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THE SPATIAL DISTRIBUTION AND AGONISTIC BEHAVIOR OF AN EASTERN GRAY SQUIRREL (*SCIURUS CAROLINENSIS*) POPULATION ON JAMESTOWN ISLAND, VIRGINIA

A Thesis
Presented to
The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

by
Marston E. Youngblood, Jr.
1979

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

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ABSTRACT

The purposes of this study were to first, apply a bivariate probabilistic home range model (Koeppl et al. 1975) to examine the spatial distribution of a natural gray squirrel population. The second aspect of this study was to examine the relations between agonistic behavior of gray squirrels with their spatial distribution. The approach-avoidance behavior of gray squirrels in response to the stimulii of urine scent marks are tested as a final aspect of this study.

Livetrapping and direct observations of squirrels were conducted for 18 months, resulting in a total capture of 37 males and 23 females which were marked and released. Gray squirrels were captured an average of 4.5 ± 0.756 times (Mean ± SE). Frequency of captures ranged from 1 to 29; approximately 35% of the animals were captured once, 60% were captured from 2-10 times, and 5% were captured more than 25 times. The results of the urine application experiment did not indicate a significant approach or avoidance response of gray squirrels towards entering urine treated live-traps. Furthermore, no scent marking was observed.

The data indicate that males on the average have larger home ranges (2.28 ha) than females (1.92 ha), but the difference is not significant. No clear age related difference in home range size is indicated. However, subadult squirrels were more mobile and had larger home range areas than adults (2.5 and 3.12 ha versus 2.34 and 1.6 ha for both males and females). Seasonal changes in home range size were not demonstrated in this study.

Significant differences in spatial distribution of the study population were indicated by changes in the percentage of home range overlap and overlap index. These differences can be attributed to both sex related and seasonal effects of the spring-summer breeding period and fall dispersal. The significant age related difference in distance to the activity center of nearest same sexed animal was linked with the increased distance between the activity centers of subadult and other males in the spring and fall/winter seasons. Avoidance by subadult males of the more aggressive and dominant adults during these periods could account for the significant age related differences.

Established animals in the Jamestown study population had stable home ranges for the duration of this study. The removal/release procedure results of this study confirm that resident gray squirrels are likely to return when released within 1 km of their home woodlot.

Adult males in this study tended to have higher Dominance Index (D.I.) scores than females, but this difference was significant only for the spring observational periods. Body weight of the animal was positively correlated with home range overlap. The data suggest that subordinate gray squirrels were avoiding contact with dominant conspecifics in the study area. Dominance was not associated with actual estimated size of home range.

The results that dominance was not shown to be associated with home range size as by Pack _et al_. (1967), and that residents were not consistently dominant over immigrants as shown by Thompson (1978) may be attributable to use of a feeding station in this study, since noticeable increases in the levels of aggressive interactions began upon its establishment on the study area. Utilization of the home range model of Koeppl _et al_. (1975) resulted in values for gray squirrel home ranges within the limits of areas reported in the literature and provided a quantifiable basis for analyzing the spatial distribution of the population.

SPATIAL DISTRIBUTION AND AGONISTIC BEHAVIOR
OF AN EASTERN GRAY SQUIRREL POPULATION

INTRODUCTION

The eastern gray squirrel, *Sciurus carolinensis*, is one of the most intensively studied small mammals in reference to home range (Flyger 1960; Taylor 1966; Doebel 1967; Donohoe and Beal 1972; Cordes and Barkalow 1972; Doebel and McGinnes 1974; Thompson 1978) and behavior (Bakken 1959; Sharp 1959; Taylor 1966; Pack *et al*. 1967; Horwich 1968; Brady 1972; Cordes and Barkalow 1972; Bland 1977; Thompson 1977a, 1977b, 1978). Studies evaluating dominance, dispersal, and social heirarchy indicate gray squirrel woodlot populations have a relatively stable social system, with an individual squirrel's position in the social heirarchy shown to be correlated with age, sex, and body size, but not conclusively associated with home range size (Flyger 1960; Cordes 1965; Taylor 1966; Pack *et al*. 1967; Thompson 1978).

D. C. Thompson (1978: 326) succinctly summarized the social system of the gray squirrel as determined by his research:

> The area used by males and females expands after weaning, then stabilizes and remains the same in location and extent for life. The home range of an established individual is broadly overlapped by the home ranges of several other animals. Each established individual is regularly in contact with only a limited number of recognized neighbors with which it has well-established dominance relationships. Individual recognition promotes lowered aggressive levels between neighbors which allows each squirrel to use its entire home range evenly. Aggressive behavior is directed toward strange squirrels, either young or immigrants, which attempt to enter this system. Thus, the established individuals hinder the settlement of new animals. Young squirrels born in a given locality have a greater chance of establishing than do immigrants.

Thompson's (1978) definition of the gray squirrel social system parallels the results of Bronson (1964) with another sciurid, *Marmota monax*. The woodchucks that he observed appeared to be organized into a complex of dominance-subordination relationships which were stable regardless of the location of an interaction within the system of overlapping home ranges.

Few recent investigators of squirrel home range and behavior have utilized descriptive probabilistic models to estimate the area used by an individual animal. The method most often used for determining squirrel home ranges is the minimal polygon method (Flyger 1960, Doebel 1967, Taylor 1966, Pack *et al*. 1967, Cordes and Barkalow 1972, Thompson 1978). Adams (1976), however, used the bivariate normal model of Jennrich and Turner (1969) to generate probability ellipses to estimate fox squirrel (*Sciurus niger*) home ranges. No researchers of squirrel behavior to date have employed the probabilistic home range model of Koeppl *et al*. (1975) to investigate the spatial distribution of a gray squirrel population. Consequently, one of the purposes of this study is to apply the bivariate, probabilistic home range model of Koeppl *et al*. (1975) to examine the spatial distribution of a natural gray squirrel population on Jamestown Island, Virginia.

The advantages that exist in studying a protected (from man) population of gray squirrels on Jamestown Island are twofold. First, it is an opportunity to study a well defined, isolated, population of a readily observable small mammal. Second, a field study presents the opportunity to observe behavior of the gray squirrel in the wild with the influences of weather, predation, and a natural habitat contributing to behavioral interaction. These important environmental factors would otherwise be lost under laboratory or semi-natural conditions.

Watson and Moss (1970) observed that behavior involving the dominance of animals over others often operates via aggression to effect patterns of spacing. In the home range system, as opposed to a territorial system, a species is attached to a fixed area of land but does not defend it; instead, the animal's portable personal sphere, the area around a solitary individual, is defended against intrusion (McBride 1971). Agonistic interactions are concerned with expelling the opposing conspecific from this area or forcing him to submit. In either case, a dominance-subordination relationship is established, thereafter expressed spatially (McBride 1971). The second aspect of this study is to examine the relations between agonistic behavior of gray squirrels with their spatial distribution.

There are reports of gray squirrels using scent marking in woodlot areas (Taylor 1966, 1968; Barkalow and Shorten 1973). Taylor (1966, 1968) hypothesized that marking points function as an act of communication among a population of squirrels. If scent marking is interpreted as a form of social behavior in the gray squirrel, then it may be a factor in individual recognition between neighboring animals and thus influence the spatial distribution of the population. The approach-avoidance behavior of gray squirrels in response to the stimuii of urine scent marks will be tested as a final aspect of this study.

REVIEW OF LITERATURE

W. H. Burt (1943) provided an early operational definition of home range. He restricted the home range concept to "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." Furthermore, he suggested that once an individual established a home range it normally remained in that area for life, with the exception of occasional exploratory movements into areas which should not be considered part of the home range.

The size of a home range may vary with sex, age, and season; and home ranges of different individuals may even overlap to varying degrees. One of the simplest methods of estimating the home range of small mammals is derived from drawing the smallest polygon which contains all the locational data points for an individual and measuring the resulting area. The problems that arise from this minimum polygon method are that the shape of the polygon and its area depend on the order in which the locational points are connected, and the areas of minimum polygons have a tendency to increase in direct proportion to the number of locational fixes in the sample (Jennrich and Turner 1969).

A circular home range model was proposed by J. C. Calhoun and J. U. Casby (1958) based on the mean recapture radius of small mammals. The capture radius (r_i) for a particular capture point ($p_i = x_i, y_i$) was defined "as the distance from p_i to the geometric center ($\overline{p} = \overline{x}, \overline{y}$) of the capture points" (Jennrich and Turner 1969: 229). A value was computed from the recapture radius and estimated home range size was determined for the defined circular area. The drawbacks to a circular home range model are that it underestimates size in comparison to long narrow ranges covering the same area, and it is based on a strict assumption of circular symmetry.

Jennrich and Turner (1969) note that many non-circular home ranges have been reported for mammals, and propose a model that could measure circular as well as non-circular home ranges. They assume that the intensity with which an animal uses its habitat is expressed by a bivariate normal distribution. In addition, this utilization distribution is best defined by concentric constant density ellipses. Home range for their elliptic model is defined as the "area of the smallest region which accounts for 95% of an animal's utilization of its habitat" (Jennrich and Turner 1969: 233). They recommend their estimate of home range because of its lack of sample size bias, the non-assumption of circularity, and an independence from orientation of home range.

A contrasting approach is presented by Van Winkle (1975) in which he discusses the elliptical home range model offered by Mazurkiewicz (1969, 1971) that uses three sample statistics to provide information on orientation of home range.

> These three statistics are the lengths of the major and minor axes (principal components) of the ellipses of concentration and the angle of inclination of the major axis with respect to the original coordinate system. Mazurkiewicz (1971) assumed that the angle of inclination was an index of direction of movement preferred by an individual and that the ratio of the principal axes was an index of the degree of preference for this direction. In her studies on the home ranges of the redback vole, Clithrionomys glareolus, no circular areas were found; in all cases the home range had the shape of a flattened ellipse, with a mean ratio of 3:1.

The bivariate normal distribution without the assumption of circularity of an individual's utilization distribution provides a general and flexible probabilistic home range model that is adequate for depicting the home ranges of many animals inhabiting homogeneous habitats (Van Winkle 1975).

Another probabilistic bivariate home range model is presented by Koeppl _et_ _al_. (1975). They propose a general model for inter- and intraspecific comparisons as well as inferences concerning internal structure of the home range. For this model, the axes of the ellipse are weighted according to the frequency of occurrence of the individual at a particular location. Biases due to orientation of locational data and sample size are corrected by the use of eigenvalues of the variance-covariance matrix derived from the data coordinates and by incorporating the F-statistic in calculation of the ellipse (Koeppl _et_ _al_. 1975). Thus, their home range model is a confidence ellipse which is utilized in determining the probability of finding an individual at a particular location.

Hayne (1949) defined a point which is the geographic center of all points of capture (or observation) of an individual as the center of activity for that animal. Koeppl _et_ _al_. (1975) believe that the activity center is more than a geometric center of a scatter of points. They postulate the concept of a center of familiarity, a location in an individual's home range in which it is most familiar and secure. The advantages of their model are that the estimated areas, A_p, reflects the confidence in home range size and location, given a finite number of home range coordinates, and that it permits inferences concerning an animal's relative familiarity with any point within its home range (Koeppl _et_ _al_. 1975).

STUDY AREA

The study site is approximately 2.4 hectares (6.01 acres) in size, and is located on Jamestown Island, Virginia, which has been under protection of the National Park Service since 1934 as part of Colonial National Historical Park. The study area is situated at the eastern edge of the New Town meadow, and is bounded on the other three sides by the James River, Orchard Run, and the Jamestown Island loop road (see Figure 1). The geologic characteristics of the area are a basal layer of sand which is topped by a few feet of clay and silt merging into topsoil, with a maximum elevation of less than 10 feet above mean low tide (Cotter 1958).

Characteristic tree species in the overstory of the study area are loblolly pine (*Pinus taeda*), pecan (*Carya illinoensis*), black cherry (*Prunus serotina*), tulip popular (*Liriodendron tulipfera*), several different oaks (*Quercus* spp.), and bald-cypress (*Taxodium distichum*). Species common to the understory are eastern redcedar (*Juniperus virginiana*), American holly (*Ilex opaca*), dogwood (*Cornus* sp.), wax myrtle (*Myrica cerifera*), and wild grape (*Vitis* sp.). Various grasses, sedges, poison ivy (*Rhus radicans*), and crownbeard (*Verbesina occidentalis*) form the ground cover of the area (Figure 2).

Figure 1. Map of study area.

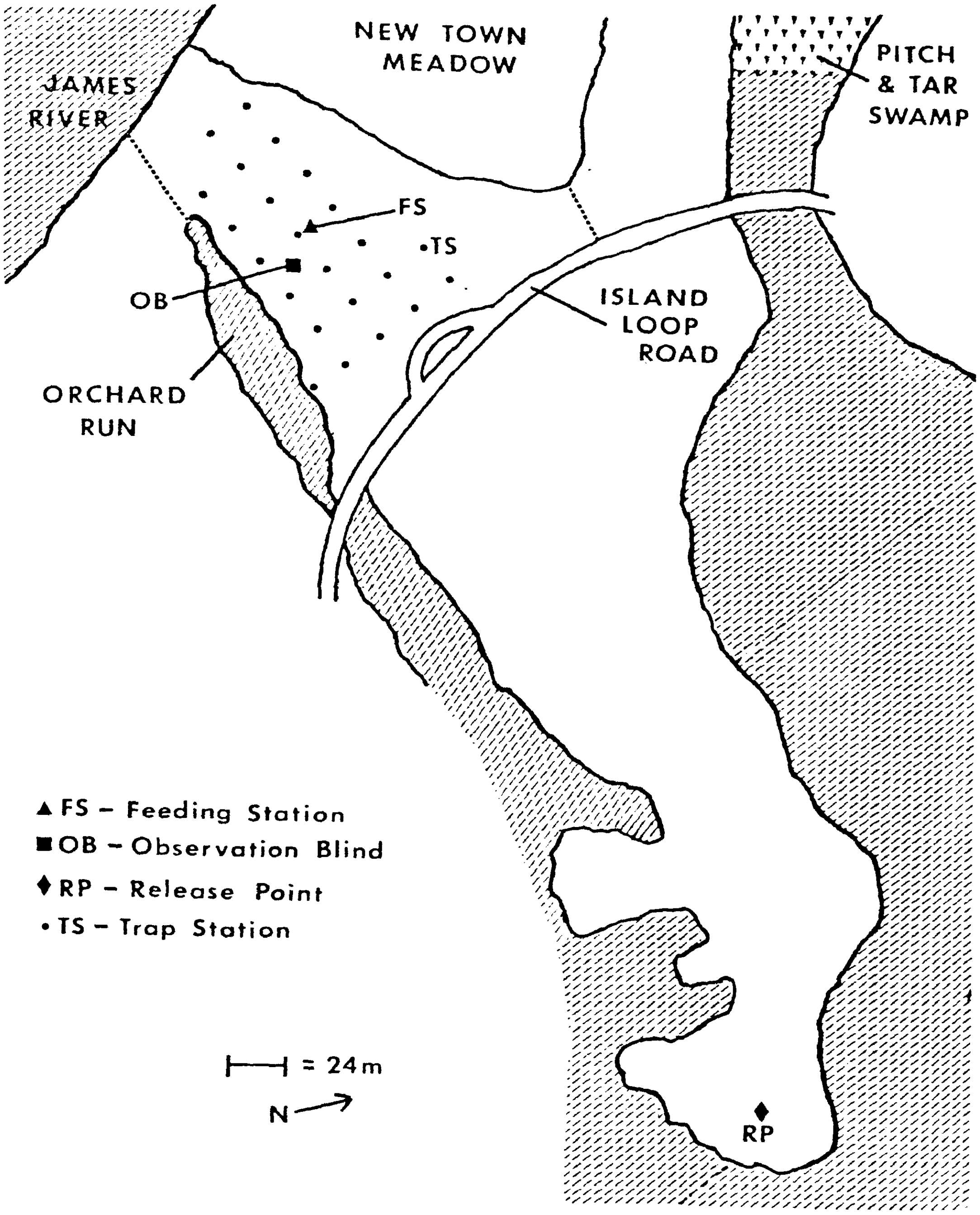
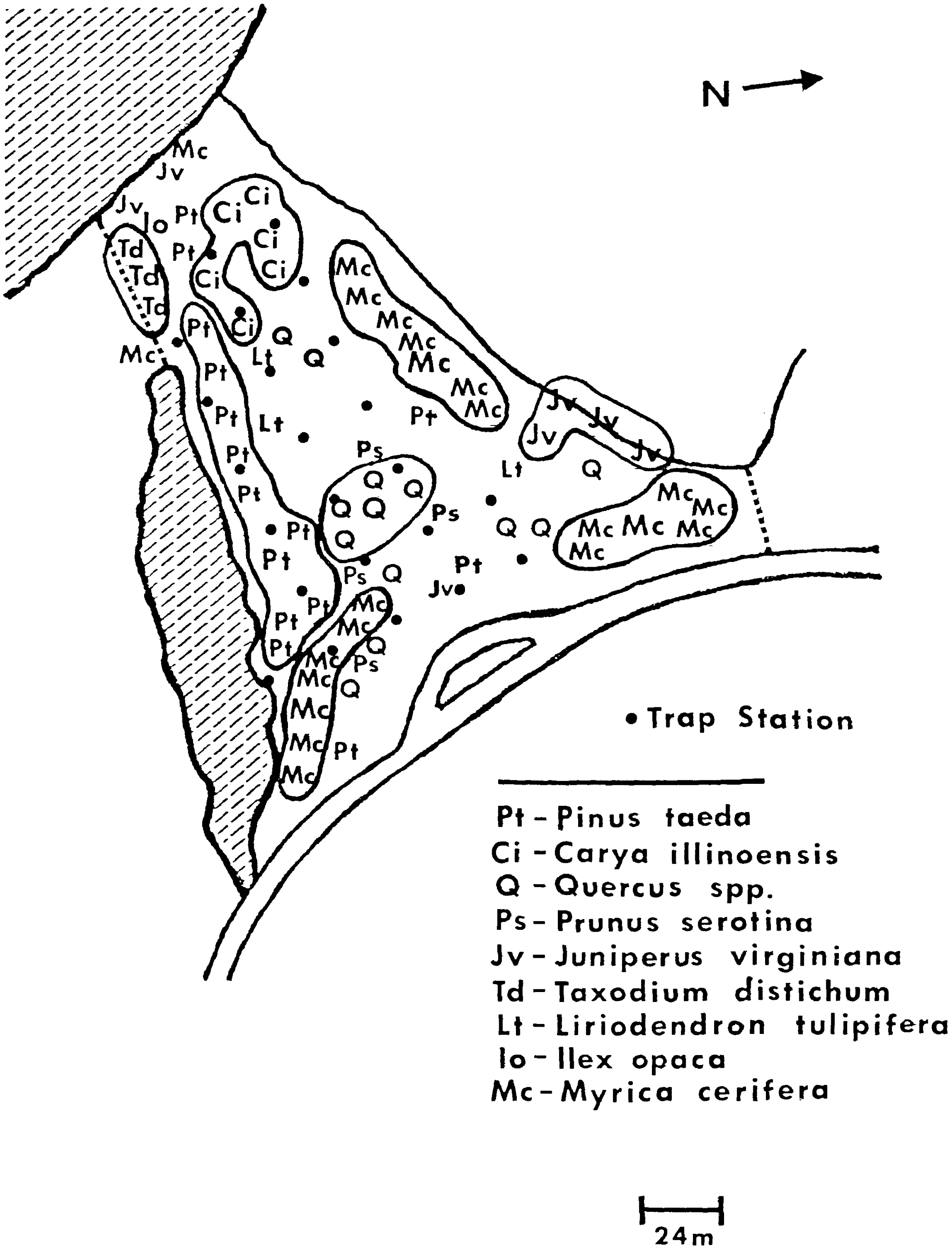

