THE BEHAVIOR OF DISPLACED GRAY SQUIRRELS

by

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INTRODUCTION

The gray squirrel (Sciurus carolinensis) is important both as a game animal and as one of the few wildlife species that can be seen by urban dwellers. Thus, information which would contribute to our understanding of this important game species should contribute to our game management efforts concerned with the squirrel as well as heighten the appreciation of this lively mammal by many urbanites.

A study of individual animal movements ". . . leads to conclusions about daily and seasonal movements, species movements (except for range extension), migratory movements, movements in defense of territory, and movements in any other category the researcher chooses to study" (Sanderson 1966:215). Knowledge of the gray squirrel's homing ability, which has been described as ". . . the basic urge, desire or instinct to return to a home territory from some point of displacement" (Wilson 1967:8), could have practical application in a stocking operation where squirrels were being introduced into an unoccupied range or to bolster a diminished population. This knowledge would also be helpful in urban situations where excess or troublesome squirrels are removed from city parks and private yards by live-trapping and displacement.

Studies of the behavior of displaced animals may also provide valuable insite on the effect that mobility may have upon present-day man.

The major objectives of this study were to determine, by sex and by age, for displaced gray squirrels:

1. The percentage of squirrels which reach home following displacement.
2. The type cover and lanes of travel utilized after displacement.
3. The effect of displacement distance on the ability of the squirrels to return home.
4. The amount of time needed to return home as related to the distance of displacement.
5. The time of day utilized for movements following displacement.

A minor objective of this study was to determine the behavior, movements, and fate of displaced squirrels which fail to return to their home area.

LITERATURE REVIEW

One of the first homing experiments with gray squirrels was carried out by Hungerford and Wilder (1941:460). These investigators displaced 15 squirrels, and this included 6 females, one of which returned, and 9 males, 5 of which returned. The maximum distance a squirrel returned was 14,800 feet in less than 4 weeks.

Shipley (1941:129-141) displaced 29 gray squirrels, 16 of which returned home. The animals which homed had been removed distances varying from 1,350 ft. to 17,140 ft.

A total of 46 gray squirrels were displaced by Wilson (1967: 21). Fourteen of them returned, however, the sex and age was known for only 12 individuals. There were 25 adults and 11 returned home, but only 1 of the 21 immature squirrels homed. Ten of 31 males and 2 of 15 females returned (Wilson 1967:23). The fartherest distance an adult male returned was 11,700 ft. in three days (Wilson 1967:32).

Allen (1943:152-153) removed more than 200 fox squirrels (*Sciurus niger*) 15 miles from one woodlot, but none was observed to come back.

A few homing experiments have been performed with other members of the Sciuridae. A female flying squirrel (*Glaucomys v. volans*) was reported to have homed over a distance of at least one half mile (McCabe 1947:404). Seidel (1961:256-257) reported homing success for eastern chipmunks (*Tamias striatus*) displaced from 150 ft. to 1,800 ft. Layne (1957:519-520) displaced 18 eastern chipmunks,

and 7 of them returned from distances up to 750 ft.

A number of homing experiments have been carried out with other small mammals as white-footed mice, Peromyscus maniculatus (Broadoaks 1961; Murie 1963; Murie and Murie 1931; Kendeigh 1964); old-field mice, Peromyscus polionotus (Gentry 1964); cotton mice, Peromyscus gossypinus (Gentry 1964); pocket mice, Perognathus porvus (Broadoaks 1961); western harvest mice, Reithrodontomys megalotis (Fisler 1966;1967); meadow vole, Microtus pennsylvanicus (Robinson and Falls 1965); California vole, Microtus californicus (Fisler 1961; 1962; 1967); and the brush rabbit, Sylvilagus backmani (Chapman 1971). Homing experiments and theories of homing for birds, fish and amphibians were reviewed by Fisler (1967). Matthews (1968) reviewed many homing experiments performed with birds and particular emphasis was placed on theories as to how birds navigated over great distances.

The natural history of certain birds and fish require that they possess a homing ability, while the life style of small mammals does not. Results from the above mentioned studies, which are relevant to the present study, will be presented in the Discussion section of this paper.

TECHNIQUES AND PROCEDURES

Study Areas

The study areas were isolated woodlots on the Virginia Polytechnic Institute and State University Farm (Fig. 1). All the squirrels used were captured on President's Hill Woods and released in Turkey Pen Woods, Price's Fork Woods (east of the U. S. 460 Blacksburg bypass), North Crumpacker Woods, Crumpacker Woods, Center Woods, and Trailer Camp Woods. All woodlots were previously known to have resident gray squirrel populations.

