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HOME RANGE AND DISPERSAL IN A NORTH CAROLINA GRAY SQUIRREL POPULATION

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ABSTRACT

Home range and dispersal patterns of gray squirrels (*Sciurus carolinensis*) in an unexploited population near Raleigh were determined by recapturing marked or tagged animals in leaf nests, live traps and artificial nest boxes during 1956-65. Adult gray squirrels occupied yearly home ranges averaging 1.8 Younger squirrels were more mobile and had larger home areas, 2.7 acres for subadults and 2.5 acres for juveniles. In all age classes males had larger average home ranges than females. Home ranges of young females and of adults were

more stable than those of young males. Squirrels known to have survived for from 1 to 8 years occupied rather small areas, indicating that individuals tended to remain in the same area for their lifetime. Young squirrels often remained with their mother for 6 months or longer. Seventy squirrels remained in the area of their birth and 9 females produced litters in the same nest boxes in which they, themselves, were born. Subadult males between 8 and 11 months of age moved more frequently and greater distances from their birth sites than females or other age classes. With the exception of a probable exodus of squirrels from the study areas in 1960-61, no appreciable annual reshuffling of the population was noted.

INTRODUCTION

The objective of this study was to determine the home range and dispersal pattern of the gray squirrel, *Sciurus carolinensis carolinensis* Gmelin, in an unexploited population. The investigation was conducted in the William B. Umstead State Park approximately six miles northwest of Raleigh, Wake County, North Carolina. The 5200-acre park is essentially a continuous tract of unbroken woodland which is almost completely surrounded by suitable habitats permitting unrestricted movement of squirrels to and from the park. Area vegetation is typical of the northern Piedmont Region being predominantly pines (*Pinus echinata* and *P. taeda*), hickories (*Carya tomentosa* and *C. glabra*), oaks (*Quercus alba, Q. Stellata, Q. velutina, Q. coccinea* and *Q. falcata*), red maple (*Acer rubrum*), and black gum (*Nyssa sylvatica*) on uplands and ridges with ravines having a dominant southern beech (*Fagus grandifolia*), red oak (*Quercus rubra*), and southern sugar maple (*Acer saccharum*) canopy. Tulip poplars (*Liriodendron tulipifera*) are abundant and pierce the canopy throughout the park. The poplars provide a readily available source of material for litter nests and an abundant May and June food supply for squirrels.

Trees of all mast-producing species have reached maturity and provide an abundant source of food during average years. Since most of the area was wooded when the park was established, canopy trees exceeding 2 feet dbh are common and some are 3 to 4 feet in diameter. Virtually all of the bottomland and ravines and much of the upland vegetation is approaching the climax. Pine stands are being replaced by hardwoods. In past years land abuse, as well as numerous springs and streams, have dissected the area into a dendritic pattern of ravines and swales creating a variety of microhabitats for a diverse ground flora and an abundant supply of water for squirrels.

The conditions under which our study was conducted were different from those reported by previous workers in that our research plots were located in a 2500-acre Natural Area which was a part of an extensive and continuous tract of woodland much of which was approaching the climax condition. The squirrel population on the research plots had minimal contact with the public since neither camping nor picnicking is permitted in the Natural Area portion of the park and no marked nature trails were located near the plots. The only supplement to the natural food supply was the corn, *Zea mays*, used at each trap site and it was available only during the actual trapping periods of approximately three weeks duration each winter and spring. Although formerly hunted and logged, the area has been protected from these disruptive activities as well as fire for over 40 years. The only effective gray squirrel predator absent from the area was the bobcat, *Felis rufus*; however, both feral house cats, *Felis catus*, and wild dogs, *Canis familiaris*, roam the area. An average of 3.2 natural den trees per acre were available to squirrels. There were no barriers to movement into or out of the research plots. One significant element of artificiality was the presence of two den boxes per acre that were available on one-half of each research plot for approximately one-third of the project's duration. Our squirrel populations appear to have been consistently lower per acre than most of those reported

from isolated woodlots and broken canopy woodlands by other workers (Flyger, 1960; Pack, 1966; Doebel, 1967; Taylor *et al.*, 1971).