NEW TOWN MEADOW
JAMES RIVER
PITCH & TAR SWAMP
FS
TS
OB
ISLAND LOOP ROAD
ORCHARD RUN
RP
▲ FS – Feeding Station
■ OB – Observation Blind
♦ RP – Release Point
• TS – Trap Station
= 24m
N

Figure 2. Distribution of Overstory and Major Understory Vegetation in Study Area.

(Encircled symbols on map indicate high density of a species.)


N
• Trap Station
Pt - Pinus taeda
Ci - Carya illinoensis
Q - Quercus spp.
Ps - Prunus serotina
Jv - Juniperus virginiana
Td - Taxodium distichum
Lt - Liriodendron tulipifera
Io - Ilex opaca
Mc - Myrica cerifera
24m

MATERIALS AND METHODS

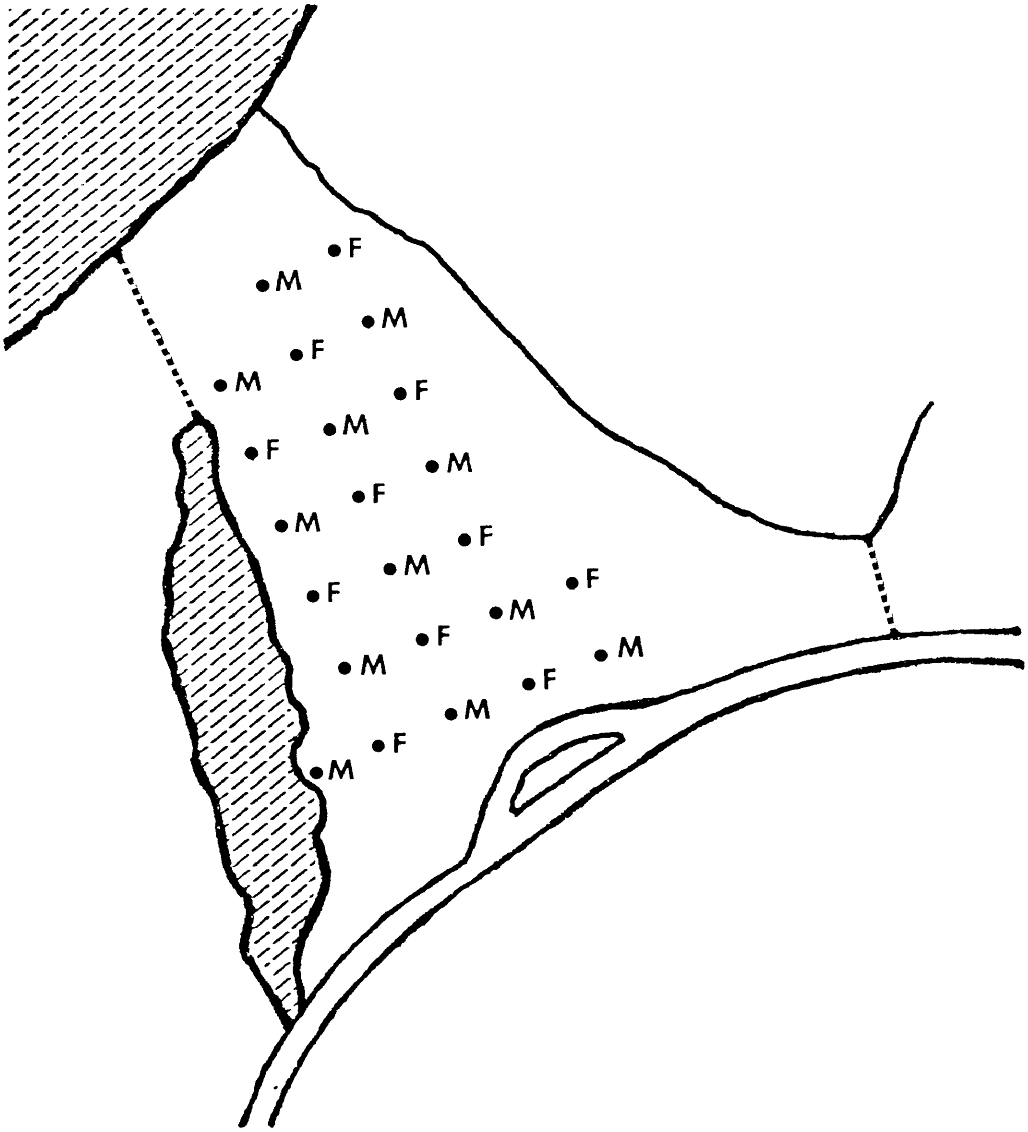
In March, 1975, a trapping grid was established on the study area. Grid lines were laid on a 5 column (23° West of North) by 7 row (67° East of North) design with 20 m inter-station spacing. The lines of the grid were shortened as necessary to conform to the natural boundaries of the study area. The result was an irregular shape for the overall grid layout (Fig. 3) of 23 trap stations. Live traps were placed two per station within 1 m of the grid stake.

Each live trap was 25 cm X 25 cm X 61 cm rectangular pine box with hardware cloth at one end for ventilation and a gravity fall trap door at the opposite end (after Mosby 1969). The hardware cloth reinforced trap door was released when the investigating animal tripped a baited treadle. Shelled feed corn, D&G lab chow, raw peanuts in the shell, and whole pecans served as bait during the course of the study.

Trapping Procedure

Fourteen-day trapping periods were conducted each month from April 5, 1975, until August 14, 1975. From September 1, 1975 to September 12, 1976, a continuous trapping schedule of 7 days set traps followed by 7 days closed traps was followed. Because of the bimodal nature of the gray squirrel daily activity period (Horwich 1968), trapping was conducted during either early morning or late afternoon hours. In the morning, traps were opened and set shortly after dawn, and were checked and closed 5 to 8 hours later. On days in which trapping was done in the afternoon, traps were opened and set at midday and checked for captured animals at sundown.

Figure 3. Urine treatment experimental trap locations.



M = MALE URINE MARKED TRAP
F = FEMALE URINE MARKED TRAP

In March, 1975, 7 adult and subadult gray squirrels were live-trapped at a private home in Williamsburg, Virginia, located approximately 5 km from the Jamestown Island study area. These gray squirrels (4 females and 3 males) were housed at the Laboratory of Endocrinology and Population Ecology of the College of William and Mary, and supplied with food (D&G Laboratory Chow) and water ad libitum. From March 22, 1976, to August 25, 1976, 6 drops of urine collected from these squirrels or 6 drops of distilled water was introduced into selected traps at the beginning of each trap day in addition to the normal bait allocation. The urine was collected by placing screen-covered aluminum foil trays underneath the wire mesh floor of solitary, caged gray squirrels and then pipetting deposited urine into clean 10 ml glass vials for storage. The urine was kept frozen until required for application to the live traps. Only urine from adult males and females was used, and urine from each sex was collected and stored separately.

Application of urine or water to the live traps was performed systematically. At each station, one trap was treated with water and the other with urine (either male or female). Six drops of the appropriate urine or distilled water was applied with a dropping pipette to the treadle of each trap as it was set for the days trapping. The total number of water controls was 23, while there were 12 male urine and 11 female urine treated traps (Fig. 3). The schedule of trapping remained unchanged (7 days set followed by 7 days closed). Traps were consistently marked with the same scent treatment from March 22, 1976, to August 25, 1976. Number of captures for each trap per station were recorded at the conclusion of each trap day.

Captive gray squirrels were removed from the live traps by placing a burlap sack over the entrance of the trap, releasing the door, and stimulating the animal to leave the trap and enter the sack by blowing through the hardware cloth end of the trap. For each captured gray squirrel, certain basic information was recorded. Squirrels were sexed, weighed with a Pesola 1000 g scale (after June 1975), and aged by pelage characteristics (Sharp 1958; Barrier and Barkalow 1967). Reproductive condition of males was assessed by noting testes descent via palpation (either testes scrotal or testes non-scrotal condition recorded) and by observing scrotal characteristics such as general size, pelage, and coloration (Pudney 1976). Mature male squirrels typically have large testes contained in well formed scrotal pouches which are usually bald and heavily pigmented (Pudney 1976). Reproductive information recorded for females included condition of the vagina (perforate or imperforate), size and pigmentation of nipples, and the presence of pregnancy or lactation as determined by palpation (Nixon and McClain 1975). Locational data (grid coordinates) for each capture were also recorded as well as general weather conditions.

Three marking techniques were employed to facilitate identification of individuals. Gray Squirrels were toe clipped according to a numerical code (Taber and Cowan 1971). Secondly, an ear punch was used to perforate each ear before inserting a Monel 5/16" ear tag (National Band & Tag) backed by a Monel washer and a colored celluloid 3/4" washer which was crimped into place. The third marking technique consisted of daubing geometric designs upon the pelage of the gray squirrel with Nyanzol D (Nyanza Inc.). This dye is a permanent, non-toxic, black dye frequently used for marking animals. Dye markings were lost as the gray squirrels shed their pelage; therefore, animals were re-marked often upon recapture to assure permanence and distinctiveness of the dye pattern. After completion of marking, examination, and physical data collection, each squirrel was released at the point of capture.

Observational Procedure

From April, 1975, until September, 1976, detailed observations and records were made on individual gray squirrel movements and behavior. Movements of animals over the study area were recorded on maps during each period of observation. Using descriptions of typical gray squirrel behavior (Bakken 1959; Sharp 1959; Taylor 1966; Pack *et al*. 1967), an ethogram of agonistic, investigative, sexual, and feeding behaviors was devised (see Appendix). The time, location, and type of behavior observed for each squirrel during the course of each observational period was logged on a recording sheet. Interactions between squirrels were recorded sequentially until the animals were lost from sight. Weather conditions for each observation period were also recorded.

Observation times were mainly confined to the principal morning and late afternoon activity periods of the gray squirrels (Bakken 1959; Horwich 1968). Morning observations were made between 06:30 and 10:30 for a period of 3 to 4 hours. Late afternoon observations were made between 16:00 and 20:30 for corresponding lengths of time. Gray squirrels were initially observed by slowly walking through the study area and pausing for 30 min. to an hr. as active squirrels were located before moving on to a different portion of the area. In June, 1975, an observation blind was placed at a central point in the study area

(Fig. 1). From June, 1975, until September, 1976, most observations of gray squirrel movements and behavior were made from the blind. Good visability of the major portion of the study area was possible due to the lack of obscuring ground cover during most seasons.

On June 21, 1976, a feeding station was placed at grid coordinate C4 (Fig. 1) approximately 12 m from the observation blind. Pack *et al.* (1967) have demonstrated that a feeding station will act as a focal point to attract gray squirrels to an area, and also serve to stimulate behavioral interactions between animals. The station was supplied daily with 15-20 pecans at the beginning of each observation period. The feeding station was discontinued on August 22, 1976, when suitable bait (pecans) became unavailable.

Removal and Release Procedure

From August 15, 1976, to August 20, 1976, 6 resident gray squirrels were removed from the study area and caged at the Laboratory of Endocrinology and Population Ecology. Residents for the purposes of this study were defined as animals that had been captured 5 times and/or observed on the study area for at least one month.

On August 20, 1976, the 7 captive gray squirrels from Williamsburg which had earlier been toe clipped and ear tagged for identification were transported from the laboratory to Jamestown Island. At 08:03 they were released at a point 488 m from the Island loop roadway boundary of the study area (Fig. 1). The live traps on the study area were then opened and set, and the observation blind occupied following standard procedures as described.

The resident Jamestown gray squirrels were held in the laboratory for at least one week from date of capture, and on August 29, 1976, at 07:30 transported back to Jamestown Island. They were released from the same point on the island at which the alien, Williamsburg gray squirrels had previously been released. Throughout the periods of resident removal, alien gray squirrel release, and then resident gray squirrel release, the standard trapping procedures and schedule were employed.

Statistical Procedures

Extensive use was made of packaged statistical computer programs at the College of William and Mary Computer Center to analyze the trapping and observational data. Biometry programs developed by F. J. Rohlf (Sokal and Rohlf 1969) were used to calculate the 95% confidence ellipses for home range estimations (Koeppl *et al*. 1975). Mann-Whitney U tests, Spearman's r, three-way ANOVA's, and Duncan's range tests were performed using the Statistical Package for the Social Sciences (SPSS) versions 7.0 and 8.0 (Nie *et al*. 1975; Nie and Hull 1977). Occasionally, statistics were manually computed using methods described in Sokal and Rohlf (1969) and Siegel (1956). The level of statistical significance employed was 0.05 unless otherwise noted.

RESULTS

Population Description

The results of 189 days of live-trap operation for the 18 month duration of the study yielded a total of 60 captured gray squirrels (Table 1). Of the total number of captures, 37 males and 23 females were marked and released. Adult animals comprised 65% (39) of the captures, while subadult and juvenile animals represented the remaining 22% (13) and 13% (8) of captures. A chi-squire test of independence of sex and age upon trap response was not significant ($X^2 = 3.83$, $0.50 > p > 0.10$), indicating no differential captures due to sex or age.

Gray squirrels were captured an average of 4.5 ± 0.756 times (mean ± std. error, Table 2). Frequency of capture ranged from 1 to 29. Approximately 35% (21) of the animals were captured once and 60% (36) were captured from 2 to 10 times. The remaining three individuals were captured more than 25 times and could be categorized as trap-addicted.

