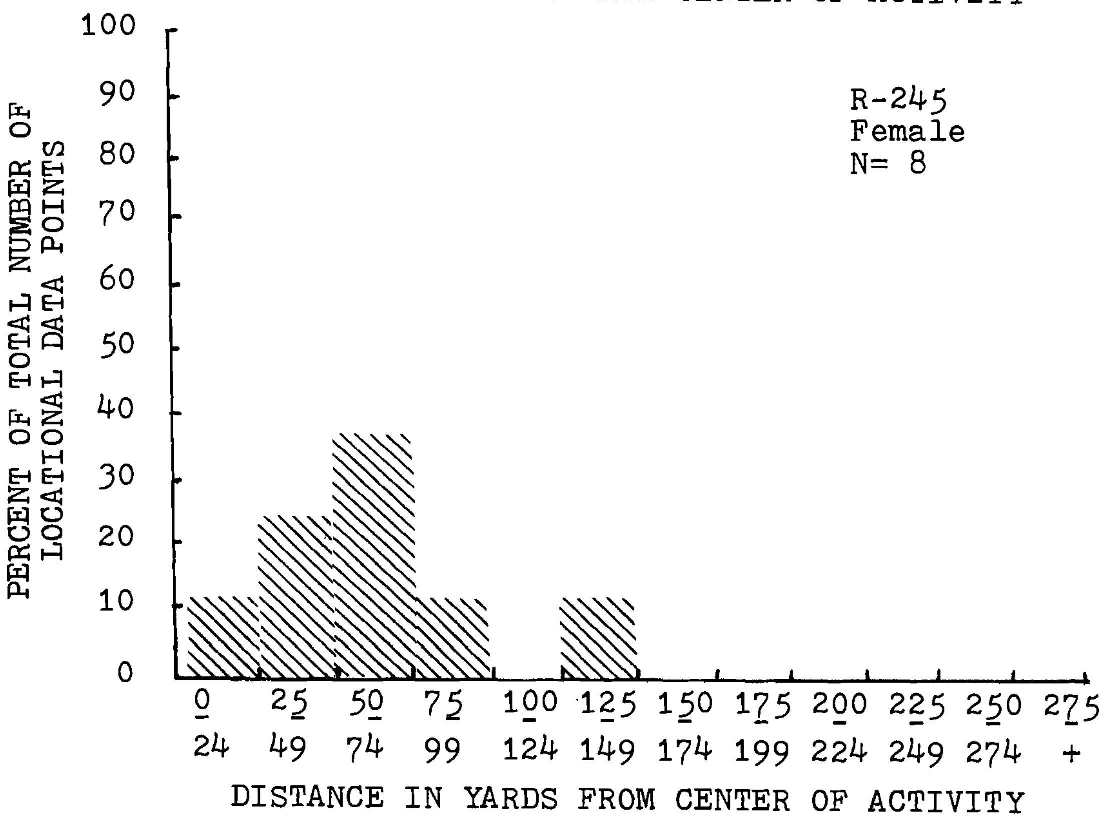


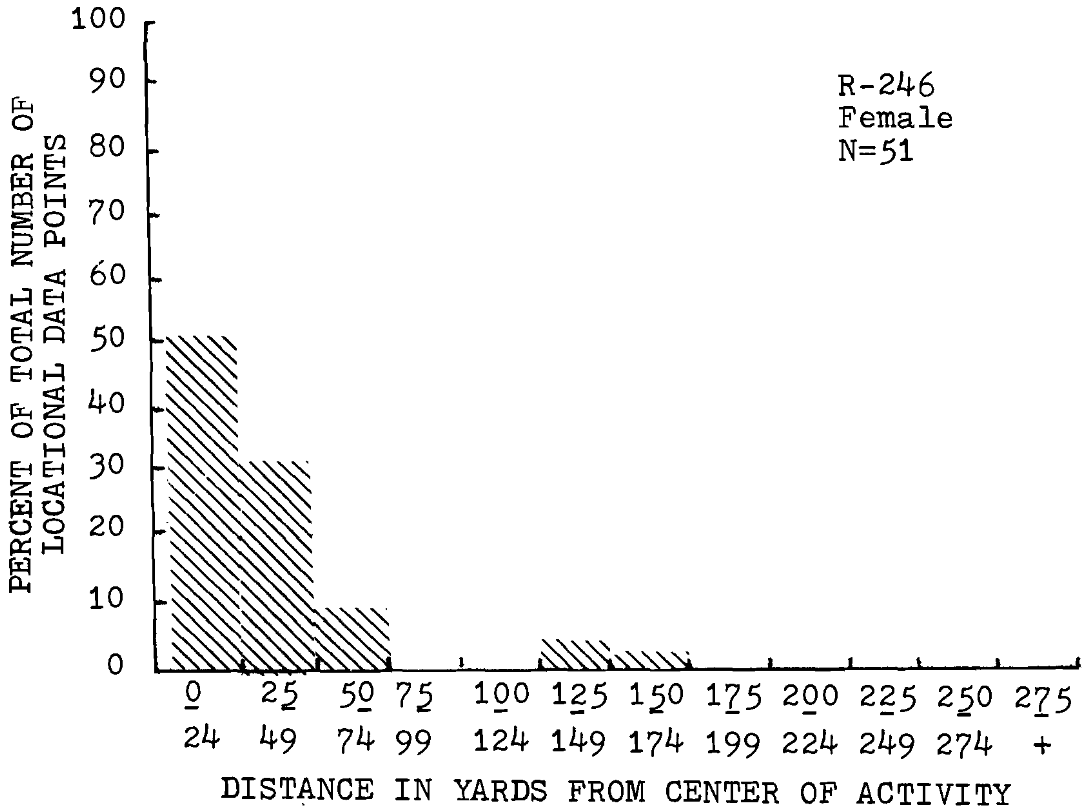
100
90
80
70
60
50
40
30
20
10
0
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
R-236
Male
N=14
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