METHODS

Two 200-acre research plots were located within the Natural Area portion of the park. Movement data were obtained by capturing gray squirrels in leaf nests, live traps and nest boxes during the period March, 1956 through May, 1965. Leaf nests were inspected for nestlings during the summers of 1958 through 1964 and also during the spring of 1962. Two nest boxes per acre were erected on one-half of each 200-acre plot for approximately one-third of the project's duration; boxes were then removed for a two-year period before being re-erected on the other half of each plot that had previously been without boxes. Nest boxes were examined during the months of March, June, September and December between the hours of 10:00 AM and 3:30 PM which was the period of least daylight squirrel activity. Occasionally boxes were examined at night. Specially designed live traps (Soots, 1964) were inspected late in the afternoon each day to insure maximum exposure to squirrels and to eliminate the possibility of animals remaining in traps overnight. Trapping periods, conducted during the winter and spring, varied in length from 2 to 6 weeks for each study area. Details of the experimental design have been discussed more fully by Barkalow and Soots (1965).

Young squirrels were individually identified by a toe-clipping system and older squirrels were ear-tagged. Individuals between 3 and 6 months of age were considered juveniles; over 6 but less than 12 months were subadults and squirrels over one year old were adults. Aging criteria used with young animals were modifications of the technique employed by Shorten (1954) and Uhlig (1955b).

An individual's home range was determined by plotting at least 5 locations of capture on a map and connecting the outermost points. The area enclosed was measured by a planimeter and converted to acres. Yearly (5 or more captures during each 10- to 14-month period) as well as long term home ranges were determined for adult animals. Home ranges of juvenile and subadult squirrels were calculated from 5 or more captures over a 1- to 3-month and a 1- to 6-month interval respectively. The maximum range for an individual was determined as the distance between the two outermost points of capture within the home range. Average values of home range and maximum range were determined for each sex and age class.

As used in this paper the term "dispersal" includes movements of young squirrels away from their birth sites, movements of individuals from an old home range to a new one, as well as one-way movements of animals out of the resident populations.

RESULTS

Social Behavior and Early Movements

During the spring, examination of nest boxes and leaf nests often caused females to carry their nestlings from one nest box or leaf nest to another. In most instances litters were transferred to the nearest adjoining nest box, rarely more than 90 yards. However, one female moved her two young 175 yards in a single day. Another female, which had just given birth to three young, was found in a leaf nest at 9:00 AM. One-half hour later she and two of her newly-born young were found in another leaf nest approximately 140 yards away. A subsequent recapture of this female and the same two young in a nest box one month later indicated that the third offspring had apparently not been moved or was lost during a transfer.

After young squirrels were capable of leaving the nest (about 8 weeks of age) they continued to remain in the vicinity with their mother. Family units were frequently recaptured together in nest boxes after 6 months and littermates were often recaptured together over longer periods. In one case two males, 32 days of age when initially found in a nest box, were recaptured 12 months later in another nest box 70 yards away. Males and females of different ages were often found sharing the same nest box, especially during the winter.

Forty-eight female and 22 male gray squirrels were known to have remained in the area of their birth. Nine of the females produced litters in the same nest box in which they, themselves, were born. Fifteen other females littered within 70 yards, and 12 others within 140 yards of their respective birth sites.

Dispersal

Ninety subadult squirrels were known to have dispersed from their respective birth places. Twenty-two individuals (10 males and 12 females) moved an average distance of 190 yards before establishing new home ranges (Table 1). The 10 males moved an average distance of 250 yards and the 12 females averaged 130 yards. Recapture records for 30 other animals (16 males and 14 females) indicated these squirrels moved off the study areas. Thirty-eight subadults (28 males and 10 females) were not recaptured enough times to adequately define their dispersal patterns.

Although dispersal was more frequently recorded for subadult animals between 8 and 11 months of age, such movements were also recorded for 9 juvenile (7 males and 2 females) and 11 adult (7 males and 4 females) squirrels. The longest record for a young squirrel was 1.3 miles for a juvenile 2 months of age. Eight other juveniles were known to have moved an average distance of 280 yards from their respective birth sites. An average dispersal distance of 1.1 miles was recorded for 8 adult animals that moved from one study area to the other. Three squirrels were killed by hunters outside the park. Two females were killed 2.0 and 1.7 miles from their last known sites of capture and a male was killed 1.2 miles from its last known capture site.

Home Range

Of 1769 marked squirrels, 183 were captured 5 times or more. Ninety-four yearly home range determinations averaged 1.8 acres for adult squirrels. Younger animals occupied larger areas, 2.7 acres for subadults and 2.5 acres for juveniles. In all age classes males had a larger average home range than females (Tables 2 and 3).