Figure 4 illustrates trends of capture effort for the duration of the study. Starting from April, 1975, the rate of 1.7 captures/day increased to the June and August, 1975, peak capture rates of 4.2 and 4.3/day. Rate of captures were lowest in September, 1975, as shown by the rate of 0.8 captures/day. The rate of captures irregularly increased during the winter to a high point in February, 1976, of 1.9/day. A decline in captures occurred in the spring, culminating in a rate of 0.0/day in May, 1976. A steady increase thereafter led

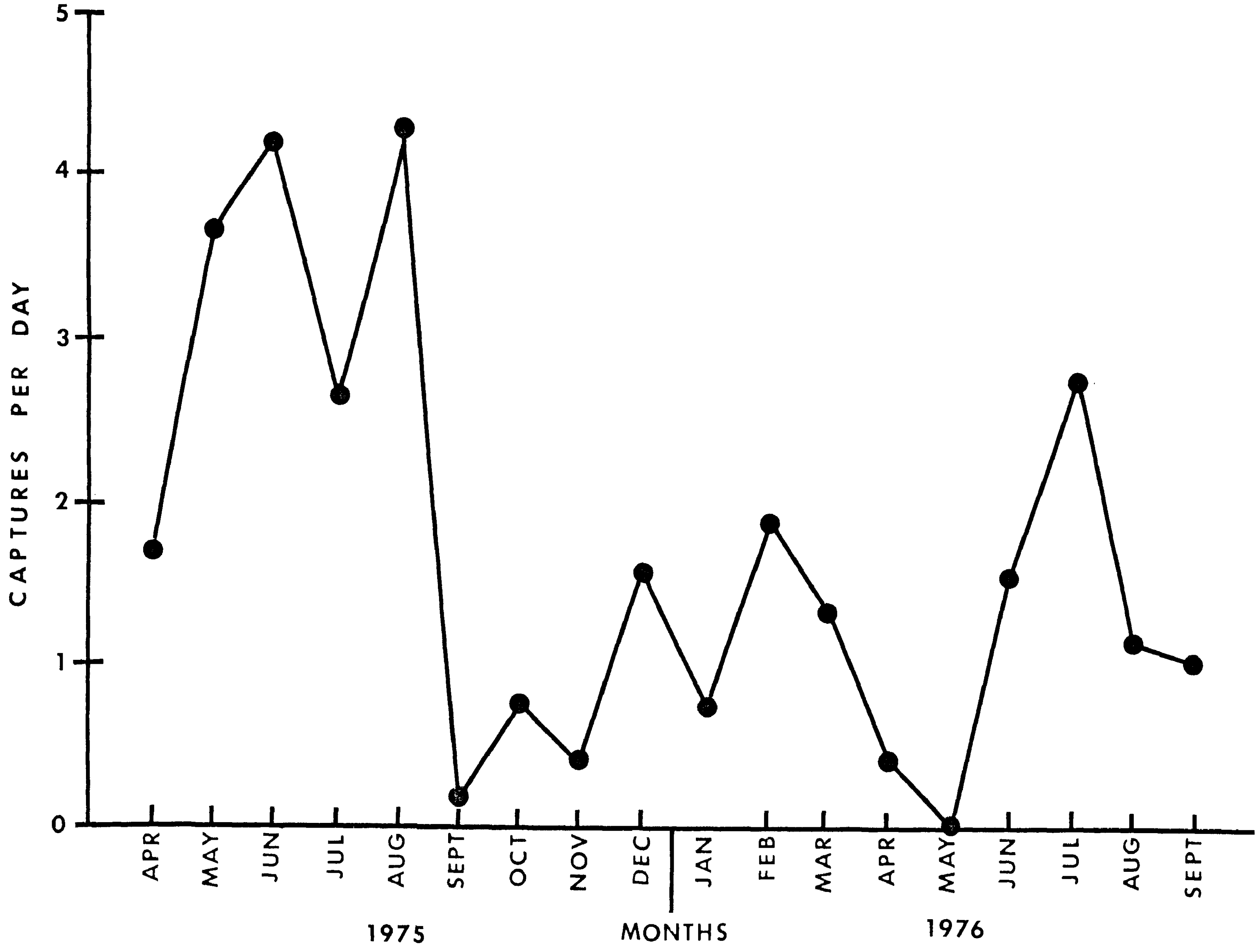
Table 1. Sex and age of gray squirrels captured by live-trapping. Chi-square test of independence of sex and age not significant, $x^2 = 3.83$, $0.10 < p < 0.50$.

	Sex			
Age	Male	Female	Total	%
Adult	27	12	39	65.0
Subadult	5	8	13	21.7
Juvenile	5	3	8	13.3
Total	37	23	60	
%	61.7	38.3		100

Table 2. Frequency of captures of squirrels in live-traps. Mean number of captures = 4.5, standard error = 0.756, standard deviation = 5.86, n= 60.

Times Captured	Number of Animals
1	21
2	9
3	8
4	3
5	3
6	3
7	3
8	3
9	2
10	2
25	1
27	1
29	1

Figure 4. Capture effort by month.


5
4
3
2
1
0
CAPTURES PER DAY
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1975
MONTHS
1976

to another summer peak in July, 1976, which then dropped off to a final low of 1.0/day at the conclusion of the study in September, 1976.

During the experimental urine application phase of live-trapping, 97 captures were recorded (Table 3). Of these captures, 43 animals were caught in the control (water marked traps) while 34 animals were captured in the male urine treatment and 20 animals in the female urine treatment. A chi-square test of independence of urine treatment and subsequent captures was not significant ($X^2 = 1.378$, $0.50 < p < 0.90$). Application of the urine treatment to live-traps did not significantly alter the trap response of gray squirrels in the study population.

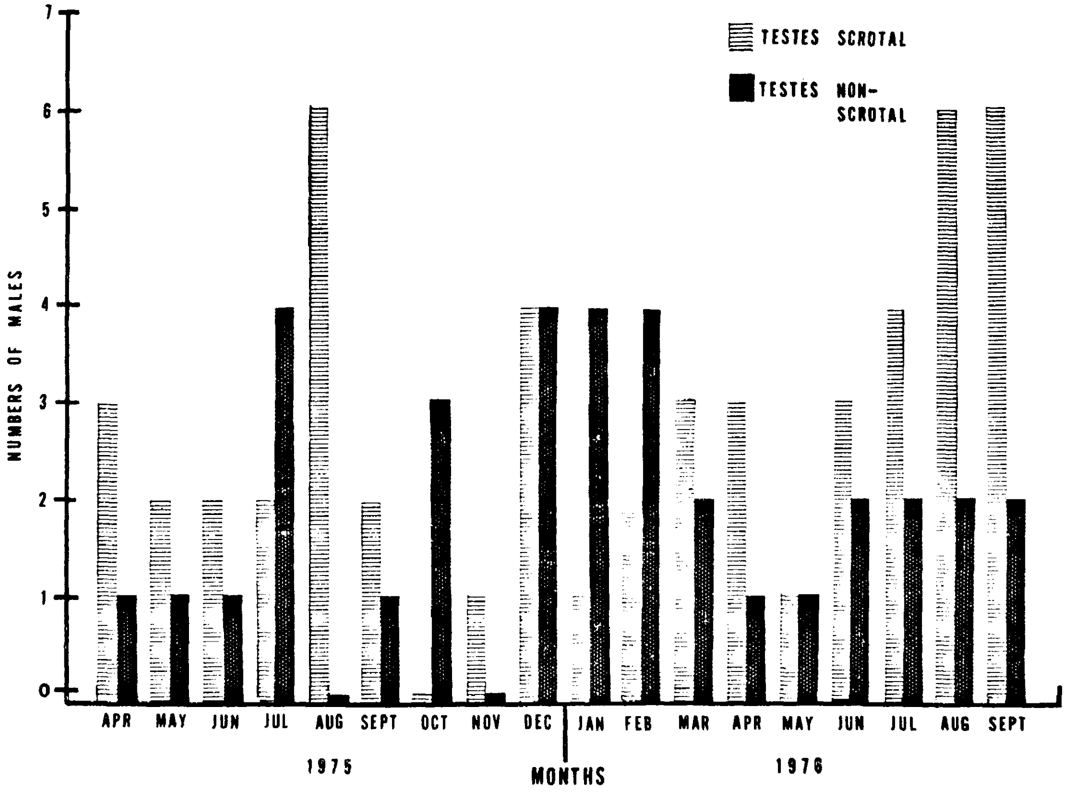
The size of the Jamestown study population was estimated using the live-trapping data for the peak summer capture periods of 1975 and 1976. The technique employed was the Maximum Likelihood Estimate (MLE) developed and tested by Nixon, et al. (1967) for estimation of squirrel abundance from live-trapping data. The equation used to determine the MLE is derived from the well known Lincoln index: $\hat{N} = \frac{\Sigma n_x}{1- (\Sigma n_x/\Sigma x n_x)}$, where $\hat{N}$ = the estimate of the population, Σn_x = the total number of animals handled, and $\Sigma x n_x$ = the total number of captures (Nixon et al. 1967). The MLE for July and August, 1975 was 38.1 animals. The same period in 1976 produced a MLE of 15.2 animals.

Reproductive condition of captured male squirrels as assessed by scrotal sac characteristics is shown in Figure 5. The largest number of males with scrotal testes were captured in August, 1975. Relatively high proportions of non-scrotal testes males were captured in July, October, and December, 1975. The number of immature males with non-scrotal testes remained high through January and February, 1976,

Table 3. Trap response of gray squirrels to urine application experiment. Chi-square test of independence of treatment and captures not significant, $x^2 = 1.378$, $0.50<p<0.90$.

Treatment	Captures		Total
	Males	Females	
Water	19	24	43
Male Urine	17	17	34
Female Urine	12	8	20
Total	48	49	97

Figure 5. Male reproductive condition during 1975 and 1976.


TESTES SCROTAL
TESTES NON-SCROTAL
NUMBERS OF MALES
0
1
2
3
4
5
6
7
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1975
MONTHS
1976

before declining. Males with scrotal testes began increasing in March and April, 1976, with a peak in male sexual development occurring in August-September 1976.

The reproductive condition of females is shown in Figure 6 for 1975 and Figure 7 for 1976. April and August, 1975, showed the highest numbers of pregnant or lactating females in the population. High numbers of females with open vaginae were captured in June, August, and December, 1975. Females having closed vaginae were only captured in April and May, 1975. In 1976, the highest number of pregnant or lactating females were captured in April. A few imperforate females were captured in the months of February and April, 1976. Mature, perforate, females were captured more frequently in June and August, 1976.

The reproductive rate for female squirrels was computed from the capture data and is detailed in Figure 8. Reproductive rate is defined here as the number of pregnant or lactating females divided by the total number of mature females. Definite spring and summer peaks of reproductive rate are evident in the study population of gray squirrels. Intermediate levels of reproductive activity (0.50 - 0.55) occurred in April and August, 1975, and July, 1976. A sustained high reproductive rate of 1.00 occurred from March to May, 1976.

Average total body weights for captured males is plotted in Figure 9, and for females in Figure 10. The body weight data (Figs. 9 and 10) must be presented with reservation due to the degree of uncertainty arising from small sample sizes with high individual variation, and the fact that the animals may have lost varying amounts of weight while in the live-traps. Adult males showed a trend for a

Figure 6. Female reproductive condition 1975.

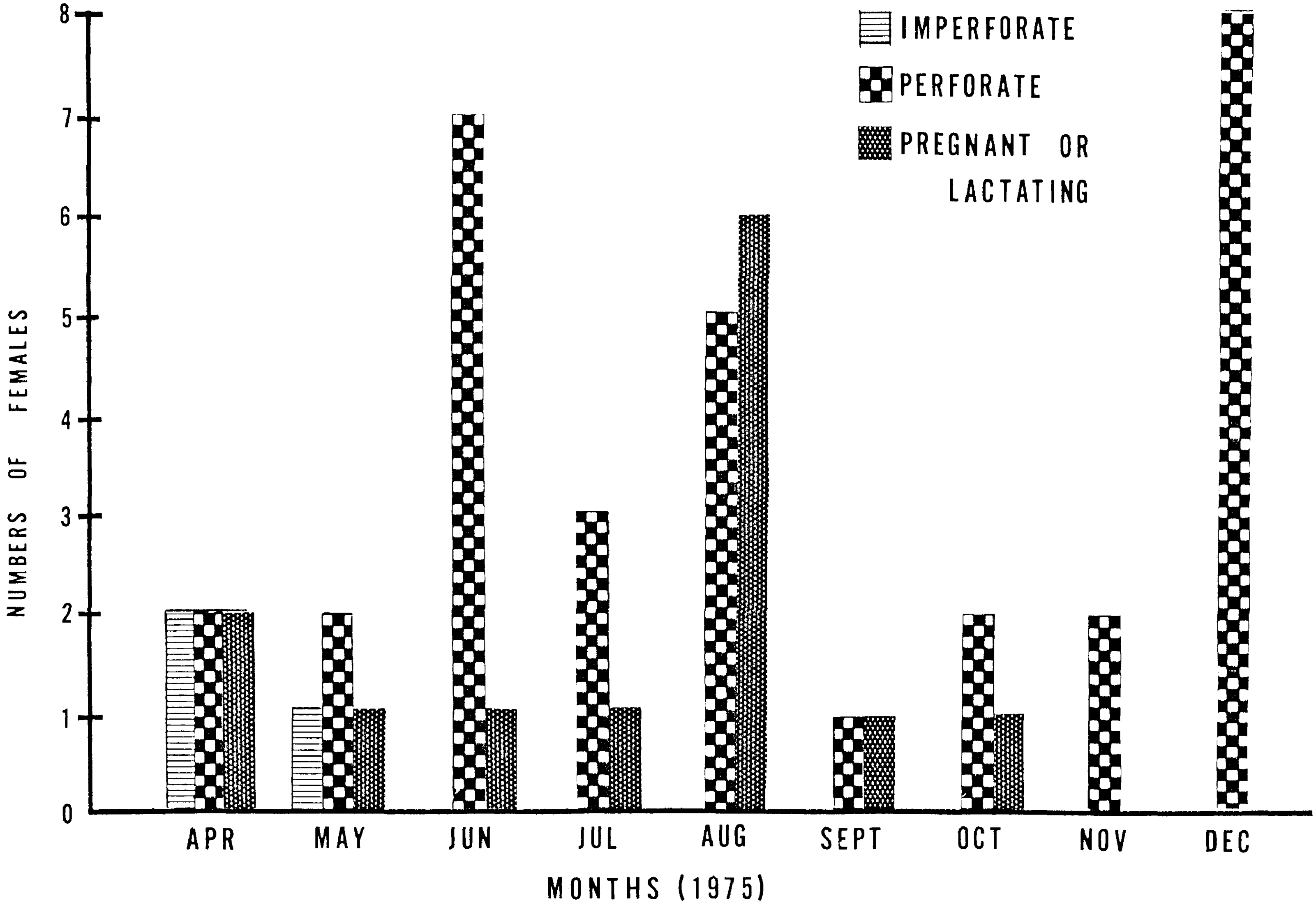

IMPERFORATE
PERFORATE
PREGNANT OR LACTATING
NUMBERS OF FEMALES
0
1
2
3
4
5
6
7
8
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
MONTHS (1975)

Figure 7. Female reproductive condition 1976

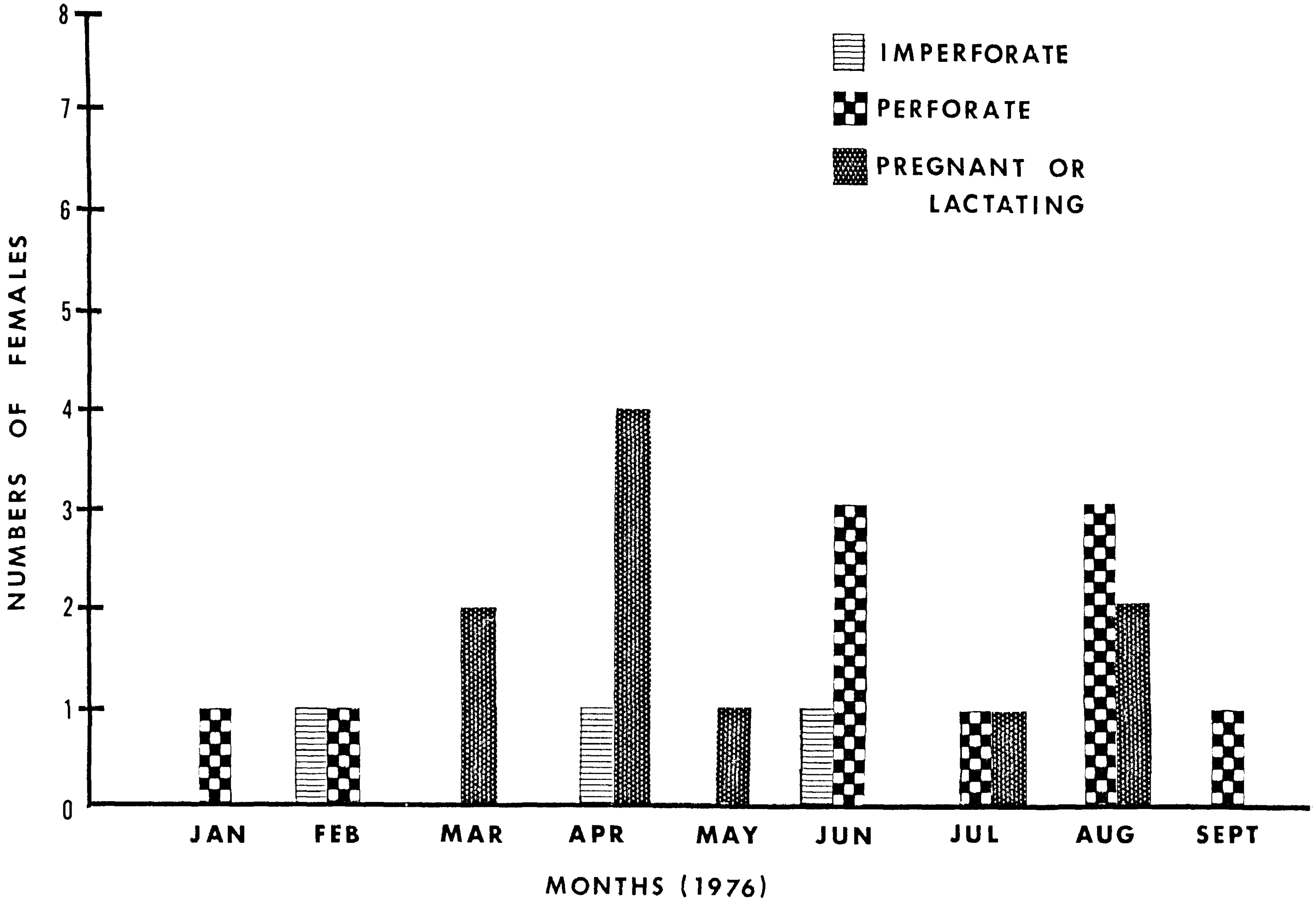

IMPERFORATE
PERFORATE
PREGNANT OR LACTATING
NUMBERS OF FEMALES
0
1
2
3
4
5
6
7
8
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
MONTHS (1976)

Figure 8. Reproductive rate of adult females (numbers in parentheses are total number of animals).