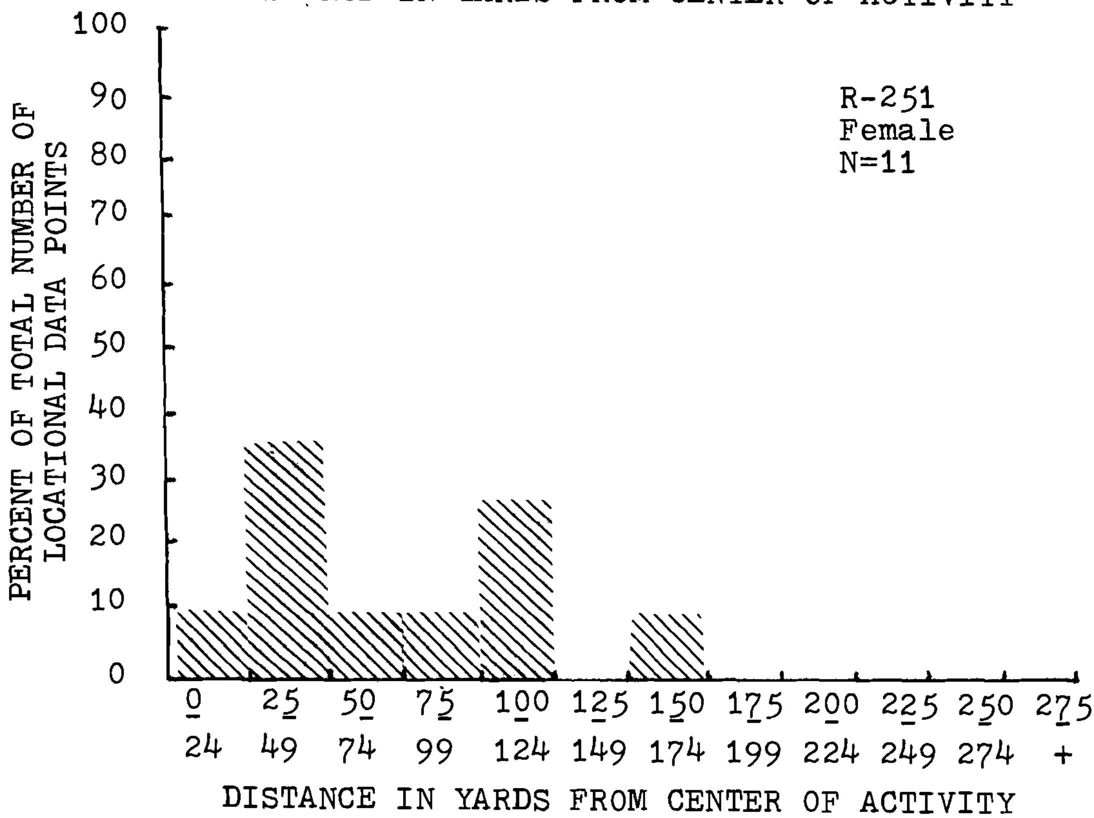

100
90
80
70
60
50
40
30
20
10
0
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
R-237
Female
N=39
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