The largest home range determined for an individual was 21.4 acres. This subadult male was captured a total of 14 times, 13 of which were within a 2-week period in March, 1961. This animal traveled within its home range a total linear distance of 2.5 miles during the 2-week period.

The greatest number of recaptures was 30 for a female captured during 4 years. The longest history was 8 years. This individual, also a female, was initially captured in a nest box at the age of 7 days. The animal was recaptured a total of 13 times in an area of less than 3 acres.

Calculated home ranges were generally larger for squirrels captured a greater number of times. This relationship, however, between size of home range and number of recaptures was less apparent with adult females than with adult males or younger squirrels of both sexes (Table 4).

Some enlargement of the home range occurred with age. Ninety-nine individuals recaptured over periods of from 2 to 8 years had larger home ranges, on the average, than squirrels taken over a one-year period (Table 2). The relationship between size of home range and length of recapture period, however, was not a linear one; little or no increase in average home range was noted for squirrels recaptured over periods of from 3 to 6 years (Figure 1).

Mapped home ranges for juveniles and subadults were generally elongate and "rectangular" in shape while those for adult squirrels were more "circular." This difference in shape of home range was reflected by the greater maximum ranges recorded for the younger age classes (Table 5). The mean maximum range for juveniles and subadults collectively was 225 yards, while that for adult squirrels was 180 yards.

DISCUSSION

Dispersal

Repeated captures of family units (female and offspring) over a period of several months indicated that young squirrels became familiar with the home range of their mother. As squirrels approached maturity, many (especially females) continued to remain in the same local area. Females commonly produced litters in the same nest box or general area in which they, themselves, were born.

The tendency to disperse appeared to be more characteristic of males. Fifty-four of 90 subadult animals known to have left the area of their birth were males. Howard (1949) reported that small rodents disperse at the time that their reproductive organs first become functional. Since we found dispersal to occur most frequently in gray squirrels 8 to 11 months of age that were approaching sexual maturity, such movements might be, in part, a response to the hormonal secretions of their reproductive organs. However, it has been pointed out that dispersal was also recorded for juvenile and adult squirrels of both sexes although much less frequently. An unusually atypical movement was recorded for a juvenile male 2 months of age. This squirrel was estimated to be 32 days of age when first captured in a leaf nest and at the age of 56 days it was caught in a trap 1.3 miles away from the original marking site. Most young squirrels do not usually leave the nest until they are somewhat older (Uhlig, 1955a; Bakken, 1959). Barkalow *et al.* (1970) hypothesized an annual average dispersal rate of 14.5 percent from our study areas.

Biologists have reported a fall shuffle or dispersal associated with population displacement (Baumgartner, 1943; D. L. Allen, 1943; J. M. Allen, 1952; Brown and Yeager, 1945; Sharp, 1959). Baumgartner (1943) pointed out that although the motivating factor for such movements is usually considered to be population pressure correlated with a shortage of food, movements occurred when food supply was greatest, almost simultaneously with the maturing of the nut crop. He suggested that such movements result from intraspecific intolerance.

During the present study no annual reshuffling of the gray squirrel population was observed. However, either an exodus, mortality or both occurred on the study areas between December, 1960 and April, 1961. The 1960 fall mast crop was poor but the squirrel population was the highest during the 10-year study. In early December of 1960, when trapping was discontinued, the population index was 468 squirrels; by April, 1961, it had dropped to only 66 animals (Soots, 1964). Since there was little indication of a high mortality and since this reduction occurred over a period of about three months, it is our opinion that there was a substantial population movement from the area.

Home Range

Recapturing marked squirrels in leaf nests, live traps and den boxes provided an effective means of determining their home ranges. Estimates of home range and maximum range obtained in this study generally agree with those reported by Flyger (1960) for Maryland gray squirrels and by Pack (1966) and Doebal (1967) for squirrels in Virginia. Our findings, however, conflict with observations made by Donohoe and Beal (1972) in Ohio and Robinson and Cowan (1954) in Canada. In the Ohio study 7 gray squirrels and 5 fox squirrels

(Sciurus niger) followed by radiotelemetry for periods of from 1 day to 2 months were found to occupy average home ranges of 11.8 and 27.9 acres respectively. An extremely large home range of 77.6 acres was reported for an adult male fox squirrel. Robinson and Cowan used both trapping and sight records to determine that introduced Eastern gray squirrels in parkland on Vancouver Island ranged over areas up to 50 acres and traveled a daily average maximum distance of 450 yards from the "home tree."