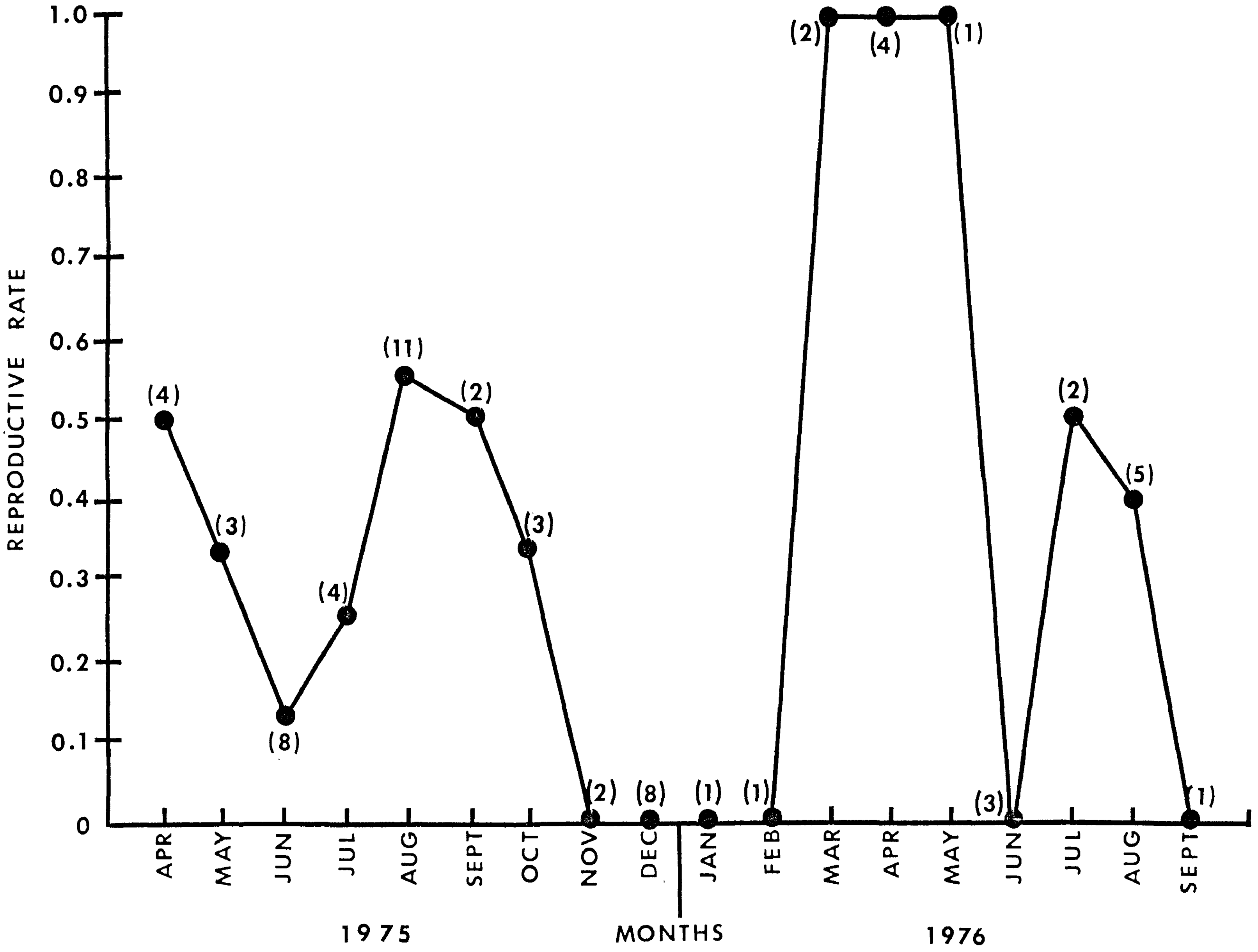

REPRODUCTIVE RATE
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
(4)
(3)
(8)
(4)
(11)
(2)
(3)
(2)
(8)
(1)
(1)
(2)
(4)
(1)
(3)
(2)
(5)
(1)
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1975
MONTHS
1976

Figure 9. Average male body weights (numbers in parentheses are number of animals).

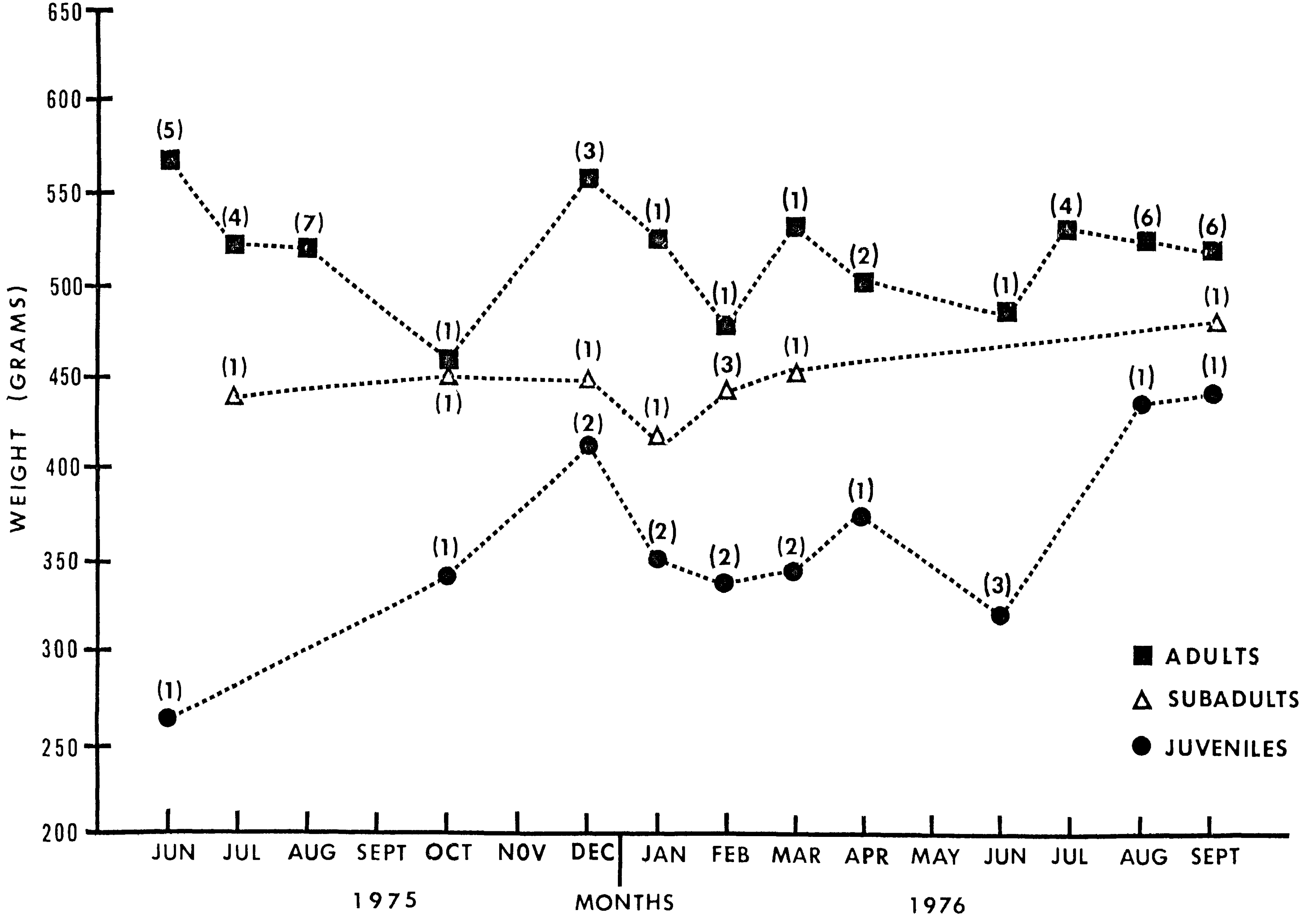
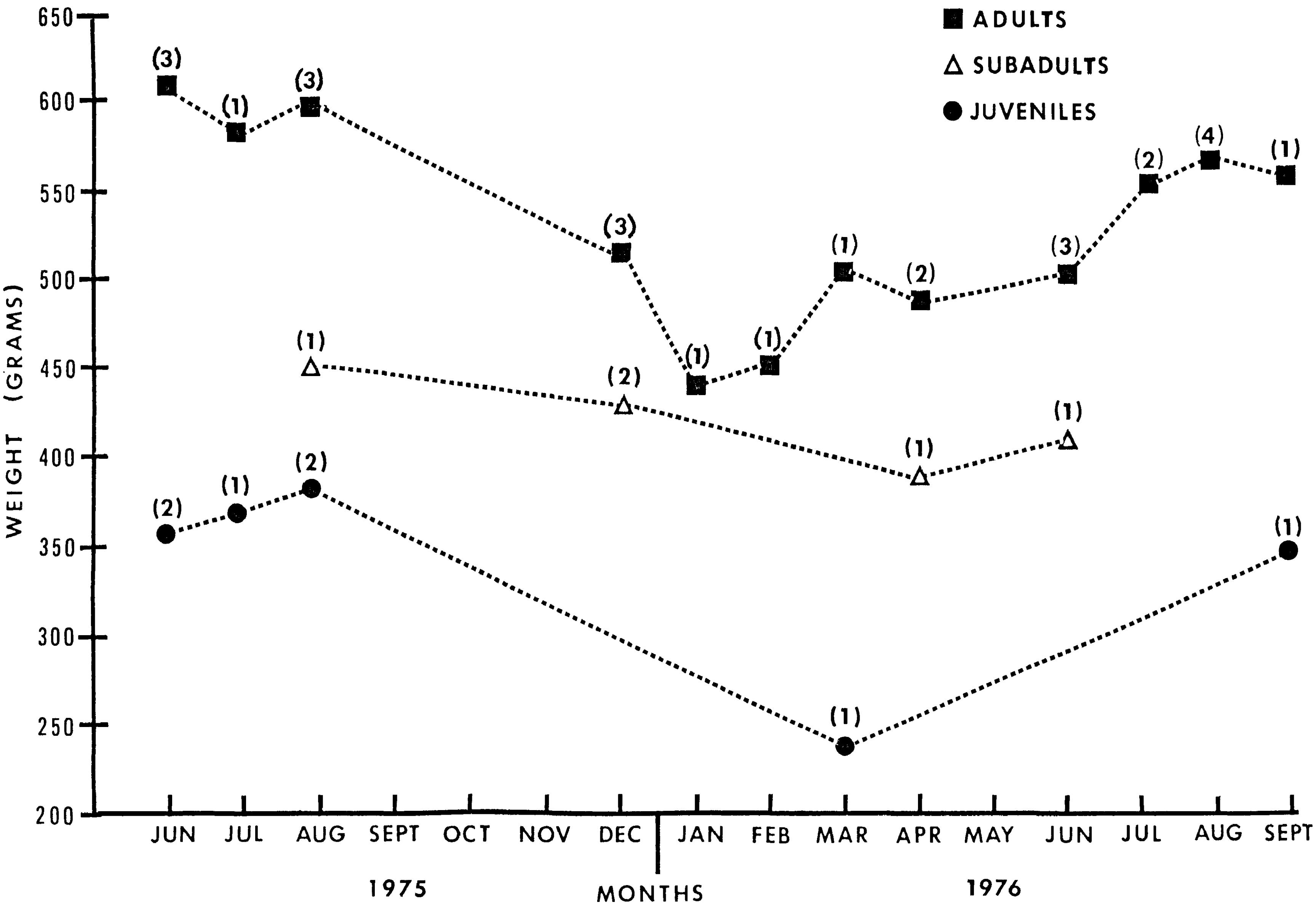

WEIGHT (GRAMS)
650
600
550
500
450
400
350
300
250
200
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1975
MONTHS
1976
■ ADULTS
△ SUBADULTS
● JUVENILES
(5)
(4)
(7)
(1)
(3)
(1)
(1)
(1)
(2)
(1)
(4)
(6)
(6)
(1)
(1)
(1)
(1)
(3)
(1)
(1)
(1)
(1)
(2)
(2)
(2)
(2)
(1)
(3)
(1)
(1)

Figure 10. Average female body weights (numbers in parentheses are number of animals).


ADULTS
SUBADULTS
JUVENILES
WEIGHT (GRAMS)
650
600
550
500
450
400
350
300
250
200
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1975
MONTHS
1976
(3)
(1)
(3)
(3)
(1)
(1)
(1)
(2)
(3)
(2)
(4)
(1)
(1)
(2)
(1)
(1)
(2)
(1)
(2)
(1)
(1)

decrease in body weight from early summer to fall, 1975, followed by a weight increase in December, 1975. The weight data for the remaining months of winter and early spring 1976 indicate an overall decline in adult male body weights. In June 1976, average weights of males began to rise again. Subadults of the 1975 year class demonstrated a slight weight gain from July to October followed by a winter weight decline to 410g in December and January. Subadult weights increased from February, 1976, onward as squirrels began to fully mature. Juvenile squirrels exhibited a dramatic weight increase from June (263g) to December (405g), 1975, and from June (313g) to September (440g), 1976, following expected developmental trends of growth (Barkalow and Shorten 1973).

Figure 10 illustrates the total body weights for captured females. Average adult female weight declined from an initial high of 603g in June, 1975, to a low of 440g in January, 1976. From January, 1976, to September adult female weights increased to 555g. Captures of subadult females were not frequent enough to show definite seasonal trends in body weight. Similarly, data from June to August, 1975, is only sufficient to indicate a steady weight gain for juvenile females in the summer, and insufficient to show developmental trends for the remainder of the sampling period.

Spatial Distribution

Home range statistics were computed using locational data obtained by live-trapping and 294 hours of field observation of gray squirrel behavior. A minimum of five locational fixes were used as input for Rohlf's program to calculate a 95% confidence ellipse (Sokal and Rohlf 1969) to estimate individual home range size and activity center

(Koeppl, et al. 1975). By analyzing the data seasonally, i.e. spring, summer, and fall/winter, 39 individual home ranges were plotted for 24 resident animals (Figures 11-15).

The average areas for the 95% probability ellipses are listed in Table 4. Home range area was computed manually by methods described in Koeppl, et al. (1975). The average yearly home range size for adult males was 2.34 ha. Subadult males had slightly larger average home ranges of 2.50 ha, and juvenile males had the smallest home ranges, averaging 2.05 ha. Male animals had an overall combined home range size of 2.28 ha. Size for the home ranges of females was 1.92 ha. Adult females had average home ranges of 1.60 ha, while subadults had an average of 3.12 ha. The single juvenile female for which data was sufficient to compute a home range utilized an estimated area of 1.81 ha.

A three-way ANOVA was calculated for the home range data to detect any significant variation in distribution of areas for males and females by sex, age, or season (Table 4). There were no significant differences in size of home range due to sex ($p = 0.209$), or season ($p = 0.846$). Additionally, no significant effects were detected between age ($p = 0.390$) and size of squirrel home ranges.

The proportion of an animal's home range ellipse that is overlapped by one or more other animal's home ranges was estimated from the home range plots (Figures 11-15) by dividing each ellipse into quadrats and approximating the percentage of area overlapped by other ellipses, and is presented in Table 5. A three-way ANOVA revealed that male home ranges overlapped less than did female home ranges (77.3% versus 92.3%), $p = 0.025$. Significant seasonal variation in overlap was

Figure 11. Home range 95% probability ellipses for resident animals during spring 1975.