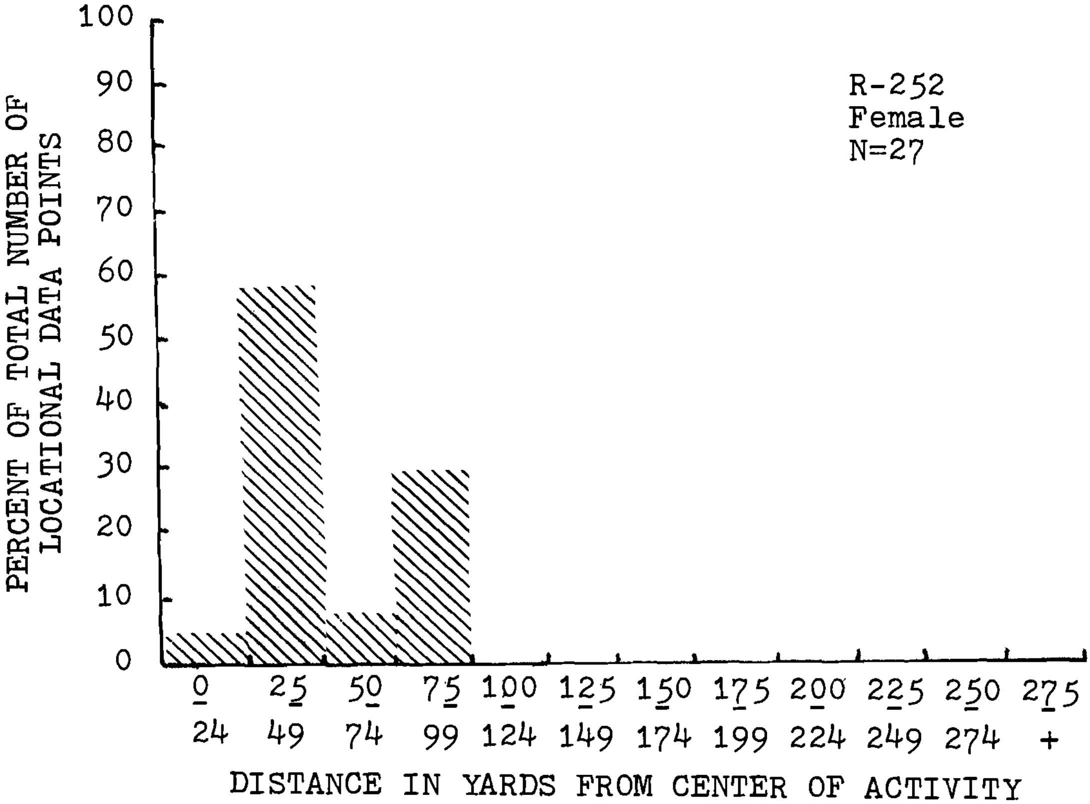

100
90
80
70
60
50
40
30
20
10
0
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
R-240
Female
N=9
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