Composition of the Woodlots

The composition of the woodlots is described thoroughly by Wilson (1967:13). The overstories consists primarily of mature to overmature white oak (*Quercus alba*) - hickory (*Carya* spp.) with a range in d.b.h. from 3 to 40 inches. The white oak is considered by Uhlig (1956:46) to be the ideal tree for gray squirrels both as a den tree and an excellent source of food. The hickory nut is the preferred food of the gray squirrel (Uhlig 1956:39).

Center Woods, Trailer Camp Woods and the eastern portion of Crumpacker Woods have a dense understory, while President's Hill Woods, Turkey Pen Woods, Price's Fork Woods, North Crumpacker Woods, and the western portion of Crumpacker Woods have a grass covered floor due to grazing or mowing.

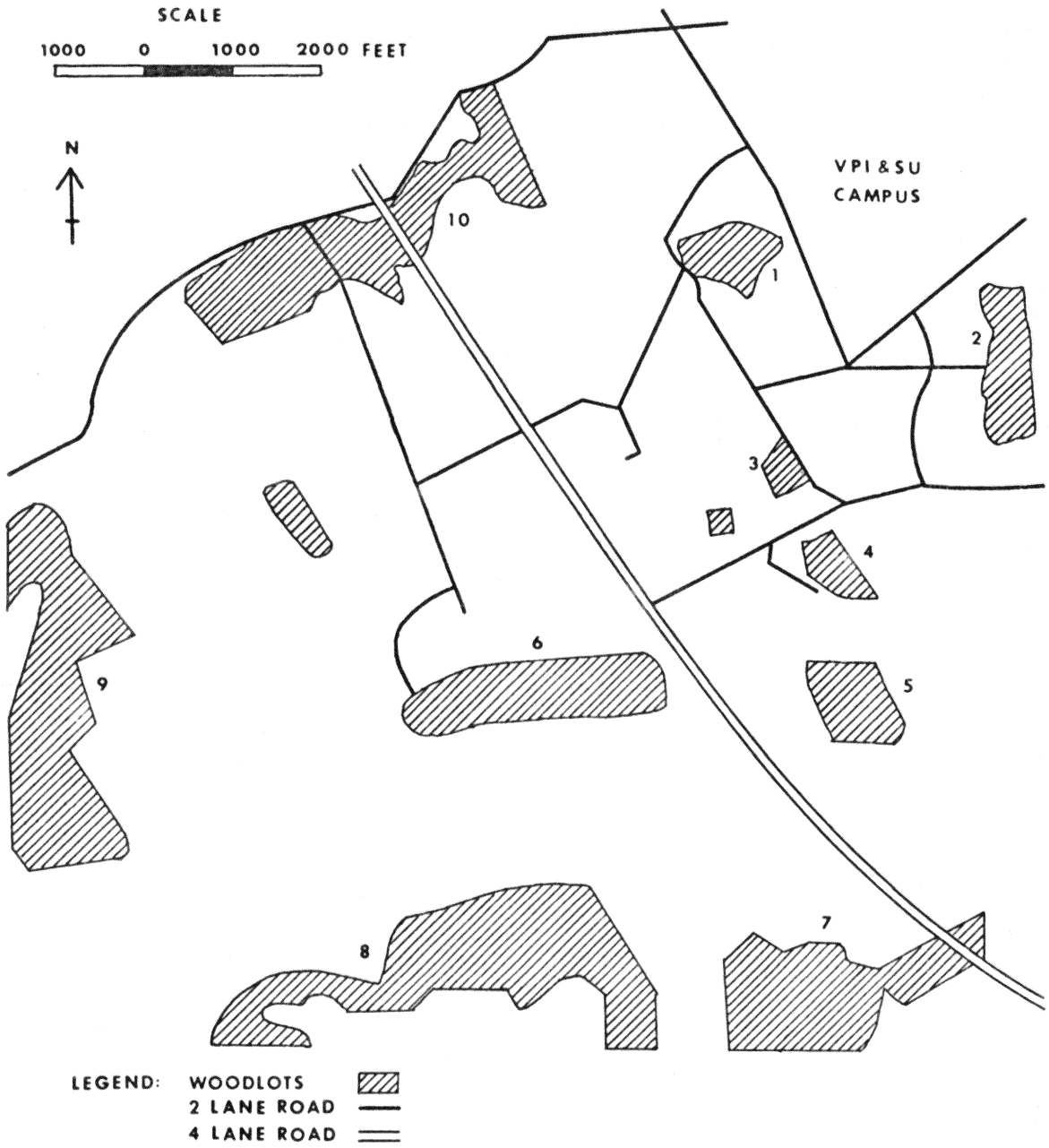

Fig. 1. Virginia Polytechnic Institute College Farm woodlots: (1) President's Hill; (2) Trailer Camp; (3) Turkey Pen; (4) North Crumpacker; (5) Crumpacker; (6) Center; (7) Dairy; (8) Boundary; (9) Heth; (10) Price's Fork.

