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INTERACTION AMONG ADULT FEMALE FOX SQUIRRELS DURING THEIR WINTER BREEDING SEASON[1]

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ABSTRACT

Radiotelemetry was used to study the interaction, spacing, and habitat utilization of adult female fox squirrels (Sciurus niger) during their winter breeding season. A total of 15 adult female fox squirrels were radio-tracked during 4 February-16 March 1976, and 24 January-26 March 1977. Enough fixes (377) were taken on eight squirrels to derive a standard diameter of 120 m, a standard range of 1.13 ha, and an approximate home range of 12.24 ha for adult females during February and March. Although females with transmitters entered the standard ranges of other females with transmitters, the main den sites and centers of activity of the radio-equipped squirrels appeared to be somewhat uniformly distributed and no closer than 50 m to the main den site and center of activity of another adult female. The average basal area per hectare of major tree species in the standard ranges of adult females was similar to the basal area per hectare of those tree species in the woods.

INTRODUCTION

Breeding females comprise the most stable portion of the fox squirrel (Sciurus niger) population (Moore, 1957:58). Therefore, adult females may be less likely to change their home ranges, once they become reproductively active, than other sex- and age-classes of fox squirrels. Studies tend to confirm that the breeding adult female is the central element in the social structure of the gray squirrel (S. carolinensis) (Taylor, 1969). Thus, a sound ecological and behavioral understanding of the adult female fox squirrel may provide a better insight into the dynamics of fox squirrel populations.

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Intraspecific interactions may affect population regulation of rodents (Sadlier, 1965; Healy, 1967; Christian, 1971). Social behavior may also affect the number of adult female gray squirrels that breed (Nixon and McClain, 1975:436, 437). Fox and gray squirrels do not exhibit the territoriality found in populations of red squirrels (Tamiasciurus hudsonicus) in coniferous forests (Smith, 1968). However, reproductively active female fox and gray squirrels defend their nests, nest trees, or areas surrounding their nest trees (Bakken, 1952; Robinson and Cowan, 1954; Taylor, 1966; Geeslin, 1970; Adams, 1973; McCloskey, 1975). Taylor (1966:233-234) indicated that pregnant and nursing female gray squirrels are intolerant of other breeding females of their species. Taylor (1977) also noted that scent marking points were often located on the nest tree of female gray squirrels and the use of these marking points may be territorial. Nixon et al. (1975:21) found that the home ranges of breeding adult female gray squirrels were nearly mutually exclusive.

The purpose of this study was to examine the interaction, spacial distribution, and habitat utilization via radiotelemetry of adult female fox squirrels during their winter breeding season in an east-central Illinois woodlot.

METHODS

Study area.--This study was conducted in Trelease Woods, a 24-ha mature mixed mesophytic forest located in Champaign County, east-central Illinois. The vegetation of Trelease Woods was described by Boggess (1964) and by Pelz and Rolfe (1977). Pelz and Rolfe (1977) tallied 22 major tree species; the leading dominants, in order of Importance Value Index, were sugar maple (Acer saccharum), hackberry (Celtis occidentalis), slippery elm (Ulmus rubra), white ash (Fraxinus americana), basswood (Tilia americana), red oak (Quercus rubra), and buckeye (Aesculus glabra). Trelease Woods is inhabited by both fox and gray squirrels, but only a few gray squirrels were present during this study.

Materials.--Radiotelemetry equipment consisted of 15, 296 MHz squirrel-type transmitters and an AVM Model 12 receiver. The transmitters were attached to neck collars. The total weight of collar and transmitter was approximately 20 g. The materials for the transmitters were purchased from AVM Instrument Co., Champaign, Illinois.

Procedures.--Fox squirrels were livetrapped in the south half of Trelease Woods during February 1976 and January 1977. Seven adult females that appeared to be reproductively active were etherized, ear-tagged, and fitted with transmitters during 4-6 February 1976; radios were also placed on eight similar females on 24 January 1977. Squirrel locations were determined by using a hand-held directional antenna connected to the radio receiver. Compass bearings to the locations of the squirrels were taken at two or more of the numbered permanent stakes set 50 m apart in Trelease Woods. The resulting "fixes" were later plotted on scaled maps of the woods.