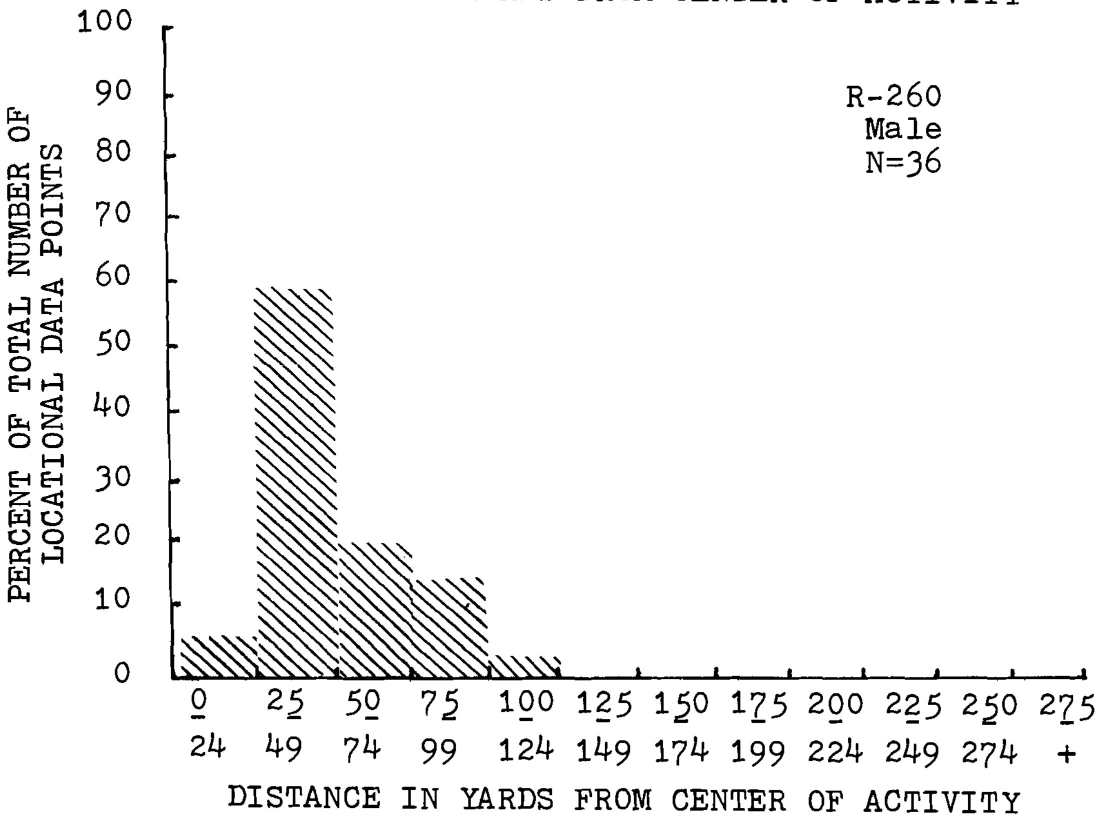

R-241
Female
N=89
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

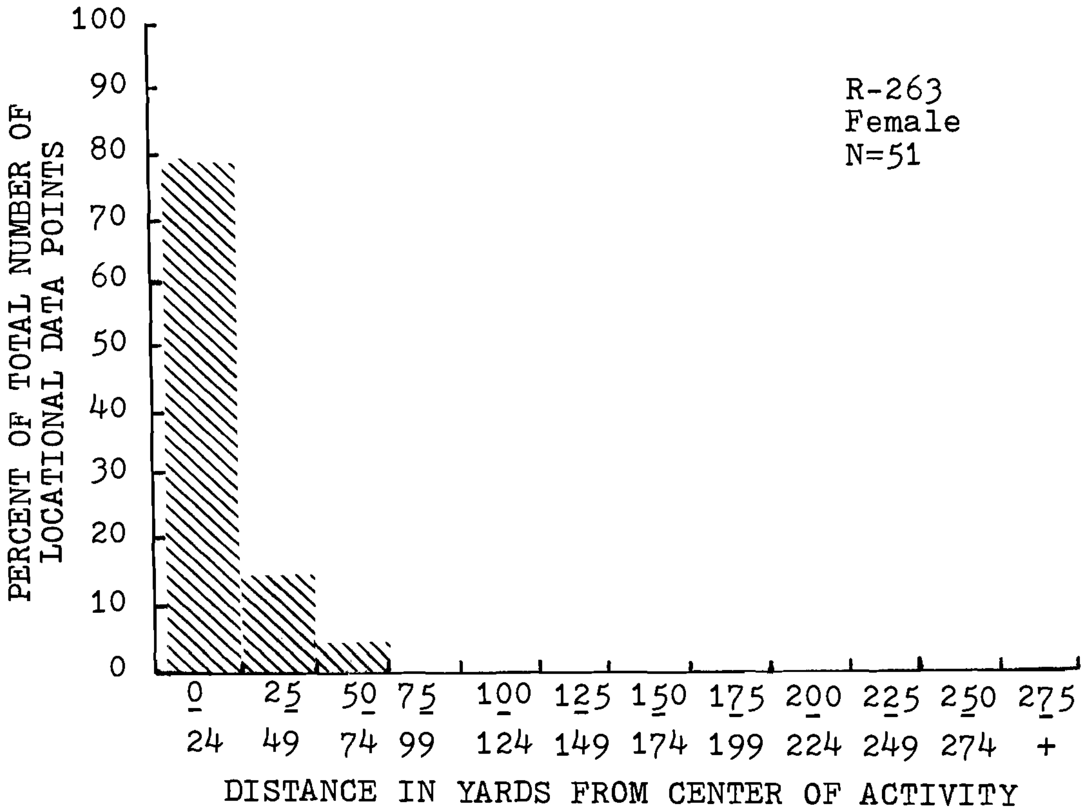

R-245
Female
N= 8
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY


R-246
Female
N=51
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

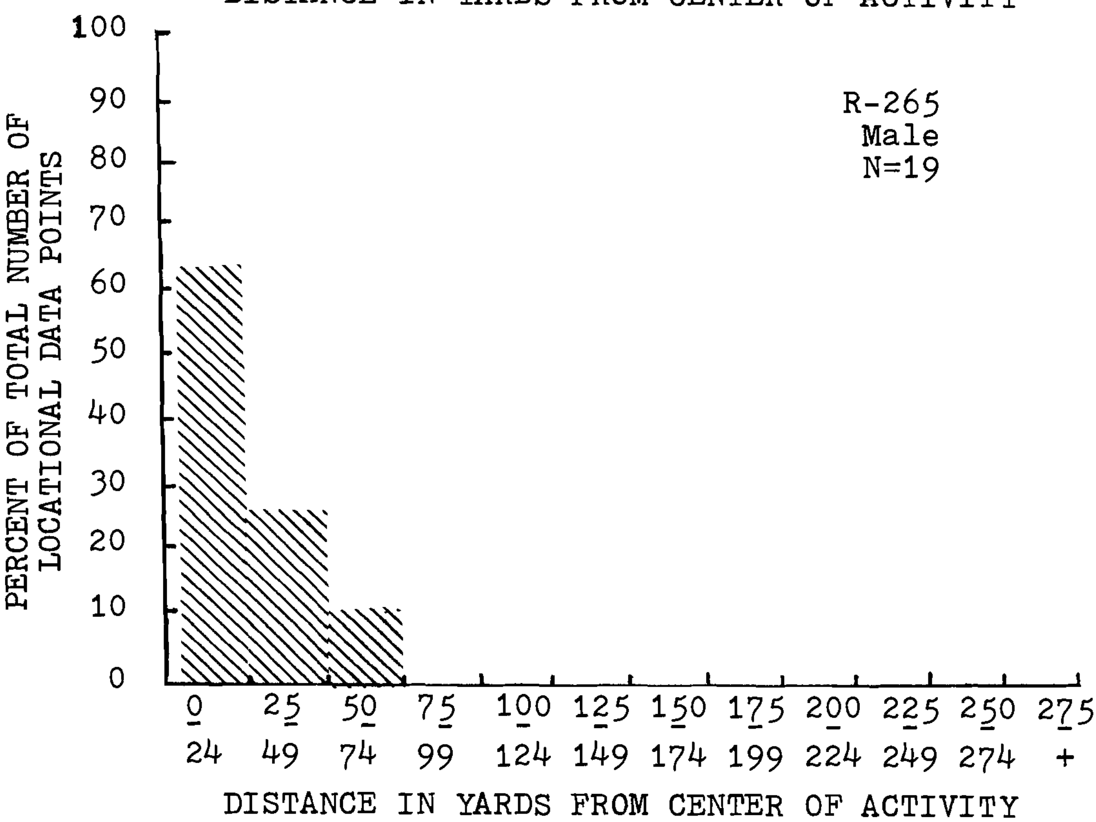

R-251
Female
N=11
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY


R-252