Connections Between Woodlots

Figure 2 shows the available travel or cover lane between the woodlots. None of the outlying woodlots is entirely connected by travel lanes to President's Hill, the home woodlot. Each returning squirrel would have to cross open areas of at least 100 feet.

The existing travel lanes consist of (1) fence rows with small trees, blackberry (Rhubus spp.) and annual weeds, (2) large individual deciduous trees either isolated in small clusters, or in rows spaced fairly evenly apart at varying distances, and (3) rows of evergreen shrubs and small trees.

The use of cover lanes to travel between woodlots has been reported for gray squirrels (Uhlig 1956:73; Johnson 1957:15) and for fox squirrels (Allen 1943:142). The straight line distance and the shortest possible distance using available cover between the home woodlot and each of the woodlots of displacement are shown in Table 1.

The U. S. 460 Blacksburg bypass was a highway which presented a major impediment to a returning squirrel. This would primarily effect squirrels displaced in Center Woods.

Investigational Techniques

Trapping

Squirrels were trapped using wooden mammal live-traps (Mosby 1955). Whole kernel corn was used as bait.

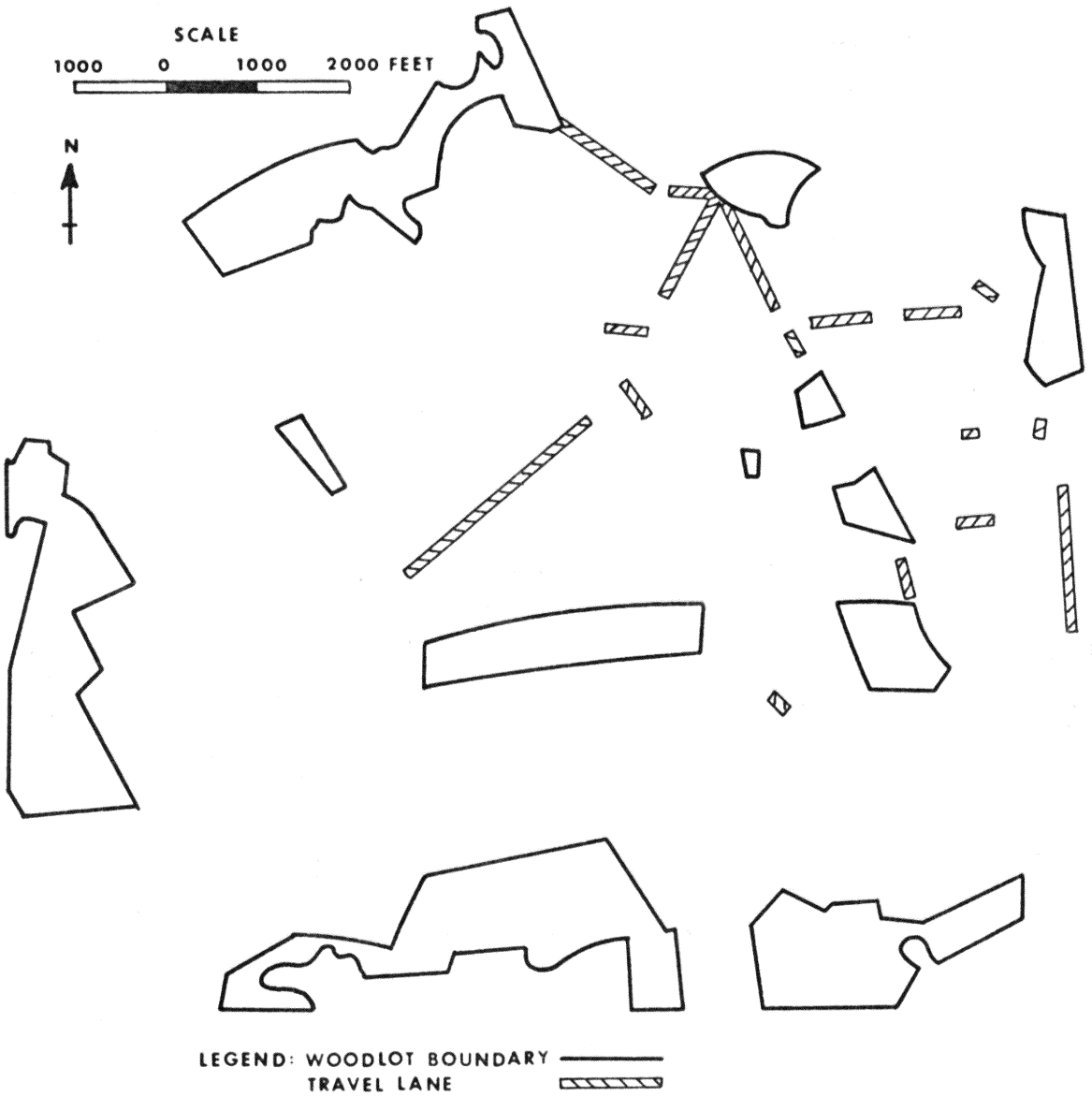

Fig. 2. Virginia Polytechnic Institute College Farm showing cover lanes between woodlots

Table 1. Distances between the center of President's Hill Woods and the location in the woodlots where squirrels were released

Woodlots	Straight line distance	Shortest possible distances using available cover
Turkey Pen Woods	2750 ft.	3250 ft.
Price's Fork Woods	3250 ft.	3624 ft.
Trailer Camp Woods	3250 ft.	5000 ft.
North Crumpacker Woods	4126 ft.	4622 ft.
Crumpacker Woods	5500 ft.	6124 ft.
Center Woods	6624 ft.	7120 ft.

Trapping of squirrels for the purpose of displacement was conducted in President's Hill Woods from September 24, 1971, to December 3, 1971, at least 5 days per week, and from January 19, 1972, to February 15, 1972, approximately 2 days per week.

Trapping was conducted in Turkey Pen Woods from February 28, 1972, to March 6, 1972, for the purpose of capturing displaced squirrels which could not be identified at a distance.

Trapping was also conducted in President's Hill Woods from March 6, 1972 to March 21, 1972, in an attempt to capture any unobserved displaced squirrels which returned home, and to obtain a population estimate of the squirrels which remained. Traps were checked twice a day to reduce shock losses as suggested by Pack (1966:16).