In 1976, the squirrels were tracked from 4 February until 16 March. In 1977, radio-tracking extended from 24 January until 26 March. Fixes were taken diurnally and almost daily, with a minimum of 1.5 hr between observations. Sufficient fixes were taken on six squirrels in 1976 and on two squirrels in 1977 to allow statistical analyses. For these eight squirrels, a total of 377 fixes were taken (range, 31-63) for an average of 47.1 per squirrel. The center of activity (Hayne, 1949) of each of these eight squirrels was determined. Fix points from these eight squirrels around their respective centers of activity were used to calculate a standard diameter, standard range, and whole range (Harrison, 1958) for adult female fox squirrels during their winter breeding season.

Each time a squirrel was located in a tree, the species of tree was noted. For trees used frequently as den sites by the squirrels (primary den sites), the species, DBH, den direction, den height (measured with an altimeter), and tree height were determined. Also, the 1976 inventory of the vegetation in Trelease Woods, furnished by D. R. Pelz, University of Illinois Forestry Department, facilitated determination of the average basal area of the leading dominant tree species per hectare within the standard range of the eight adult female squirrels and the basal area per hectare of the same tree species in the entire woodlot.

RESULTS

The center of activity (Hayne, 1949), which is the geographic center of all fixes for a particular squirrel, is shown for six adult female fox squirrels for February and March, 1976, in Figure 1 and for two adult female squirrels for January-March, 1977, in Figure 2. The primary den sites and breeding condition of these eight squirrels and other squirrels wearing transmitters are also shown with their corresponding ear-tag numbers in the figures. The localities of two adult female fox squirrels without radios in 1976 (#541 and #547) are shown in Figure 1. These two squirrels (both lactating) were livetrapped at least three times during attempted retrieval of the radios after completion of the first spring of study. The average distance between the centers of activity for the closest adjacent adult females was 152 $\pm$ 25 m (SE) (N = 5, range = 92 - 215 m) in 1976 and 1977. The average distance between the primary den site of an adult female and the primary den sites of its two closest neighbors was 116 $\pm$ 8 m (SE) (N = 30, range = 51 - 221 m). The farthest fix of a squirrel from its center of activity was 200 m.

Harrison (1958:193) utilized the idea of a series of concentric probability zones surrounding the center of activity and within which an animal spends varying proportions of its time. From this concept Harrison (1958:198) formulated a standard diameter that "defines, by implication, a 'standard range,' the circle of standard diameter, which will contain 68.26 percent of all trappings." The standard diameter can be estimated by plotting the normal deviates of the frequency of radio fixes against the observed diameters around the center of activity, drawing the line of best fit, and noting where it