Female
N=27
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

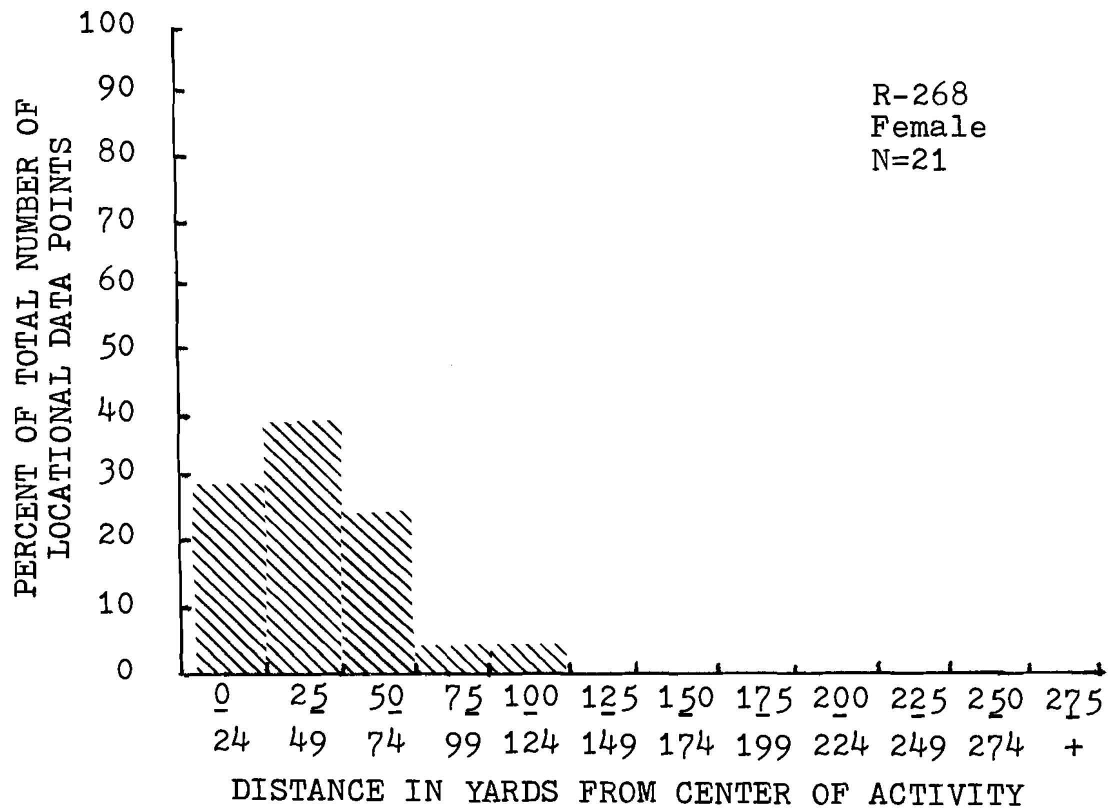

R-260
Male
N=36
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

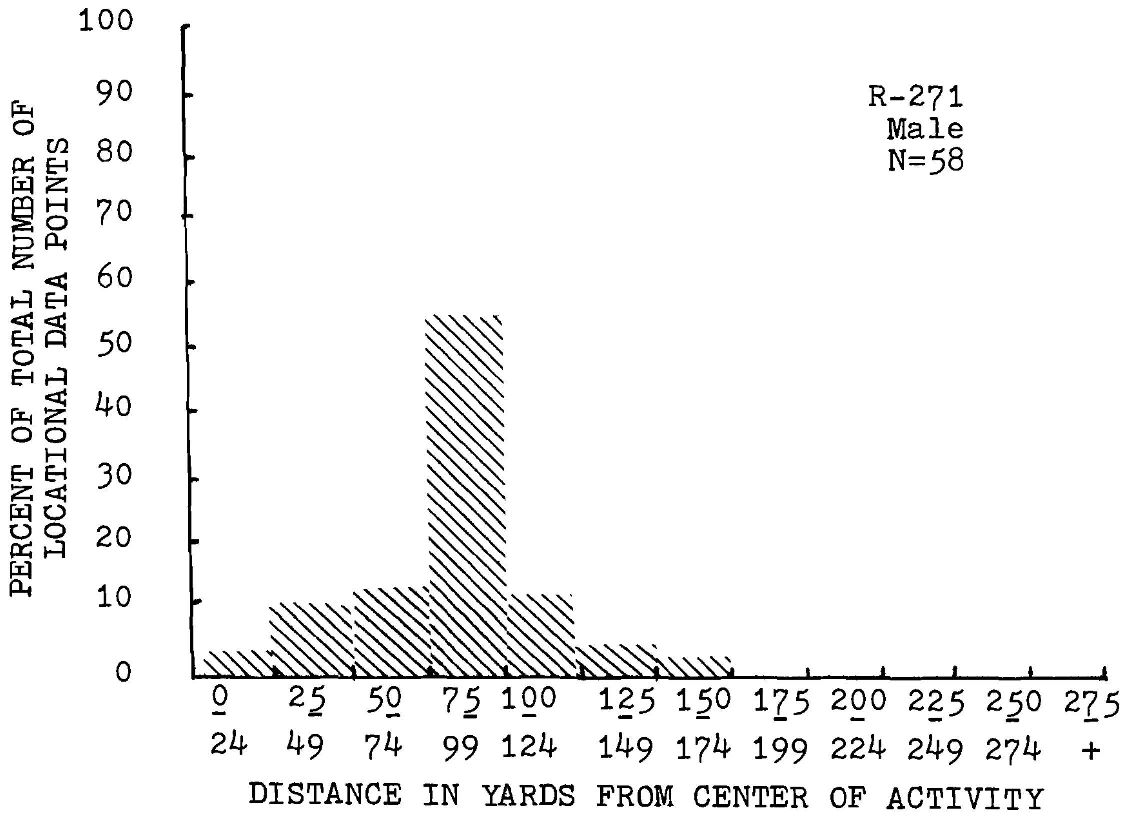