For positive identification each individual squirrel was labeled with a numbered monel tag in each ear (manufactured by the National Band and Tag Company, Newport, Kentucky). In order to distinguish between sexes, the hair on the terminal portion of the tail was clipped for females, and the hair on the basal portion of the tail was clipped for males (Fig. 3 and Fig. 4). For individual identification at a distance, each squirrel was marked with Nyanzol D, a black fur dye, in a coded pattern (Fig. 3 and Fig. 4). Nyanzol D dye and complete instructions for its use are available from Nyanzol Incorporated, P. O. Box 899, Laurence, Massachusetts.

Dye for identification purposes is lost during the spring molt (April) and the fall molt (October), and the tail hair will regrow during the fall molt (Flyger 1955:381-2). Some of the squirrels

Fig. 3. Photograph of squirrel #2145-2146, a subadult male. Hair on basal portion of tail was clipped. The front section and right rear leg were dyed with Nyanzol D fur dye.

Fig. 4. Photograph of squirrel #2131-2132, a subadult female. Hair on the terminal portion of the tail was clipped. The front and midsection were dyed with Nyanzol D fur dye.

which were dyed and clipped during October could not be individually identified at a distance after about three weeks and had to be recaptured for positive identification.

Determination of Sex and Age

Sex was determined by examination of external genitalia, and age was determined by tail pelage (Sharp 1958). The squirrels were placed in one of three age categories: juveniles, under six months of age; subadults, between 6 and 18 months of age; and adults, greater than 18 months of age (Sharp 1958:30).

Displacement of Squirrels

After being dyed, each squirrel was placed in a small retaining cage and transported in the trunk of an automobile to one of the selected woodlots previously mentioned, where it was released.

Radiotracking

Originally this study was to have used radiotracking as the principal method of gathering data. Unfortunately only one radio-transmitter was obtained, and it was lost after being used on one squirrel.

The radiotransmitter was similar to the one used by Doebel (1967) and was built by Research Support Services, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. The method of attaching the transmitter to the squirrel was described in detail by Doebel (1967).