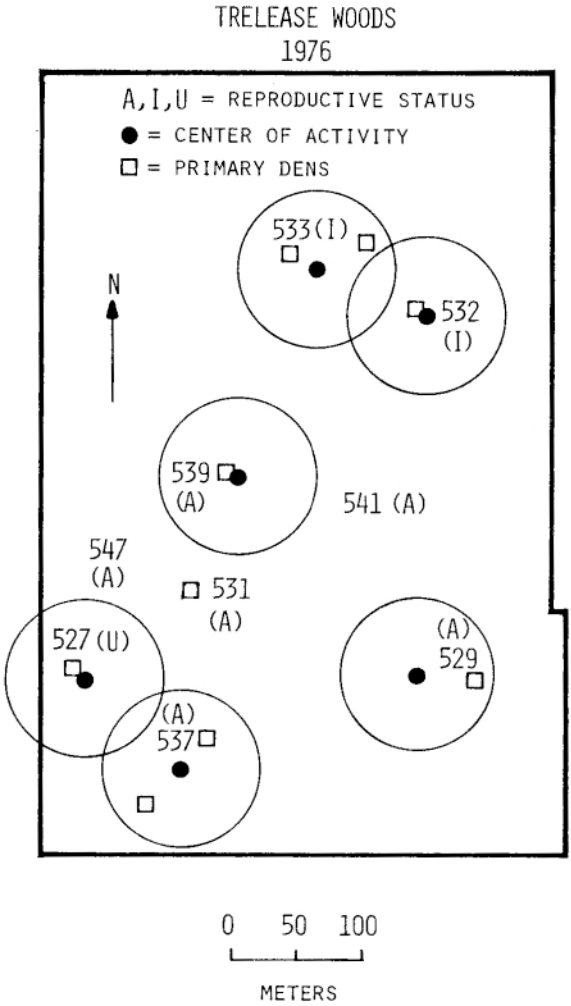

Figure 1. Ear-tag numbers, primary den sites, and centers of activity with standard ranges of six radio-collared adult female fox squirrels in Trelease Woods during February-March 1976. Squirrels with ear-tag numbers 541 and 547 were livetrapped at least three times in their respective localities at the completion of the 1976 radio study. Reproductive status is denoted as active (lactating or pregnant) = A, inactive = I, and unknown = U.

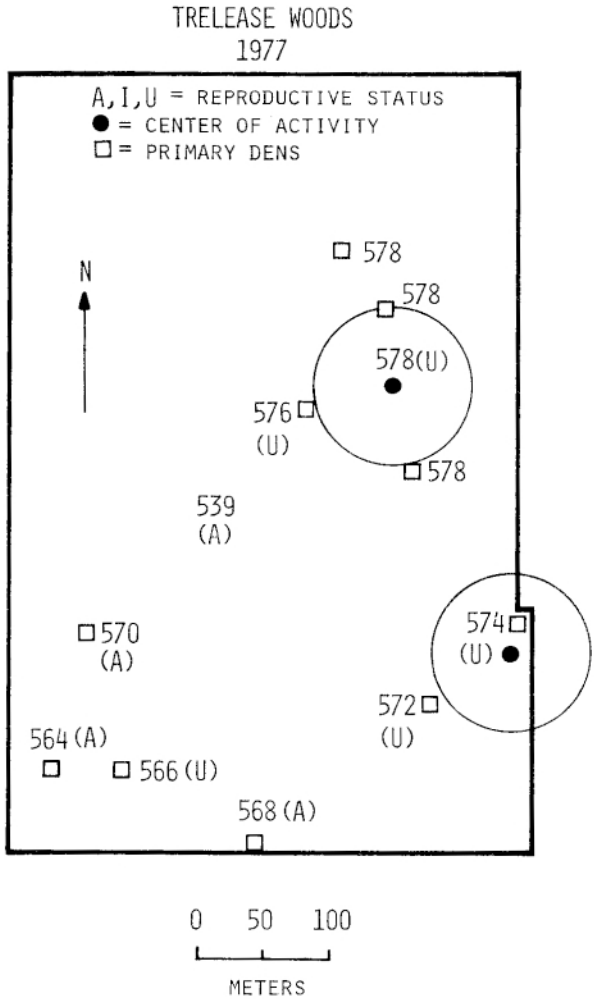

Figure 2. Ear-tag numbers and primary den sites of radio-collared adult female fox squirrels in Trelease Woods during January-March 1977. Centers of activity with standard ranges are shown for numbers 574 and 578. Squirrel number 539 was found dead in its designated location before the onset of the radio study in January 1977. Reproductive status is denoted as active (lactating or pregnant) = A, inactive = I, and unknown = U.

cuts the abscissa of unit deviate. Utilizing 377 total fixes for eight adult female fox squirrels in this manner (Table 1), a standard diameter of 120 m was determined (Fig. 3). Thus, 68.26 percent of the calculated activity of adult female fox squirrels in late winter took place within a circle (a standard range) with a standard diameter of 120 m around their centers of activity. The area of this standard range is 1.13 ha. Correspondingly, Harrison (1958:204) stated that an animal would spend 99.9 percent of its time within a diameter of 3.29 standard diameters; this calculation resulted in a whole range area of 12.24 ha for the average breeding adult female fox squirrel in Trelease Woods during this study.