Differences in home range estimates reported by various workers are probably more related to habitat characteristics and to squirrel population density than to methodology used in determining home range. Flyger (1960) found little difference between ranges produced from sight-record data and those produced from trapping data for the same squirrels. Doebal (1967) used both radiotelemetry and observation-trapping methods to determine average home ranges of less than 1.5 acres for Virginia gray squirrels. In our study, population density was less than 3 squirrels per acre and home ranges averaged somewhat larger than those reported for Maryland (Flyger, 1960) and Virginia (Pack, 1966; Doebal, 1967) squirrels on small isolated woodlots where population densities were 7.5 and 5.5 individuals per acre respectively. As pointed out by Flyger (1960) the extensive movements reported by Robinson and Cowan (1954) for the exotic Vancouver Island gray squirrels may have been the result of the very low population density, in this case 0.7 squirrels per acre.

Since we found squirrels between the ages of 8 and 11 months to be highly mobile and "dispersal-prone", it is conceivable that workers might mistake movements away from a birth site or from an old home range to a new one for movements within some larger home area. When such movements are plotted inflated home range values result. If correct age determinations are made such movements may be anticipated in the 8 to 11 month old category.

Young squirrels seem to exhibit two behavior patterns of movement following weaning; they may establish a home range which includes the nest site in which they were born, or they may disperse varying distances away from the original nest site before establishing a well-defined home area. Some young may continue their dispersal movement for some distance and may well be removed from the population before establishing a home range. The maximum distance we could follow a dispersal movement on our research areas was approximately two miles and a few young animals were known to have exceeded this distance and left the area without establishing a home range.

Average home range and maximum range values recorded for squirrels in each age class suggest that males are more mobile than females. Taylor *et al.* (1971) similarly found clear differences in the maximum recorded distances moved by male and female gray squirrels during a 6-year study of the species in Britain. These workers clearly demonstrated that the larger size of male ranges did not result from any tendency for males to re-enter traps more readily than females.

Since females more often remained in the area of their birth after becoming sexually mature, while males showed a stronger tendency to disperse, it is suggested that home ranges of young female gray squirrels are more stable than those of young males. It is further suggested that, although gray squirrels may initially enlarge and/or shift their home areas, a stabilized home range is firmly established after 3 or 4 years.

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Table 1. Distances 22 subadult gray squirrels dispersed from their birth places before establishing new home ranges.

Distances Moved (yards)	Males	Females
70 - 99	1	4
100 - 129	0	2
130 - 159	1	1
160 - 189	1	4
190 - 219	2	0
220 - 249	1	0
250 - 279	0	0
280 - 309	0	0
310 - 339	1	1
340 - 369	0	0
370 - 399	3	0

Mean Distance Moved by Both Sexes = 190.

Table 2. Means, standard deviation, and standard error of home ranges (acres) of adult gray squirrels recaptured over various periods during 1956-65.

ıng 1956-65.

Recapture Period (years)	Females					Males				
	N	H.R.	Range	S.E.	S.D.	N	H.R.	Range	S.E.	S.D.
1	64	1.7	0.2 - 5.3	0.1	1.2	30	2.2	0.2 - 6.9	0.4	2.0
2	20	2.5	0.2 - 10.0	0.5	2.3	11	3.1	0.6 - 11.7	0.9	3.0
3	21	3.5	0.5 - 15.6	0.8	3.5	15	4.9	0.5 - 8.5	0.6	2.5
4	9	4.2	1.0 - 8.2	1.0	3.0	5	5.3	1.8 - 7.2	1.2	2.6
5	8	3.4	1.0 - 7.0	0.7	2.0	6	5.4	2.0 - 10.3	1.3	3.1
6	3	3.9	0.8 - 6.6	1.7	2.9					
8	1	3.5								

Table 3. Means, standard deviation, and standard error of home ranges (acres) of juvenile and subadult gray squirrels recaptured during 1956-65.