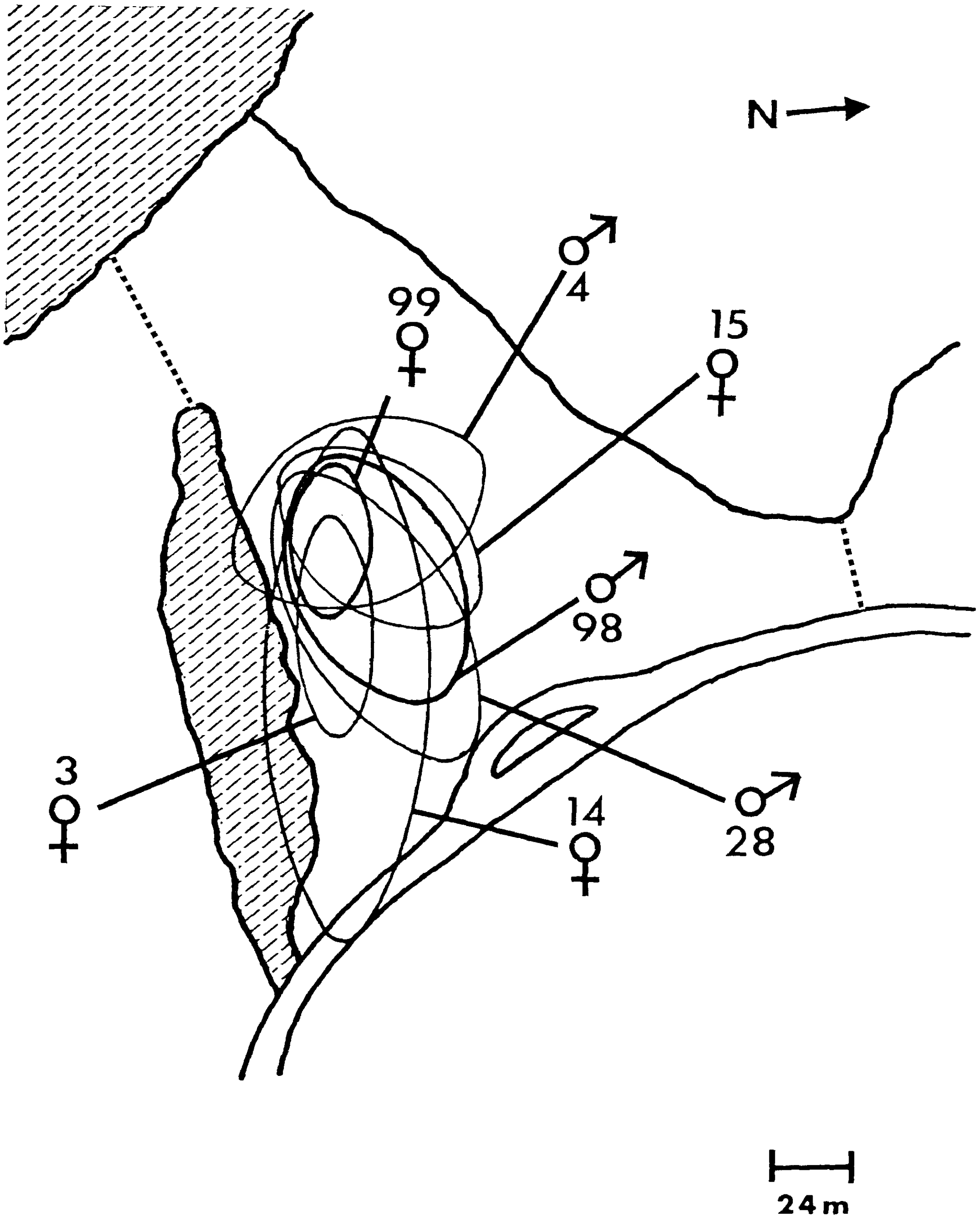

N
4
99
15
98
3
28
14
24m

Figure 12. Home range 95% probability ellipses for resident animals during summer 1975.

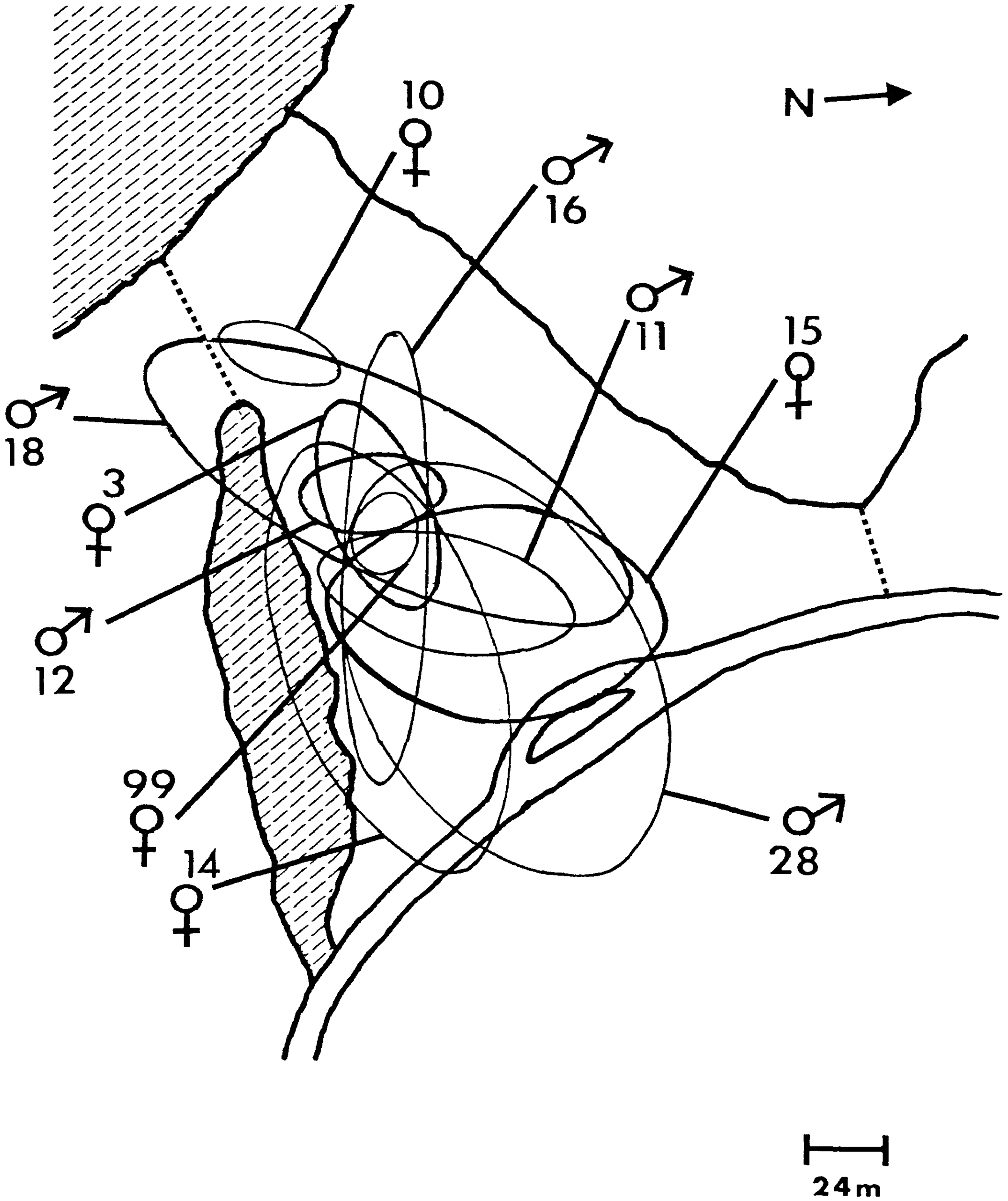

N
10 ♀
♂ 16
♂ 11
15 ♀
♂ 18
3 ♀
♂ 12
99 ♀
14 ♀
♂ 28
24m

Figure 13. Home range 95% probability ellipses for resident animals during fall/winter 1975.

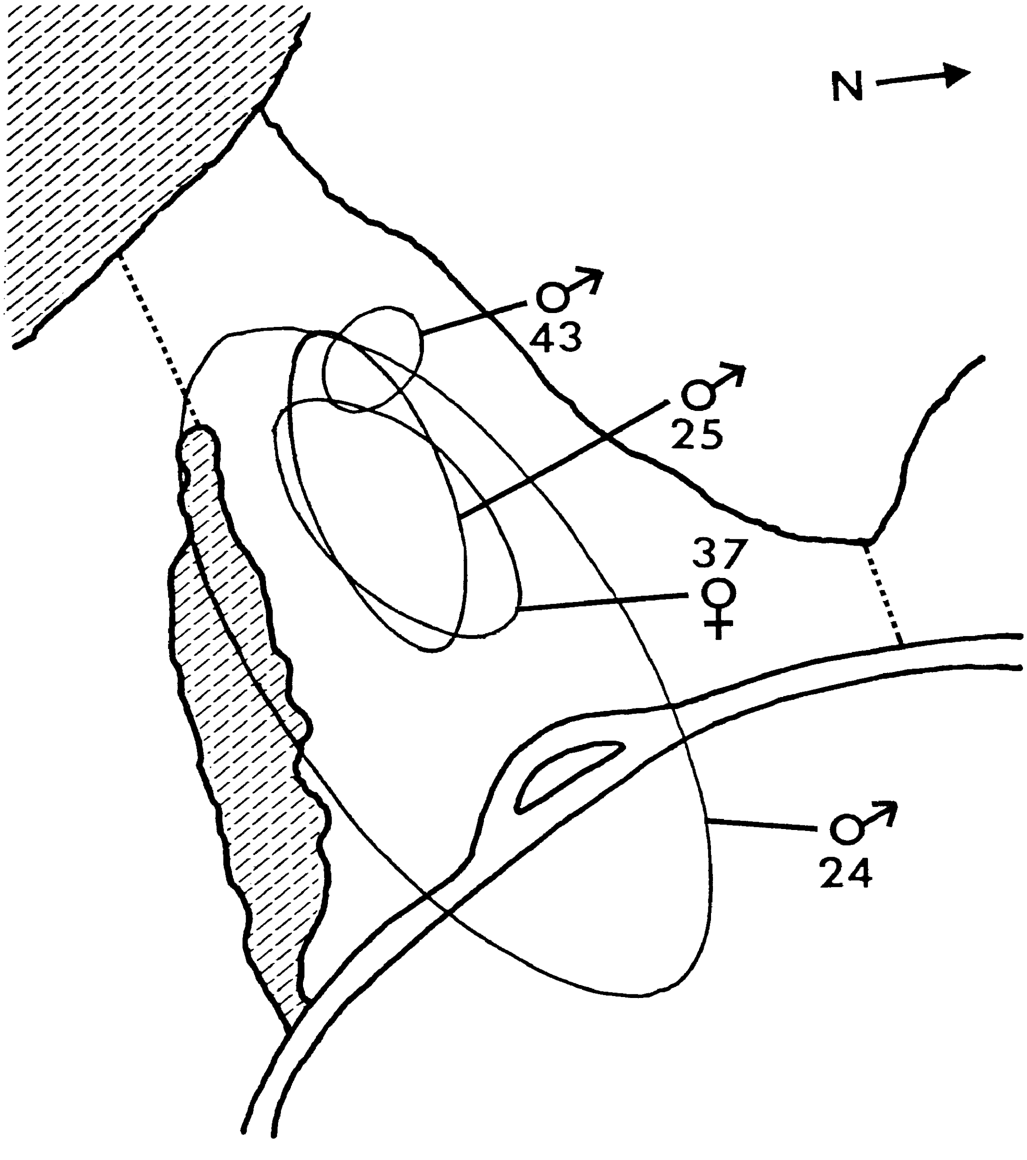
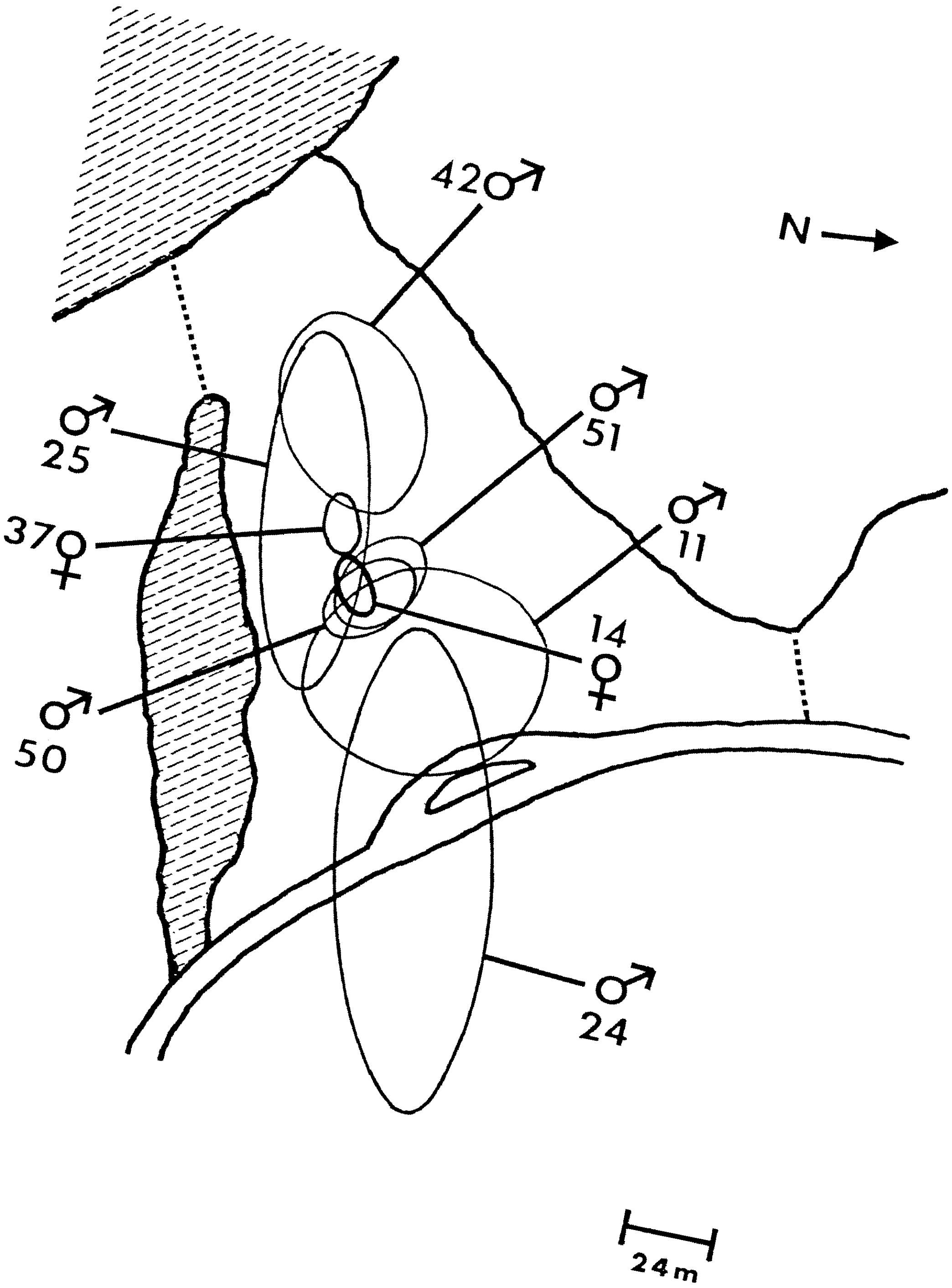
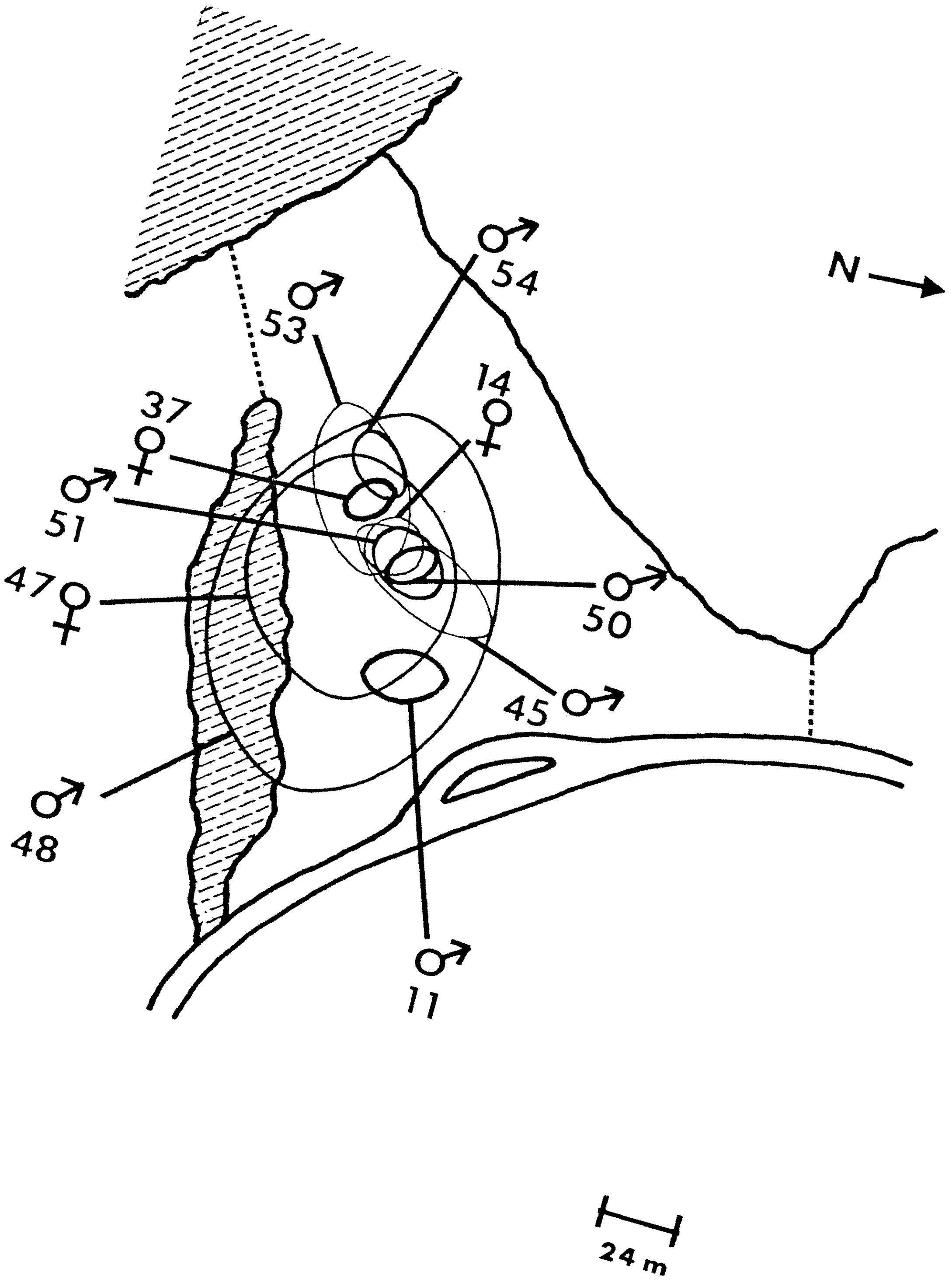

N
♂ 43
♂ 25
37 ♀
♂ 24
24 m

Figure 14. Home range 95% probability ellipses for resident animals during spring 1976.