Table 1. Percentage of radio fixes in circles of increasing diameters, located around the calculated centers of activity of eight adult female fox squirrels during February-March 1976 and January-March 1977 in Trelease Woods, Champaign County, Illinois.

Diameter of Circle (m)	Number of Fixes	Cumulative Number of Fixes	Percent of Total	Probits
40	107	107	28.4	0.3638
80	103	210	55.7	0.7688
120	81	291	77.2	1.2055
160	36	327	86.7	1.5063
200	12	339	89.9	1.6449
240	20	359	95.2	1.9774
280	7	366	97.1	2.1808
320	7	373	98.9	2.5556
360	1	374	99.2	2.6521
400	3	377	100.0	

The standard ranges, based on a standard diameter of 120 m, for six squirrels (at least three of which were reproductively active) are shown in Figure 1 and for two squirrels are shown in Figure 2. In 1976 (Fig. 1), the reproductive status of the squirrels was as follows: squirrels #529, 531, 537, 539, 541, and 547 were active (A = lactating or pregnant); squirrels #532 and 533 were inactive (I); and squirrel #527 was unknown (U). The standard ranges of #527 (U) and #537 (A) overlapped as did the

standard ranges of #532 (I) and #533 (I) (Fig. 1). Besides the overlap of the standard ranges of these squirrels, the following intrusions of the standard range of a radio-marked squirrel by another radio-marked squirrel occurred: #533 (I) was found twice in the standard range of #532 (I); #533 (I) was found five times in the standard range of #539 (A); and #537 (A) was found once in the standard range of #527 (U).

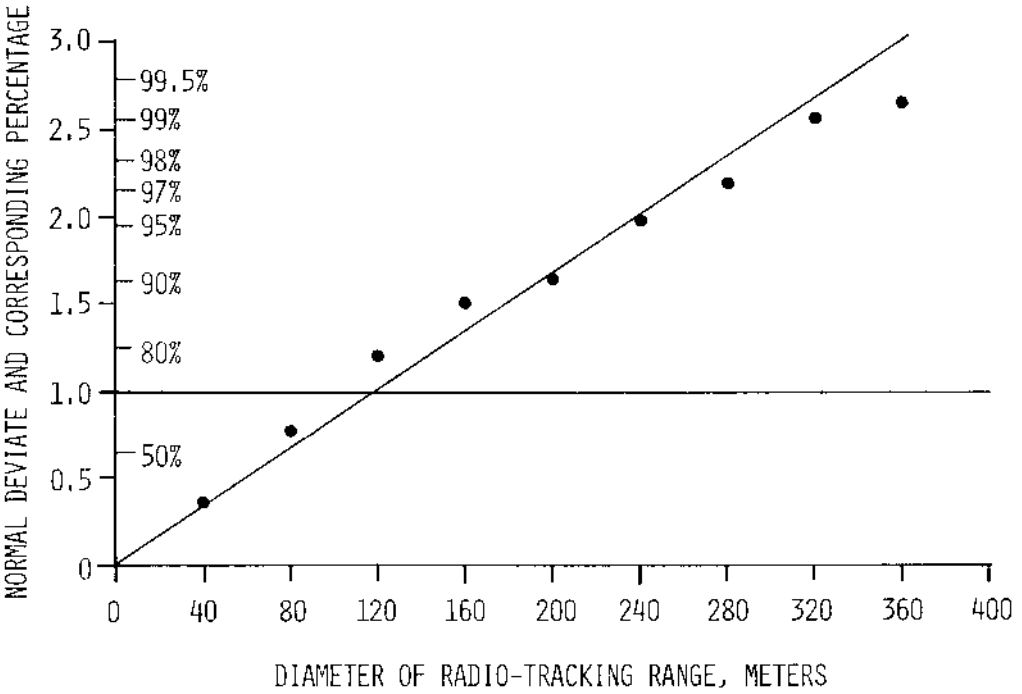

Figure 3. Plot of the normal deviates of the frequency of radio fixes within the diameters of circles around the centers of activity against the observed diameters of the circles for eight adult female fox squirrels. The standard diameter for the squirrels is 120 m.