Age Class	Females					Males				
	N	H.R.	Range	S.E.	S.D.	N	H.R.	Range	S.E.	S.D.
Juvenile	14	2.4	0.9 - 6.6	0.4	1.6	4	2.7	0.8 - 6.8	1.1	2.3
Subadult	19	1.9	0.2 - 6.1	0.4	1.7	21	3.4	0.5 - 21.4	1.0	4.5

Table 4. Average home ranges (acres) of adult, subadult, and juvenile gray squirrels according to number of recaptures.[1]

Number of Recaptures	Adult[2]		Subadult		Juvenile	
	Females	Males	Females	Males	Females	Males
5	1.4 (30)	1.3 (14)	1.4 (11)	1.1 (7)	1.9 (7)	
6	1.5 (16)	2.2 (12)	2.0 (2)	2.7 (4)	2.3 (4)	3.1 (3)
7	1.3 (6)	4.4 (3)	1.4 (3)	2.0 (2)	2.3 (2)	1.5 (1)
8	1.0 (2)		6.1 (1)	3.5 (1)	6.6 (1)	
9	3.8 (4)	6.9 (1)		2.4 (2)		
10	2.9 (4)		2.7 (1)	4.9 (2)		
11	2.0 (1)		4.0 (1)	5.5 (1)		
12	1.6 (1)					
13				4.5 (1)		
14				21.4 (1)		

[1]Figure in parentheses refers to number of individual home range values.
[2]Average yearly home range.

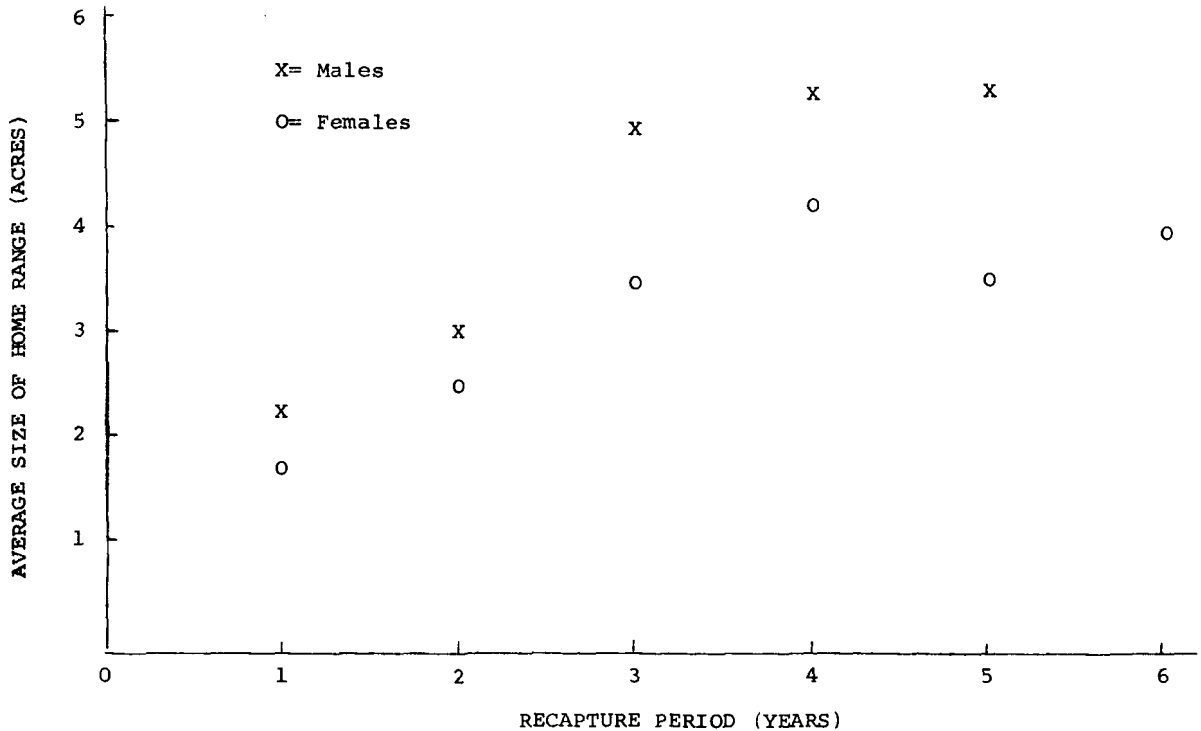

Figure 1. Relationship between average home range size and length of recapture period for adult male and female gray squirrels.

Table 5. Means, standard deviation, and standard error of maximum ranges (yards) of juvenile, subadult, and adult gray squirrels recaptured during 1956-65.

	Females					Males				
Age Class	N	H.R.	Range	S.E.	S.D.	N	H.R.	Range	S.E.	S.D.
Juvenile	14	205	95 - 290	20	70	4	240	160 - 335	45	95
Subadult	19	210	80 - 375	20	90	21	245	95 - 800	35	170
Adult[1]	64	165	70 - 290	5	50	30	210	75 - 600	20	115

[1]Maximum range calculated for yearly home ranges only.

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