42♂
N
25♂
51♂
37♀
11♂
14♀
50♂
24♂
24m

Figure 15. Home range 95% probability ellipses for resident animals during summer 1976.



N
♂ 54
♂ 53
14 ♀
37 ♀
♂ 51
47 ♀
♂ 50
45 ♂
♂ 48
♂ 11
24 m

Table 4. Home range areas of resident animals, categorized by sex and age during seasonal trapping and observation periods (area in hectares, n = number of animals) with three-way ANOVA.

		Seasons			
		Spring	Summer	Fall/Winter	All Seasons
Males	$\bar{X}$ ± SE (n)	2.49 ± 0.401 (9)	2.07 ± 0.321 (12)	2.46 ± 0.613 (3)	2.28 ± 0.227 (24)
Adults	$\bar{X}$ ± SE (n)	2.54 ± 0.615 (4)	2.26 ± 0.355 (10)	- -	2.34 ± 0.297 (14)
Subadults	$\bar{X}$ ± SE (n)	2.96 ± 0.925 (2)	- -	1.60 (1)	2.50 ± 0.699 (3)
Juveniles	$\bar{X}$ ± SE (n)	2.11 ± 0.861 (3)	1.13 ± 0.230 (2)	2.89 ± 0.755 (2)	2.05 ± 0.458 (7)
Females	$\bar{X}$ ± SE (n)	1.74 ± 0.316 (6)	1.88 ± 0.427 (8)	3.26 (1)	1.92 ± 0.269 (15)
Adults	$\bar{X}$ ± SE (n)	1.73 ± 0.316 (5)	1.49 ± 0.463 (6)	- -	1.60 ± 0.295 (11)
Subadults	$\bar{X}$ ± SE (n)	- -	3.05 ± 0.260 (2)	3.26 (1)	3.12 ± 0.166 (3)
Juveniles	$\bar{X}$ ± SE (n)	1.81 (1)	-	-	1.81 (1)

Table 4. (continued) Analysis of variance of home range areas by sex, seasons, and age.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main effects	4.625	5	0.925	0.761	0.584
Sex	1.994	1	1.994	1.641	0.209
Season	0.409	2	0.205	0.168	0.846
Age	2.354	2	1.177	0.969	0.390
Residual	38.875	32	1.215		
Total	43.500	37	1.176		

detected ($p = 0.034$) as well as a difference between age classes ($p = 0.010$). The overlap of spring home ranges was significantly less than the overlap of summer ranges (comparison of means by Duncan's range test, $p < 0.05$). There was no significant difference between the overlap of home ranges for either the fall/winter and spring, or fall/winter and summer seasons. Females did not show a significant difference in overlap between spring and summer home ranges; however, males appeared to contribute more to seasonal variation in overlap than did females ($p = 0.025$). Fall/winter female home range data was insufficient for further testing of overlap.

To investigate age related differences in home range overlap a Duncan's multiple range test at the 0.05 level was also performed (Table 5). The range test revealed no significant difference between juvenile and adult home range overlap. Subadult home ranges, however, showed significantly less overlap in comparison to both juvenile and adult home ranges.

The percentage of overlap of home ranges (Table 5) was adjusted for seasonal changes in the number of resident animals to produce the home range overlap index data (Table 6). The overlap index was calculated by dividing each percentage overlap value in the raw data set by the number of animals categorized as residents during a trapping and observation season. The density compensation of home range overlap (Table 5) resulted in a qualitative change for three aspects of the home range overlap index (Table 6) when tested for differences by sex and season, as well as age. First, the overall yearly difference in home range overlap between sexes decreased in significance from the level of $p = 0.025$ to $p = 0.044$ (three-way

Table 5. Average percent overlap of squirrel home ranges, categorized by sex and age during seasonal trapping and observation periods (n = number of animals) with three-way ANOVA.

		Seasons			
		Spring	Summer	Fall/Winter	All Seasons
Males	$\bar{X} \pm$ SE	52.2 ± 8.46	90.0 ± 5.06	71.7 ± 23.51	77.3 ± 5.38
	(n)	(9)	(12)	(3)	(24)
Adults	$\bar{X} \pm$ SE	67.5 ± 13.78	88.0 ± 5.93	-	82.1 ± 6.04
	(n)	(4)	(10)	-	(14)
Subadults	$\bar{X} \pm$ SE	40.0 ± 10.00	-	25.0	35.0 ± 7.64
	(n)	(2)	-	(1)	(3)
Juveniles	$\bar{X} \pm$ SE	70.0 ± 15.28	100.0 ± 0.00	95.0 ± 5.00	85.7 ± 8.12
	(n)	(3)	(2)	(2)	(7)
Females	$\bar{X} \pm$ SE	89.2 ± 7.12	93.7 ± 4.09	100.0	92.3 ± 3.51
	(n)	(6)	(8)	(1)	(15)
Adults	$\bar{X} \pm$ SE	95.0 ± 5.00	95.8 ± 4.17	-	95.5 ± 3.05
	(n)	(5)	(6)	-	(11)
Subadults	$\bar{X} \pm$ SE	-	87.5 ± 12.50	100.0	91.7 ± 8.33
	(n)	-	(2)	(1)	(3)
Juveniles	$\bar{X} \pm$ SE	60.0	-	-	60.0
	(n)	(1)			(1)

Table 5. (continued) Analysis of variance of percent overlap by sex, season, and age. Asterisk indicates significant probability less than critical level of 0.05.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main effects	8794.965	5	1758.993	4.877	0.002*
Sex	2002.594	1	2002.594	5.552	0.025*
Season	2705.870	2	1352.935	3.751	0.034*
Age	3895.385	2	1947.693	5.400	0.010*
Residual	11541.828	32	360.682		
Total	20336.793	37	549.643		

Duncan's range test at p = 0.05. Homogenious subsets of means are underlined.

Subadult	Juvenile	Adult	Spring	Fall/Winter	Summer
56.0	82.5	88.0	73.00	78.75	91.50

Table 6. Average overlap indices of squirrel home ranges, categorized by sex and age during seasonal trapping and observation periods (n = number of animals) with three-way ANOVA.

		Seasons			
		Spring	Summer	Fall/Winter	All Seasons
<u>Males</u>	$\bar{X} \pm SE$	8.2 ± 0.94	9.2 ± 0.51	17.9 ± 5.86	9.9 ± 1.02
	(n)	(9)	(12)	(3)	(24)
Adults	$\bar{X} \pm SE$	9.4 ± 2.09	9.0 ± 0.60	-	9.1 ± 0.68
	(n)	(4)	(10)	-	(14)
Subadults	$\bar{X} \pm SE$	5.1 ± 1.25	-	6.3	5.5 ± 0.83
	(n)	(2)	-	(1)	(3)
Juveniles	$\bar{X} \pm SE$	8.8 ± 1.92	10.0 ± 0.0	23.8 ± 1.25	13.4 ± 2.79
	(n)	(3)	(2)	(2)	(7)
<u>Females</u>	$\bar{X} \pm SE$	12.2 ± 0.90	9.4 ± 0.41	25.0	11.5 ± 1.10
	(n)	(6)	(8)	(1)	(15)
Adults	$\bar{X} \pm SE$	12.8 ± 0.67	9.6 ± 0.42	-	11.1 ± 0.63
	(n)	(5)	(6)	-	(11)
Subadults	$\bar{X} \pm SE$	-	8.8 ± 1.25	25.0	14.2 ± 5.46
	(n)	-	(2)	(1)	(3)
Juveniles	$\bar{X} \pm SE$	8.6	-	-	8.6
	(n)	(1)			(1)

Table 6. (continued) Analysis of variance of overlap index by sex, season, and age. Asterisk indicates significant probability less than critical value of 0.05.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main effects	355.158	5	71.032	8.177	0.000*
Sex	38.259	1	38.259	4.404	0.044*
Season	224.837	2	112.418	12.941	0.000*
Age	128.450	2	64.225	7.393	0.002*
Residual	277.974	32	8.687		
Total	633.132	37	17.112		

Duncan's range test at p = 0.05. Homogenious subsets of means are underlined.

Subadult	Adult	Juvenile	Summer	Spring	Fall/Winter
6.78	9.98	12.8	9.25	9.80	19.7

ANOVA's). Second, the significant effects due to age increased noticably from $p = 0.010$ to $p = 0.002$. Third, the degree of home range overlap in the fall/winter season was significantly different from the overlap in spring and summer (Duncan's range test, $p < 0.05$). The overlap index results indicate that squirrels in the fall/winter had home ranges that tended to overlap more with the home ranges of neighboring animals than during either the spring or summer seasons. Meanwhile, subadult animals had overlap indices more similar to adults than to juveniles (Duncan's range test, $p < 0.05$).

The average distance between activity centers of the nearest same sexed animals was calculated from the 95% probability ellipses using the formula $D_c = U\,[(X-\bar{x})^2 + (Y-\bar{y})^2]^{\frac{1}{2}}$ given by Koeppl _et_ _al_. (1975) for computing the Euclidean distance between the activity center and a specified location. The yearly average distance between males of 16.5 m (Table 7) was not significantly different ($p = 0.712$) from the average distance between females of 17.8 m. Likewise, no significant difference was indicated for seasonal variation in distances between activity centers for males and females ($p = 0.199$). A significant effect was revealed between age and distance to the same sex ($p = 0.020$). Subadult activity centers were less closely spaced than were the activity centers of adults and juveniles (Duncan's range test, $p < 0.05$). In summary, the subadult age class had a significantly greater mean distance to same sexed animals than adults or juveniles; thus, subadult squirrels of the same sex were spaced significantly farther apart on the yearly average than were juvenile or adult animals of the same sex.

The distance between activity centers of the nearest opposite sexed animals was computed utilizing the 95% probability ellipses and the

Table 7. Average distance (meters) between activity centers (A.C.) of same sex animals, categorized by sex and age during seasonal trapping and observation periods (n = number of animals) with three-way ANOVA.

		Seasons			
		Spring	Summer	Fall/Winter	All Seasons
<u>Males</u>	$\bar{X} \pm SE$ (n)	20.8 ± 5.28 (9)	10.2 ± 2.27 (12)	28.9 ± 1.71 (3)	16.5 ± 2.63 (24)
Adults	$\bar{X} \pm SE$ (n)	17.3 ± 5.10 (4)	11.4 ± 2.56 (10)	- -	13.1 ± 2.34 (14)
Subadults	$\bar{X} \pm SE$ (n)	41.5 ± 9.08 (2)	- -	28.1 ± 2.56 (2)	37.9 ± 6.36 (3)
Juveniles	$\bar{X} \pm SE$ (n)	11.8 ± 7.97 (3)	4.05 ± 0.0 (2)	30.6 (1)	14.2 ± 4.89 (7)
<u>Females</u>	$\bar{X} \pm SE$ (n)	12.3 ± 2.01 (6)	22.0 ± 5.44 (2)	- -	17.8 ± 3.39 (14)
Adults	$\bar{X} \pm SE$ (n)	13.6 ± 1.97 (5)	21.6 ± 7.11 (6)	- -	17.9 ± 4.01 (11)
Subadults	$\bar{X} \pm SE$ (n)	- -	23.1 ± 8.34 (2)	- -	23.1 ± 8.34 (2)
Juveniles	$\bar{X} \pm SE$ (n)	6.3 (1)	-	-	6.3 (1)

Table 7. (continued) Analysis of variance of distance to same sex A.C. by sex, season, and age. Asterisk indicates significant probability less than critical level of 0.05.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main effects	1754.982	5	350.996	2.694	0.038*
Sex	18.098	1	18.098	0.139	0.712
Season	442.005	2	221.002	1.696	0.199
Age	1156.001	2	578.000	4.436	0.020*
Residual	4169.063	32	130.283		
Total	5924.047	37	160.109		

Duncan's range test at p = 0.05. Homogenious subsets of means are underlined.

Juvenile	Adult	Subadult
13.24	15.22	31.95

general formula cited above (Koeppl et al. 1975) for distance to same sexed animals. Table 8 presents the resulting distance to opposite sexed animals activity centers. No seasonal, age, or sex related differences were statistically significant for distances between activity centers of opposite sexed animals as determined by a three-way ANOVA (Table 8).

Another aspect of the population spatial distribution that was investigated was the change in location of individual activity centers over time. Table 9 lists average distances for shifts in activity centers by sex and season. The overall average movement of an activity center was 18.9 m. Males shifted activity centers an average distance of 23.7 ± 9.21 m (Mean ± SE), while females had an average shift of 14.7 ± 5.00 m. However, the difference in degree of shift of activity centers exhibited between the sexes was not significant ($p > 0.20$). No significant seasonal movement of individual centers of activity was indicated from overall Mann-Whitney U tests, $p > 0.20$ (Table 9, fall/winter data not included because of small sample size).

Removal and Release

The results of the removal and release procedure at the conclusion of 16 days trapping and observation indicated that resident squirrels could return to their home ranges when released at a distance of 488 m (1600 ft). Exactly 50% (3/6) of the resident squirrels returned to their home range areas. Animal 11, an adult male, was recaptured on the study area one day after being released. Animal 45, also an adult male, was observed on the study area the second day after release and subsequently recaptured the following day. Animal 14, an adult female, was recaptured on the study area on the eighth day after release. None

Table 8. Average distance (meters) between activity centers (A.C.) of nearest opposite sex animals, categorized by sex and age during seasonal trapping and observation periods (n = number of animals) with three-way ANOVA.

		Season			
		Spring	Summer	Fall/Winter	All Seasons
Males	$\bar{X} \pm SE$	23.2 ± 7.54	10.7 ± 2.80	22.5 ± 7.43	16.8 ± 3.40
	(n)	(9)	(12)	(3)	(24)
Adults	$\bar{X} \pm SE$	18.5 ± 5.54	12.4 ± 3.07	-	14.2 ± 2.70
	(n)	(4)	(10)	-	(14)
Subadults	$\bar{X} \pm SE$	44.1 ± 32.15	-	18.7	35.6 ± 20.40
	(n)	(2)	-	(1)	(3)
Juveniles	$\bar{X} \pm SE$	15.5 ± 9.30	2.0 ± 1.32	24.4 ± 12.43	14.2 ± 5.65
	(n)	(3)	(2)	(2)	(7)
Females	$\bar{X} \pm SE$	11.9 ± 1.44	11.8 ± 4.67	12.0	11.9 ± 2.47
	(n)	(6)	(8)	(1)	(15)
Adults	$\bar{X} \pm SE$	11.5 ± 1.70	11.3 ± 6.01	-	11.4 ± 3.22
	(n)	(5)	(6)	-	(11)
Subadults	$\bar{X} \pm SE$	-	13.6 ± 8.03	12.0	13.1 ± 4.66
	(n)	-	(2)	(1)	(3)
Juveniles	$\bar{X} \pm SE$	13.9	-	-	13.9
	(n)	(1)			(1)

Table 8. (continued) Analysis of variance of distance to opposite sex A.C. by sex, season, and age.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main effects	1562.007	5	312.401	1.585	0.193
Sex	228.758	1	228.758	1.160	0.289
Season	519.836	2	259.918	1.318	0.282
Age	748.804	2	374.402	1.899	0.166
Residual	6309.129	32	197.160		
Total	7871.137	37	212.733		

Table 9. Comparison of average shift (meters) in gray squirrel activity centers. Mann-Whitney U tests for difference in distribution by season and sex not significant, $p>0.20$ (season: $n_1 = 10$, $n_2 = 5$, $U = 37$; sex: $n_1 = 8$, $n_2 = 7$, $U = 37$). Sample size in parentheses.