In 1977, the rate of winter breeding of adult female fox squirrels was exceptionally high in other study areas. The reproductive status of the radio-equipped squirrels was as follows: squirrels #539, 564, 568, and 570 were active; the remaining squirrels were unknown. We assume that most of the adult female squirrels in this study during 1977 were reproductively active. Standard ranges of squirrels #574 (U) and #578 (U) did not overlap (Fig. 2). However, #572 (U) was found once within the standard range of #574 (U), and the primary den site of #572 was at the fringe of the standard range of #574. Also, the primary den site of squirrel #576 (U) was at the edge of the standard range of #578 (U) and undoubtedly entered this range.

The basal areas for all tree species in the standard ranges of the eight squirrels were tallied. The average basal areas per hectare for the leading dominant tree species in the standard ranges of the squirrels were compared by chi-square analyses with the basal areas per hectare of the leading dominant tree species for Trelease Woods (Table 2). These leading dominant tree species are well distributed throughout Trelease Woods (Pelz and Rolfe, 1977). There were no significant differences in the basal areas per hectare of the dominant tree species in the squirrel ranges as compared with the basal areas per hectare of these species available to the squirrels in the entire woodlot. Apparently, these squirrels did not show preference regarding tree species for their areas of greatest activity. However, 47 percent of the fixes taken when the squirrels were active occurred in red oak trees. This percentage is significantly higher than the percentage of red oak trees in Trelease Woods (1 percent; Pelz and Rolfe, 1977). However, red oak acorns were the prime food source for fox squirrels during February and March in Trelease. The tree species with the second highest percentage of fixes for active squirrels was sugar maple which accounted for 27 percent of the fixes. This is similar to the percentage of sugar maples in Trelease (26.6 percent) (Pelz and Rolfe, 1977).

The female squirrels also used mostly red oaks and sugar maples for their primary den sites (Table 2). Sanderson et al. (1976) found that gray squirrels frequently used red oaks and sugar maples as den sites. Sanderson et al. (1976:613) determined that gray squirrels preferred live trees 40 cm DBH or larger for den trees. We found that the average DBH of primary den trees used by fox squirrels was 65 cm (Table 3), that most dens faced south to easterly, and that the average height of primary dens was 11.3 m, or approximately 44 percent of the average height of the den trees.

DISCUSSION

We were not primarily concerned with the shape of the adult female fox squirrels' home ranges in this study. As Sanderson (1966:230) noted, the "shape of the home range appears to have little significance in itself. . . ." Instead, Sanderson (1966) suggested that investigators should concentrate on ecological relationships, because movement patterns are established and regulated by such factors as species density, reproductive activity, food supply, and physiographic arrangement of the habitat. Thus, we calculated the centers of activity and standard

diameters for the squirrels from radio-tracking data to investigate the interaction of adult female fox squirrels during their critical late-winter breeding season. In addition, the standard diameter gives a figure useful for comparative purposes, and an area figure--the standard range--can be calculated if desired.

Table 2. Average basal area for the leading dominant tree species (DBH > 6.60 cm) within the standard range of eight adult female fox squirrels and the basal area of the leading dominant tree species in Trelease Woods.