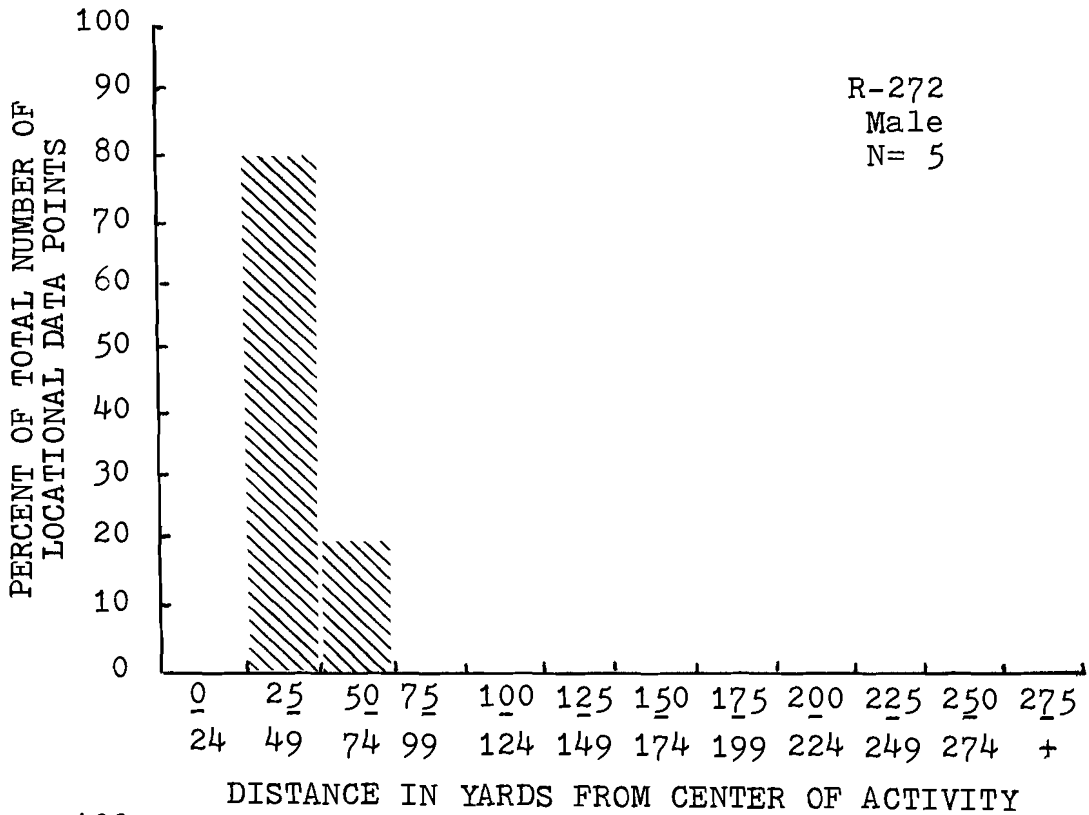
100
90
80
70
60
50
40
30
20
10
0
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
R-263
Female
N=51
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY

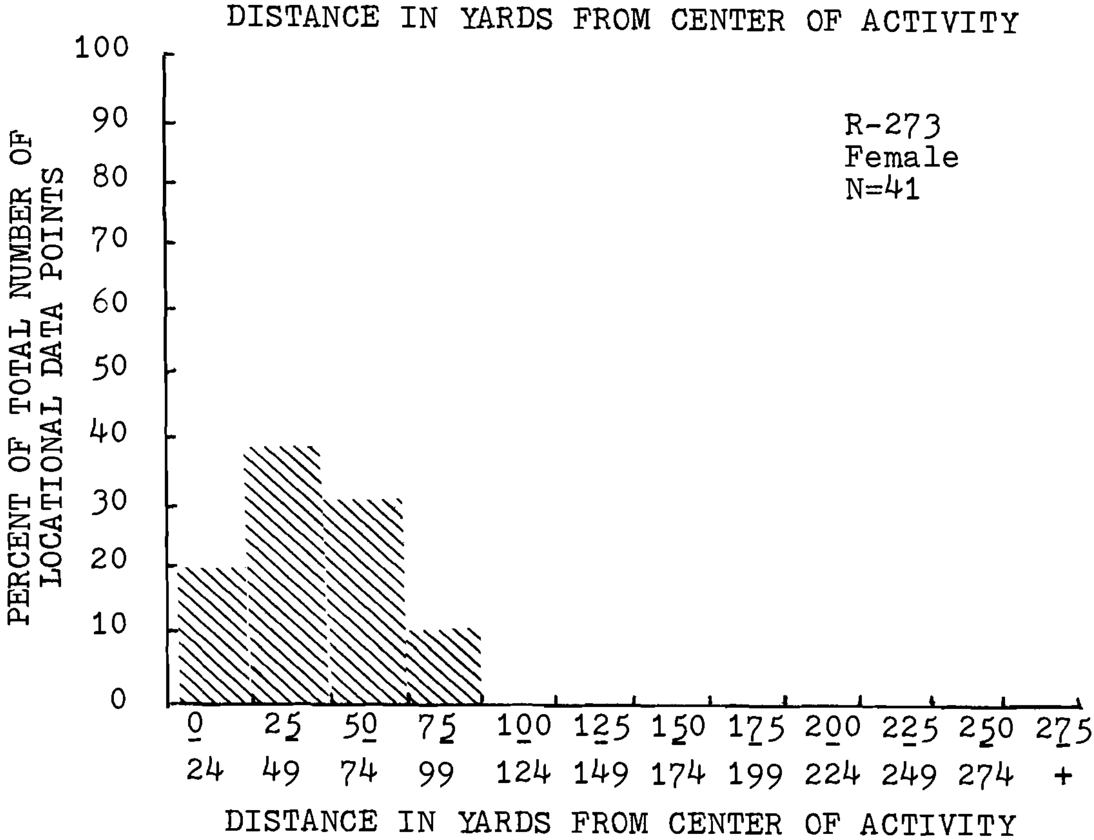


100
90
80
70
60
50
40
30
20
10
0
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
R-265
Male
N=19
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY


PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
R-268
Female
N=21
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY


PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
R-271
Male
N=58
0 24
25 49
50 74
75 99
100 124
125 149
150 174
175 199
200 224
225 249
250 274
275 +
DISTANCE IN YARDS FROM CENTER OF ACTIVITY


R-272
Male
N= 5
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0-24
25-49
50-74
75-99
100-124
125-149
150-174
175-199
200-224
225-249
250-274
275+
DISTANCE IN YARDS FROM CENTER OF ACTIVITY


R-273
Female
N=41
PERCENT OF TOTAL NUMBER OF LOCATIONAL DATA POINTS
100
90
80
70
60
50
40
30
20
10
0
0-24
25-49
50-74
75-99
100-124
125-149
150-174
175-199
200-224
225-249
250-274
275+
DISTANCE IN YARDS FROM CENTER OF ACTIVITY