Season	Males X ± SE	(n)	Females X ± SE	(n)
Spring to Summer	14.9 ± 3.79	(4)	14.0 ± 6.27	(6)
Summer to Spring	35.4 ± 21.10	(3)	16.8 ± 10.80	(2)
Total	23.7 ± 9.21	(7)	14.7 ± 5.00	(8)

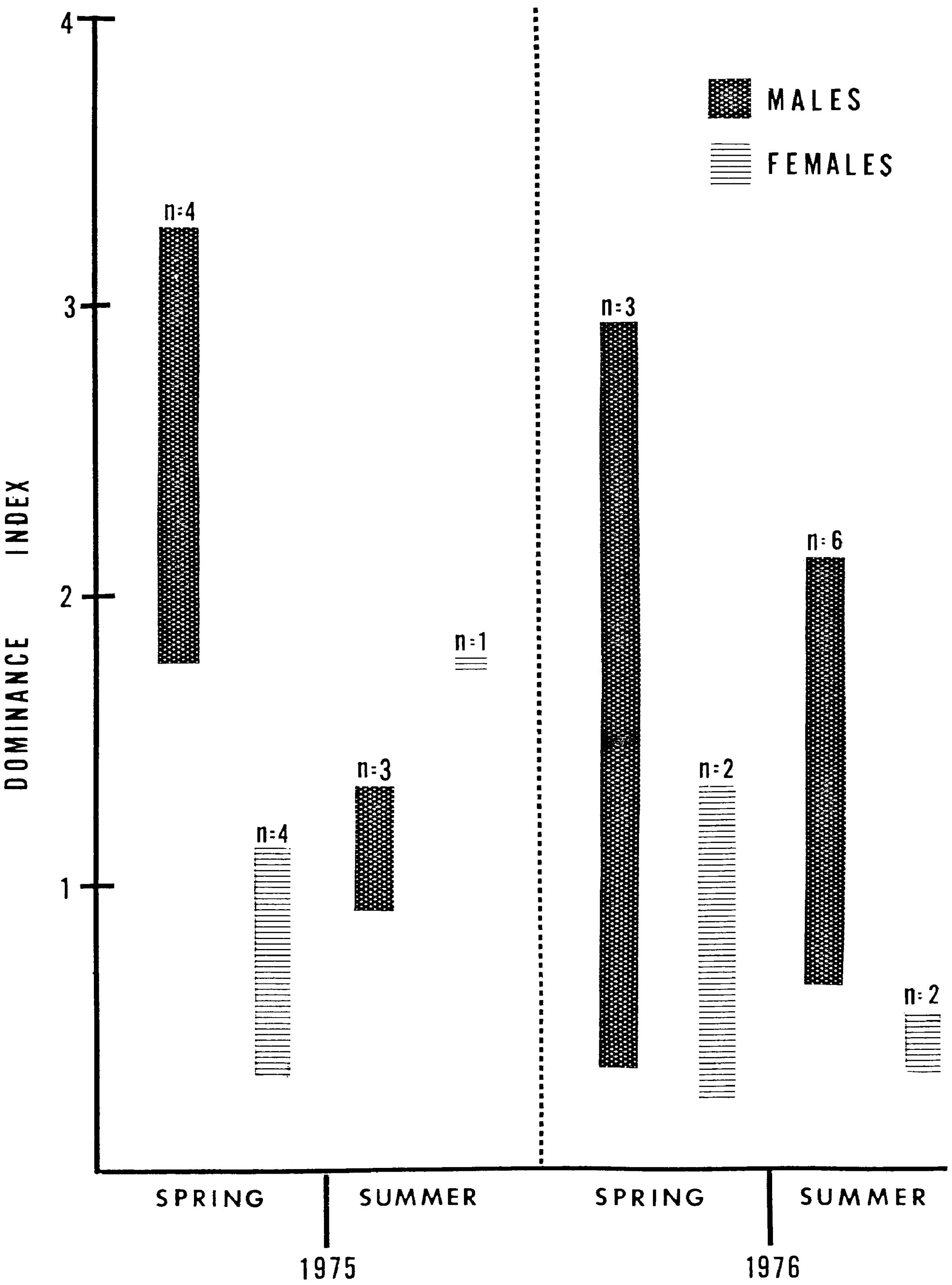
of the alien Williamsburg squirrels immigrated to the study area. Two out of the seven aliens were observed on separate occasions within 80 m of the release point. Resident animals were not observed in the release point area. A Fisher's exact test for independence of homing rates by resident and alien squirrels yielded a borderline significance value of p = 0.0699. Thus, while resident animals displayed a tendency to return to the study area at a rate better than the alien squirrels could randomly immigrate, this difference was not significant.

Behavioral Observations

Field observations of gray squirrel behavior for 294 hours yielded 247 recorded agonistic interactions between 18 animals. The frequency of observable interactions for the fall/winter period was insufficient to include for analysis; consequently, comparisons were only made for the spring and summer behavioral data. A Dominance Index, similar to the A/S ratio used by Swenson (1977) for prairie deermice, was developed to quantify the intensity of agonistic interactions exhibited by individual squirrels. The index was computed using square root transformed raw data in the following manner. The Dominance Index (D.I.) is equal to the number of dominant outcomes divided by the number of submissive outcomes of observed agonistic interactions: $\text{D.I.} = \dfrac{\sqrt{\text{nDom.} + \frac{1}{2}}}{\sqrt{\text{nSub.} + \frac{1}{2}}}$

Figure 16 illustrates the mean Dominance Index (D.I.) scores and their 95% confidence intervals for males and females during 1975 and 1976. There appears to be a trend for males to have higher D.I. scores than females upon inspection of the amount of overlap shown by the 95% confidence limits (Fig. 16). The D.I. score of the sole pregnant adult female for summer 1975 is an exception to the trend. Mann-Whitney U

Figure 16. Dominance Index scores for males and females (95% confidence limits shown, n=number of animals).


4
3
2
1
DOMINANCE INDEX
MALES
FEMALES
n=4
n=4
n=3
n=1
n=3
n=2
n=6
n=2
SPRING
SUMMER
1975
SPRING
SUMMER
1976

tests (Table 10) of D.I. by sex and season indicated a significant difference between the D.I. scores for males and females. Males had significantly higher D.I. than females in the spring ($n_1 = 7$, $n_2 = 6$, $U = 39$, $0.01 < p < 0.02$), but no significant difference was found for the summer scores ($n_1 = 9$, $n_2 = 3$, $U = 18$, $p > 0.20$).

Previous studies (Bronson 1964, Brenner *et al.* 1978) have shown that the dominant animal in an agonistic encounter often has a higher body weight than the subordinate animal. Table 11 lists some Spearman rank correlations of body weight and D.I. scores. Male squirrels had a significant positive correlation $r_s = 0.453$, $p < 0.05$ between D.I. score and body weight, while females had a positive, but not significant correlation $r_s = 0.539$, $p > 0.10$ for the same two parameters.

Dominance Index scores were tested for correlation with home range overlap and area (Table 11) to ascertain if some aspect of spatial relationships were associated with dominance. Home range area was not significantly correlated with D.I. scores for either males or females. A significant negative correlation ($r_s = -0.496$, $p < 0.009$) was found between D.I. scores and home range overlap. Dominant animals, as defined by having a high D.I. score, would tend to have a smaller percentage of their home range overlapped by the ranges of other animals.

To quantify levels of aggressive behavior, Figure 17 presents the mean number of agonistic interactions per hour of observation for 1975 and 1976. The addition of a feeding station to the study area in June, 1976, corresponded with an increase in the number of observed interactions between squirrels. However, levels of agonistic interactions were not significantly different between summers (Mann-Whitney

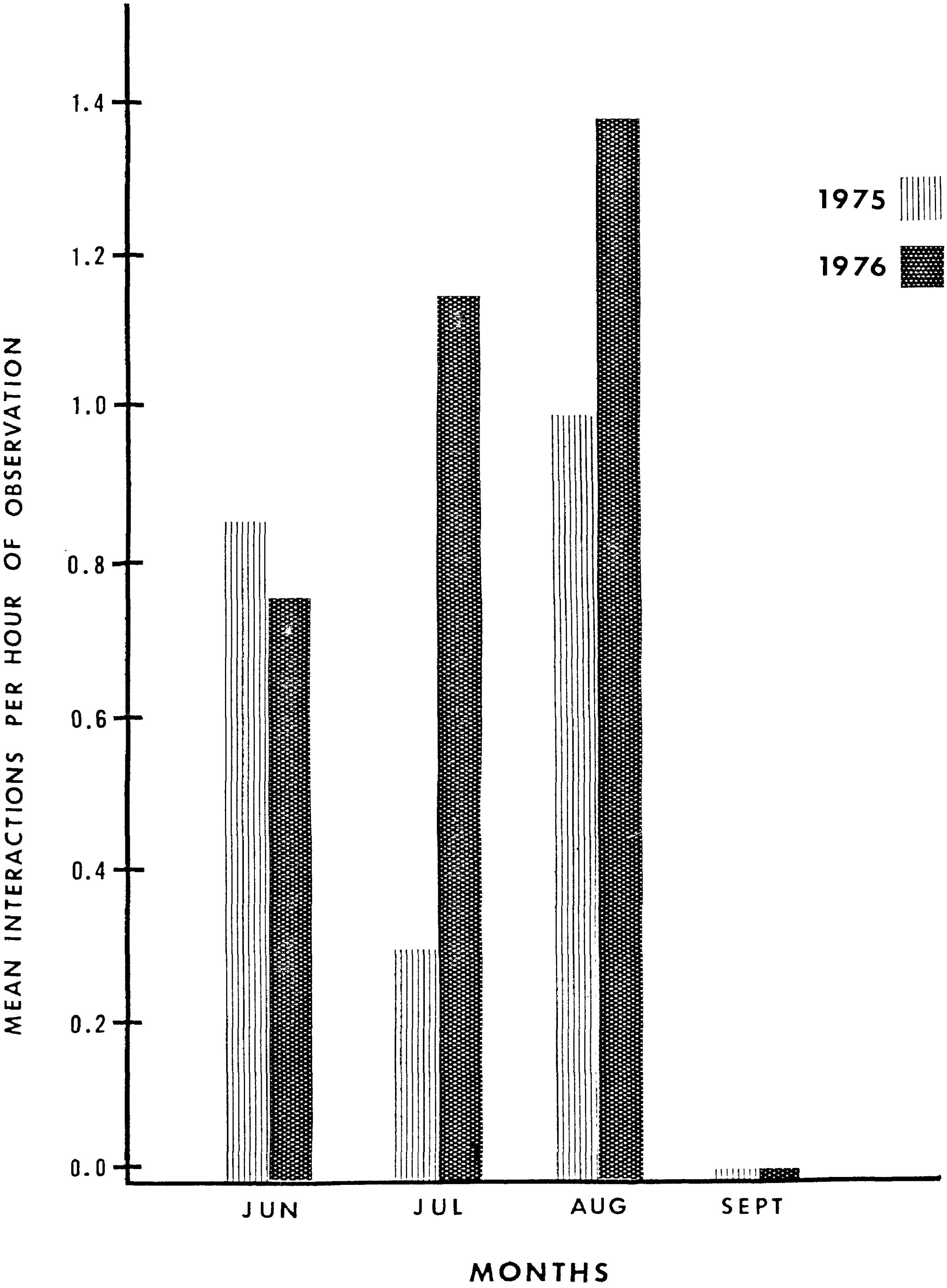
Table 10. Comparisons of dominance index (D.I.) by sex and season. Mann-Whitney U tests for differences in distribution significant by sex, $0.01 < p < 0.02$ ($n_1 = 9$, $n_2 = 16$, $U = 115.5$), but not significant by season, $p > 0.20$ ($n_1 = 12$, $n_2 = 13$, $U = 98.5$).

Season		Male $\bar{X} \pm$ SE	(n)	Female $\bar{X} \pm$ SE	(n)	Overall D.I. $\bar{X} \pm$ SE	(n)
1975	Spring	2.6 ± 0.80	(4)	0.7 ± 0.42	(4)	1.6 ± 0.41	(8)
	Summer	1.1 ± 0.20	(3)	1.7	(1)	1.3 ± 0.17	(4)
1976	Spring	1.7 ± 1.16	(3)	0.8 ± 0.39	(2)	1.3 ± 0.43	(5)
	Summer	1.4 ± 0.89	(6)	0.4 ± 0.07	(2)	1.1 ± 0.31	(8)
Overall D.I.		1.7 ± 0.94	(16)	0.8 ± 0.49	(9)	1.4 ± 0.18	(25)

Table 11. Spearman rank correlations (r_S) of Dominance Index with body weight, percent overlap, and home range area. Asterisks indicate significance.

Sex	Index with Overlap	Index with Body Weight	Index with Area
Males	$n = 13$	$n = 15$	$n = 13$
	$r_S = -0.391$	$r_S = 0.453$	$r_S = 0.234$
	$0.05 < p < 0.10$	$0.01 < p < 0.05$*	$0.40 < p < 0.50$
Females	$n = 9$	$n = 8$	$n = 8$
	$r_S = 0.272$	$r_S = 0.539$	$r_S = 0.539$
	$0.40 < p < 0.50$	$0.50 > p > 0.10$	$0.05 < p < 0.10$
Combined	$n = 22$	$n = 23$	$n = 21$
	$r_S = -0.496$	$r_S = 0.281$	$r_S = 0.298$
	$p < 0.009$*	$0.05 < p < 0.10$	$0.05 < p < 0.10$

Figure 17. Levels of aggressive interactions during summer 1976 and 1976.


MEAN INTERACTIONS PER HOUR OF OBSERVATION
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1975
1976
JUN
JUL
AUG
SEPT
MONTHS

$U = 0.5$, $p > 0.20$). Adjusting the data (Figure 18) for population density during the two summers, dividing number of interactions per hour by the MLE population values, reveals more of a disparity in the levels of aggressive behavior (Mann-Whitney $U = 12.5$, $p < 0.10$). If the months of June, July, and August only are considered for comparison, then a significant difference (Mann-Whitney $U = 9.0$, $p < 0.05$) is apparent in levels of aggressive interaction between the summers of 1975 and 1976.

The orientation of aggressive interactions during the summer of 1975 and 1976 is presented in Figure 19. The format of the orientation of interactions as given in Figure 19 (*e.g.*, Resident: Immigrant) places the dominant animal to the left of the colon and the subordinate animal to the right of the colon designating a type of dyadic interaction. Resident: Immigrant (*i.e.*, dominant animal: subordinate animal) agonistic interactions declined from 38% to 13%, comparing July, 1975, with July, 1976, while the reciprocal Immigrant: Resident interactions rose from 12% to 35% of total interactions. By August, 1976, feeding priorities at the feeding station between residents and immigrants were more established than in July, 1976, with Resident: Immigrant interactions dropping from 13% to 9%, and Immigrant: Resident interactions declining from 35% to 18% of observed agonistic encounters. As Immigrant: Resident and the corresponding reciprocal type of encounter (Resident: Immigrant) declined, Resident: Resident interactions increased from 17% in July, 1976, to 55% in August, 1976.

Figure 18. Levels of aggressive interactions adjusted for population density during 1975 and 1976.