Species	Average Basal Area in Standard Range of Adult Female Fox Squirrels (m^2/ha)	Basal Area in Trelease Woods (m^2/ha)[a]
Sugar maple (*Acer saccharum*)	8.56	8.05
White, green, and blue ash (*Fraxinus americana*, *F. pennsylvanica*, *F. quadrangulata*)	3.70	4.15
Red oak (*Quercus rubra*)	2.28	2.57
Hackberry (*Celtis occidentalis*)	1.85	3.07
American and slippery elm (*Ulmus americana* and *U. rubra*)	1.65	2.02
Basswood (*Tilia americana*)	1.28	1.70
Black walnut (*Juglans nigra*)	1.19	1.51
Bur oak (*Q. macrocarpa*)	1.15	1.42
Ohio buckeye (*Aesculus glabra*)	1.03	1.33

[a] Pelz and Rolfe (1977:448).

Table 3. Characteristics of trees having cavities used as primary den sites by radio-collared adult female fox squirrels in Trelease Woods, Champaign County, Illinois.

Tree Species	DBH (cm)	Canopy[a]	Tree Height (m)	Den Height (m)	Direction of Den Opening
Red oak (*Quercus rubra*)	86.4	Cod	33.2	16.2	N
	67.1	Dead	24.4	15.9	
	86.4	Cod	30.5	14.3	S
	80.5	Cod	27.7	11.9	SE
	78.2	Dead	19.8		
	68.1	Cod	26.2		
	93.0	Cod	30.2		
Sugar maple (*Acer saccharum*)	101.6	Dom	31.0	10.4	SW
	45.7	Sup	16.8	9.1	NW
	38.4	Sup	23.5	9.1	E
	54.6	Cod	23.2	11.6	W
	46.0	Cod	29.3	13.1	S
	46.2	Cod	28.4	9.8	E
	50.8	Cod	27.4		
Basswood (*Tilia americana*)	49.3	Cod	27.4	9.8	SE
	63.5	Cod	25.3	6.1	S
White ash (*Fraxinus americana*)	65.3	Cod	29.9	17.1	SE
Kentucky coffee tree (*Gymnocladus dioicus*)	39.1	Sup	25.9	10.1	SE
Silver maple (*A. saccharinum*)	66.8	Dead	7.0	5.5	E
Mean	64.6		25.6	11.3	

[a] Cod = codominant; Dom = dominant; Sup = suppressed.

During the late-winter breeding season for fox squirrels in Illinois, pregnancy peaks in February and lactation peaks in March (Brown and Yeager, 1945:477). Although fox squirrels have another breeding period in late summer, the late-winter breeding period may be more important to fox squirrel populations. Brown and Yeager (1945:487) found that a higher percentage of adult fox squirrels bred during the winter breeding period than during the summer breeding season (78 percent vs. 44 percent). In addition, young fox squirrels born during the winter season may have

higher survival than young born during the summer season, as reported for gray squirrels (Barkalow et al., 1970:498; Nixon and McClain, 1975:16).

The importance of the winter breeding season in conjunction with the apparent pugnaciousness and intolerance of breeding female squirrels for other squirrels during this period is ecologically significant. Each breeding female may require or demand a certain minimum area to successfully feed and raise a spring litter. If this is true, then the spacing of reproducing female squirrels may limit the population density of female fox squirrels.

We found that den locations and centers of activity of radio-tracked adult female fox squirrels during the winter breeding season appeared to be somewhat uniformly distributed (Figs. 1 and 2). The shortest distance between primary den sites of adjacent adult females was 51 m and the closest centers of activity were 92 m apart. Apparently, the defense by breeding female fox squirrels of nest trees and immediate areas around nest trees (Adams, 1973; McCloskey, 1975) may result in a distribution that approaches uniformity. However, radio-collared adult females did enter the standard ranges of radio-tracked breeding females during our study.