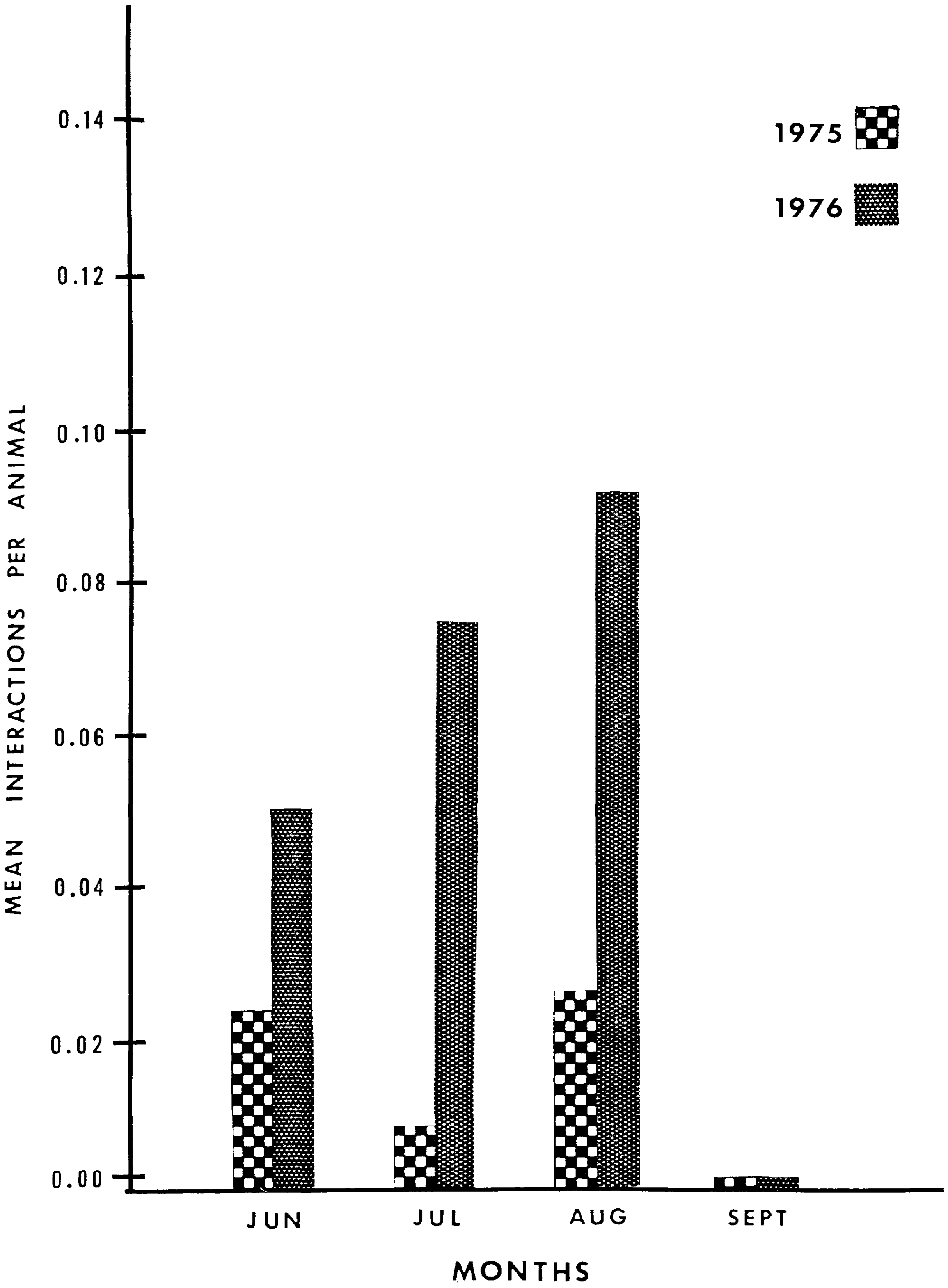
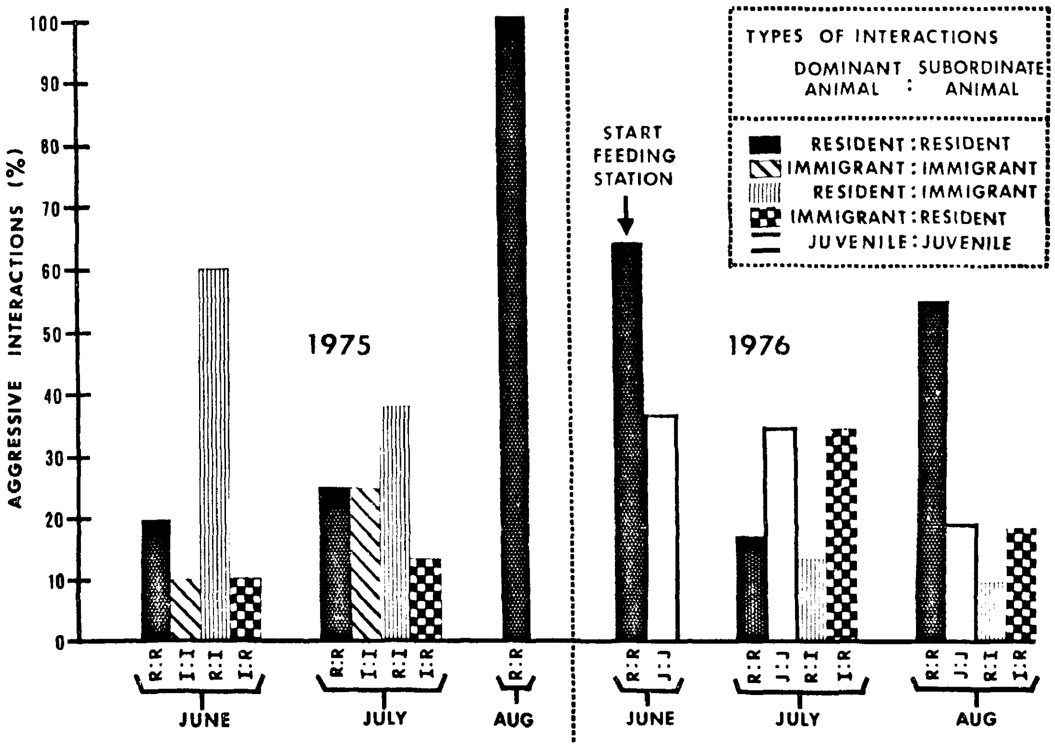

1975
1976
MEAN INTERACTIONS PER ANIMAL
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
JUN
JUL
AUG
SEPT
MONTHS

Figure 19. Orientation of aggressive interactions during summer of 1975 and 1976.


AGGRESSIVE INTERACTIONS (%)
0
10
20
30
40
50
60
70
80
90
100
1975
1976
START FEEDING STATION
R:R
I:I
R:I
I:R
J:J
JUNE
JULY
AUG
TYPES OF INTERACTIONS
DOMINANT ANIMAL : SUBORDINATE ANIMAL
RESIDENT : RESIDENT
IMMIGRANT : IMMIGRANT
RESIDENT : IMMIGRANT
IMMIGRANT : RESIDENT
JUVENILE : JUVENILE

DISCUSSION

The study population of gray squirrels on Jamestown Island was comparable to other populations in the eastern United States. The characteristic May-July breeding season (Taylor 1966; Nixon and McClain 1975; Thompson 1977a) was evident, but no winter breeding period was observed. Failure of female winter breeding has been reported for other gray squirrel populations (Cordes 1965; Barkalow and Shorten 1973). This decline in reproductive rate is often associated with a poor mast crop the preceding autumn; typically, male squirrels develop normally but the females do not come into estrus (Cordes 1965; Barkalow and Shorten 1973). Both perforate females and scrotal males were captured on the study area during the winter. Since the fall 1975 mast crop on the study area was not quantified, one can only speculate as to why no winter breeding occurred.

The decline in numbers of the population from an estimated 38 animals in June, 1975, to 15 animals in June, 1976, could be due to the winter decline in female reproductive rate, and either increased rates of emigration or mortality. Trap derived census techniques such as the Maximum Likelihood Estimate (Nixon et al. 1967) cannot distinguish between a reduction in captures due to variables such as sex, age, capture status, and climatological factors, or increased emigration and mortality. Perry et al. (1977) noted the high intrinsic variability that characterized gray squirrel trap response, and cite the need to adjust for environmental variation to obtain accurate mark-recapture population statistics. Nevertheless, the MLE provides an adequate estimate for gray squirrel population size in comparison to other commonly used population statistics (Nixon _et_ _al_. 1967).

Johnson (1973) notes that scent marking behavior can serve a number of functions, and that it is probable that scent marking serves different functions in different species. Scent marking by the gray squirrel has been observed to act as a stimulus to attract males to estrus females (Barkalow and Shorten 1973). Yet, the function of scent marking must be more than a sexual attractant since Taylor (1968) observed that peaks of marking activity occurred both during and outside of the breeding seasons. It is possible that scent marking in the gray squirrel functions more broadly as an indicator of individual identity, perhaps including information on sexual status as well as age and dominance as suggested by Johnson (1973).

In this study, no clearly defined scent marking behavior was seen during 294 hours of observation. The results of the urine application experiment did not indicate a significant approach or avoidance response of gray squirrels to enter urine treated live-traps. Perhaps if the proven stimulus of urine from females in estrus had been used the phenomenon of male attraction may have been observed as reported by Taylor (1966, 1968) and Barkalow and Shorten (1973). More experimental field research is required to clarify the function of scent marking in the eastern gray squirrel.

The size of gray squirrel home range ellipses in this study (Table 4) fall within the range of areas reported by other researchers utilizing convex polygons as estimates (Flyger 1960; Taylor 1966; Doebel 1967; Donohoe and Beal 1972; Cordes and Barkalow 1972; Bland 1977; Thompson 1978). Although not directly equivalent, convex polygons yield comparable size estimates to ellipses when corrected for sample size bias (Jennrich and Turner 1969). Reported average home range values range from 0.77 ha (Flyger 1960) to 9.75 ha (Bakken 1959) for adult males, and from 0.48 ha (Flyger 1960) to 4.01 ha (Bakken 1959) for adult females. Subadult home ranges vary from 15.2 ha (Adams 1976) to 1.09 ha (Cordes and Barkalow 1972). The data indicate that males on the average have larger home ranges (2.28 ha) than females (1.92 ha), but the difference is not significant. No clear age related difference in home range size is indicated by the data. However, the data tend to agree with the results of Cordes and Barkalow (1972) and Adams (1976) in that subadult squirrels were more mobile and had larger home range areas than adults (2.5 and 3.12 ha, versus 2.34 and 1.6 ha for both males and females). Seasonal changes in home range size as reported by Bland (1977) and Thompson (1978) were not demonstrated in this study.

Significant differences in spatial distribution of the study population were indicated by changes in the percentage of home range overlap and overlap index. These differences can be attributed to both sex related and seasonal effects. Male home ranges overlapped significantly less than female home ranges; this difference lies in the seasonal patterns of male overlap, whereby male ranges overlap significantly less in spring and summer, while overlap is significantly greater in fall/winter. The trends for decreased male home range overlap would be consistent with the demonstrated avoidance of more aggressive animals by subordinates during spring-summer breeding period (Farentinos 1972; Thompson 1977a) and increased overlap would be consistent with subadult movements during fall dispersal (Cordes and Barkalow 1972).

The significant age related difference in distance to the activity center of nearest same sexed animals was linked with the increased distances between the activity centers of subadult males and the activity centers of other males in the spring and fall/winter seasons. More frequent mobility of male squirrels has been reported during breeding seasons (Farentinos 1972; Bland 1977; Thompson 1977a, 1978) and fall dispersal (Cordes and Barkalow 1972). Avoidance by subadult males of the more aggressive and dominant adults during these periods could account for the significant age related difference found in the distances between activity centers of same sexed animals.

The results of Cordes and Barkalow (1972) and Thompson (1978) indicate that established gray squirrels have relatively stable home ranges over time. In this study, the activity centers of 15 animals for which data was complete, 7 males and 8 females, showed no significant seasonal shifting of individual activity centers. The data indicate that established animals in the Jamestown study population had stable home ranges for the duration of this study.

The stability of the gray squirrel home range system is further demonstrated by the results of the removal/release procedure. Half of the resident Jamestown animals successfully returned from a distance of 488 m, a rate of return indicating better orientation than shown by the random movements of the alien Williamsburg squirrels, and an indication of a definite tendency for residents to return to their center of familiarity. Hungerford and Wilder (1941) first observed the homing ability of gray squirrels by trapping animals and releasing them at points 914 m to 6.1 km distant. Forty per cent of the animals were later retrapped; the maximum distance from which animals returned was 4.5 km (Hungerford and Wilder 1941). Taylor et al. (1971) found that of 57 squirrels trapped within their study area and released 2.6 km away, 16 squirrels were known to have settled within 3.2 km of their point of release and 4 of these squirrels returned to sites near their point of capture. Brady (1972) trapped and displaced 53 gray squirrels from their home woodlot to other woodlots up to 2.2 km distant. Forty three per cent of the animals became residents where released; seventeen per cent of the animals actually returned to their home woodlot, and no animals returned home when displaced at distances greater than 1.1 km (Brady 1972). The removal/release procedure results of this study confirm that gray squirrels are likely to home ($p = 0.069$) when released within 1 km of their home woodlot.

The work of Pack et al. (1967) and Thompson (1978) reveal that gray squirrels have a social system based on a dominance heirarchy among a population of neighboring aniamls. Social dominance is related to both sex and age of the animal (Pack et al. 1967; Thompson 1978), with oldest adult males being at the top of the heirarchy followed by similarly aged adult females. Adult males in this study tended to have higher Dominance Index scores than females, but this difference was significant only for the spring observational periods. A larger sample size in this study would have increased the power of the tests used to determine if more conclusive sex related differences in dominance existed as demonstrated by other researchers (Bronson 1964; Pack et al. 1967, Thompson 1978). Body weight of the animal was positively correlated with Dominance Index scores. Dominance was also found to be negatively correlated with home range overlap. Animals with high D.I. scores had home ranges that overlapped less than the home ranges of neighboring low D.I. score animals. The data suggest that subordinate gray squirrels were avoiding contact with dominant conspecifics in the study area. Dominance was not associated with actual size of home range as in Pack _et_ _al_. (1967).

Bronson (1964) noted that the prevalence of wounding in female woodchucks reached a peak during lactation from May-June and that aggressive interaction rates declined steadily thereafter. Similarly, the reproductive condition of female gray squirrels can influence their Dominance Index score. The D.I. score of animal 99, an adult female, tripled when the animal was pregnant during the summer 1975 season. Taylor (1966) and Sharp (1959) also report increased aggressiveness in pregnant female gray squirrels. It would be of interest to determine if male squirrels in breeding condition also exhibited similar changes in dominance. However, due to the uncertainty in accurate assessment of actual male reproductive condition (active spermatogenesis versus regressing or recrudescing testes) in the field by external genital examination (Pudney 1976) it is inappropriate to include such an analysis in this study.

Utilization of a feeding station for a portion of this study did increase the number of observable agonistic interactions among squirrels on the study area. Pack _et_ _al_. (1967) also report the high number of social interactions observed among squirrels at feeding stations. This study differs from that of Pack _et_ _al_. (1967) in that use of a feeding station was limited to summer 1976 (3 months) instead of the entire study. Population density adjusted data indicated a significant difference in levels of aggressive behavior for the summer of 1975 and 1976. A qualitative difference also existed in the orientation of agonistic interactions between the summer 1975 and 1976 observation periods. This is exemplified by a reversal in percentages of Resident: Immigrant and Immigrant: Resident type of dyadic interactions for the two summers. The feeding station appeared to attract immigrant squirrels from adjacent woodlots as well as to present an interactive focal point for the resident squirrels on the study area. Pack *et al.* (1967) conducted their study in discrete woodlots and therefore did not observe immigrant animals interacting with residents as in this study.

Thompson (1978) observed peaks of aggressive behavior comparable to this study in his gray squirrel population during summer and early fall. The home range expansion of spring born animals was associated with the summer peak, while the early fall aggression peak corresponded to the fall movement period during which immigrants arrived on the study area (Thompson 1978). During both peaks of aggression, adult resident animals were dominant in 86.7% and 91.8% of the Adult: Juvenile, and Resident: Immigrant interactions (Thompson 1978). Orientation of aggressive interactions changed from Resident: Immigrant to Immigrant: Resident simultaneously with establishment of the feeding station on the study area. Two aggressive adult male immigrants actually succeeded in establishing priority at the feeding station over resident squirrels. The feeding station was such an attractive stimulus to immigrants that the resulting intensive agonistic interactions with residents deviated from the norms of the previous summer, and the observations of Thompson (1978).

The findings of this study lend direct support to the work done by Bland (1977) and Thompson (1978) on the spatial distribution of a gray squirrel population. The results that dominance was not shown to be associated with home range size as by Pack *et al*. (1967), and that residents were not consistently dominant over immigrants as shown by Thompson (1978) may be attributable to use of a feeding station in this study, since noticeable increases in the levels of aggressive interactions began upon its establishment on the study area. Utilization of the home range model of Koeppl *et al*. (1975) resulted in values for gray squirrel home ranges within the limits of areas reported in the literature and provided a quantifiable basis for analyzing the spatial distribution of the population.

APPENDIX

Ethogram of Gray Squirrel Behavior

Aggressive (A)

(1) Low intensity threat - squirrel in upright position, ears fully raised, eyes may be slitted; accompanied by squeak growl and possibly rapid tail flicking.

(2) High intensity threat - squirrel crouched, eyes slitted and ears partially raised; accompanied by growl and/or teeth chattering.

(3) Chase - squirrel in close pursuit of opponent; often accompanied by attempts to bite tail of fleeing squirrel.

(4) Attack - squirrel engaged in locked scratching and biting fight with opponent.

Submissive (S)

(1) Pawing - squirrel faces attacker and strikes with forepaws; may be accompanied by squeak growl and teeth chattering.

(2) Defensive - crouched position, tail curved over back, eyes wide open; Kuk-kuk....quaa vocalization may also be given.

(3) No change - ignores other animal.

(4) Avoidance - alters established position by moving, or makes a detour around other squirrel; movements stiff and jerky, hair erect.

(5) Flight - flees, pursuer, may be accompanied by squealing.

Sexual (X)

(1) Investigative approach - male sniffs ground and nearby trees adjacent to female, and approaches her position with slow hesitant movements.

(2) Mating chase - male follows female persistently, sniffing at females genital region as both animals move.

(3) Circling - male circles female slowly, continuing to sniff the females anogenital region, accompanied by some licking also.

(4) Mounting - male mounts female for period of 5-16 seconds; female being held in position by the hindquarters.

(5) Genital grooming - male licks penis; generally occurs after several mounts have culminated in ejaculation.

Grooming (G)

(1) Automanipulative - squirrel grooms itself.

(2) Social - squirrel grooms another animal.

Miscellaneous (M)

(1) Foraging - animal moves over ground, sniffs at substrate, and digs for food object.

(2) Travel - animal rapidly traverses ground w/o stopping.

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