Benson (1975:28) and McCloskey (1975:50) found that the home ranges of adult female fox squirrels only partially overlapped. Nixon et al. (1975:21) suggested that the low occurrence of captures of different nursing female gray squirrels in the same live trap during the same trapping period indicated that the home ranges of breeding adult female gray squirrels may be largely mutually exclusive. We have livetrapped two upland hardwood study areas in Vermilion County, Illinois, which contain primarily fox squirrels. One study area was livetrapped for six consecutive springs (March-May) and falls (October). The other area was livetrapped for two springs (March). We calculated an index of home range overlap between and within sexes by using the sequence of capture of individual squirrels in traps as explained by Hansen (1978:56). Based on 287 total captures of adult fox squirrels in the spring and 137 captures in the fall, a chi-square test of homogeneity of trap captures showed a significant difference in overlap values from expected values in the spring but not in the fall (Table 4). Of the 287 spring captures, there were 46 captures of different squirrels in the same live trap during the same trapping period (Table 4). However, only four of these double captures were different adult females, well below the expected value of 14.4. Thus, this low occurrence of double female captures contributed most to the chi-square value (Table 4). The avoidance evident between adult females apparently did not occur in October, when most fox squirrels have finished breeding and are actively seeking and storing mast supplies for the approaching winter.

Why, then, should breeding female squirrels maintain some minimal distance among themselves during the reproductive season? Geeslin (1970:109) surmised that the spacial arrangement of the home ranges of fox squirrels seemed to be primarily a function of food supply. Bakken (1952:113) noted that nest sites and food may be the principal factors determining the occupation of an area by squirrels. Another

Table 4. Chi-square analysis of overlap (different squirrels caught in same trap during the same trapping period) of adult fox squirrels based upon 287 spring livetrap captures and 137 fall captures in upland hardwood timber, Vermilion County, Illinois.

	Spring			Fall		
	♂♂	♂♀	♀♀	♂♂	♂♀	♀♀
Observed	13	29	4	2	6	5
Expected	8.9	22.7	14.4	2.6	6.6	3.9
Chi-square	= 1.88	+ 1.77	+ 7.54	0.15	+ 0.05	+ 0.29
		= 11.19[a]			= 0.49	

[a] $p < 0.005$, 2 df.

possible reason may be related to intraspecific stress. Christian (1971) demonstrated that the reproductive functions of female animals are hampered by social stress. Female squirrels may confine their breeding activities and caring of young to areas near their centers of activity. Thompson (1977:1180) noted that female gray squirrels mated no farther than 30 m from their centers of activity. Ruff (1971) found that after conception, female Uinta ground squirrels (Spermophilus armatus) defended limited areas around their burrows and that this territoriality acted to reduce heart rate and, therefore, stress.

We calculated a standard diameter of 120 m for eight adult female fox squirrels in this study. Doebel and McGinnes (1974:865) found a standard diameter of 93 m for adult gray squirrels and an average standard diameter of 88 m for all sex- and age-classes of gray squirrels. We determined a standard range of 1.13 ha and an approximate home range of 12.24 ha for our squirrels. Other home range estimates of adult female fox squirrels range from 0.44 to 5.3 ha (Bakken, 1952:156; Geeslin, 1970:109; Donohoe and Beal, 1972:12; Adams, 1973:12; Benson, 1975:31; Chesemore, 1975:325; McCloskey, 1975:49). However, the activity of female fox squirrels may be reduced in February and March by cold weather (Allen, 1943:154; Brown and Yeager, 1945:464; Geeslin, 1970:62; Adams, 1973:104) and by decreased movement of pregnant and lactating females (Goodrum, 1937:501; Bakken, 1952:167; Taylor, 1966:234; Geeslin, 1970:58; Adams, 1973:80). However, lactating females undoubtedly increase their activities during April and May when the energy cost of lactation substantially increases (Havera, 1978).

Although the female squirrels did not show any preference in the vegetational makeup of their standard ranges (Table 2), they apparently selected red oaks for daytime activity (feeding) and for den sites (Table 3). Red oak acorns are poorer nutritionally for fox squirrels

than other mast diets in Trelease Woods (Havera, 1978), but little other mast was available to the squirrels in Trelease during February and March 1976 and 1977.

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