The receiver was designed and built by Mr. Lee Wilkins, Deerfield, Virginia. It is a modified form of the D-11 receiver described by Cochran (1963) and Doebel (1967).

The technique used for locating the one squirrel radiotracked was to turn the receiver until the strongest signal was obtained, and then move toward the direction in which the signal became stronger. The observer would then sit quietly and wait until the squirrel was seen.

Methods of Observation

Of all the displaced squirrels, 47 were observed for about 15 minutes after being released or until they disappeared from sight; 10 of the displaced squirrels (including the one with the radiotransmitter) were followed continuously on the day of release, and an attempt was made to locate the squirrel on the day following its release by arriving in the area where the squirrel was last seen about one-half hour before sunrise.

The woodlots where squirrels had been released were periodically visited during the course of this study. The early morning and late afternoon were found to be the best times for observing squirrel activity as was reported by Bakken (1959:393). Each time that a marked squirrel was observed, the date, time of day, activity, including type and result of any social encounter, and general weather conditions were recorded.

The home woodlot, President's Hill, was also under observation periodically during the duration of this study. Trapping was

carried out in this woodlot during the times previously mentioned, and returning animals were often trapped.

Neighboring woodlots other than the ones where squirrels were displaced were also visited occasionally in an attempt to determine if any of the displaced animals had moved to these woodlots.

Squirrels were observed with the aid of 7 x 50 binoculars. The observer sat quietly on the ground, or on a log or in a vehicle when the ground was frozen enough to drive a vehicle into the woodlots.

Determination of Random Wandering Probabilities

The method of calculating the probability that a displaced squirrel would move from the woodlot where released to another woodlot was taken from Chapman (1971:688). The probability was calculated by dividing by 360 the angle subtended by the other woodlot at the point of release. It is emphasized that this is a maximum since it gives the probability that the squirrel would be in the sector formed by the angle which extends for an infinite distance. The probability that a squirrel would move a particular distance would have to be multiplied with the probability that the squirrel would be in the sector formed by the angle to obtain the actual probability of a squirrel reaching a particular woodlot by random wandering.

RESULTS

Squirrels Which Remained in Woodlot Where Released

Of the 53 squirrels which were displaced, 23 (43%) became residents of the woodlot where they were released. A squirrel was considered to have become a resident of the woodlot where released if it was sighted in that woodlot 14 days or more after release. Two squirrels later homed after being sighted where released 15 and 19 days following release. These two squirrels were not included among those which took up residence in the woodlot where released.

Size of Woodlot Where Released

A greater proportion of displaced squirrels did not necessarily remain in large woodlots than in smaller woodlots (Table 2), although the fate of 20 displaced squirrels was unknown.

Influence of Season of Release, Sex, and Age

Although the sample sizes are unequal, it appeared that displaced squirrels were more likely to establish residence when released in the fall than in the winter (Table 3). Twenty-two (46%) of 48 squirrels released in the fall (September 24, 1971 to December 3, 1971) established residence at the release site, while only 1 (11%) of 9 squirrels released in the winter (January 19, to February 14, 1972) established residence.

Seven (27%) of 26 displaced male squirrels and 16 (52%) of 31 displaced female squirrels established residence where released

Table 2. Relationship between the size of the woodlot where released and the number of displaced gray squirrels remaining in the woodlot where released; VPI College Farm, Sept. 1971-Feb. 1972

Woodlots where released	Size of woodlot (acres)	Number released*	Squirrels remaining in woodlot where released	
			No.	%
Turkey Pen	4.8	18	8	44
North Crumpacker	7.9	2	1	50
Trailer Camp	15.8	1	0	0
Crumpacker	17.9	16	6	38
Price's Fork (east of U.S. 460 bypass)	31.2	16	8	50
Center	46.5	4	0	0

* This includes four squirrels which were displaced a second time after homing. Each was displaced to a different woodlot: two in Crumpacker, one in Price's Fork, and one in Trailer Camp. One squirrel was known to have remained in Crumpacker Woods.

Table 3. The influence of season of release, sex, and age on displaced gray squirrels establishing residence in woodlots where released; VPI College Farm, Sept. 1971-Feb. 1972

Age Class	Squirrels released- Male	Female	Total- No.	%	Squirrels which remained in woodlots where released- Male	Female	Total- No.	%
			Fall Displacement					
Adult	7	12*	19	39	2	6	8	36
Subadult	10	10	20	42	3	5	8	36
Juvenile	3	6	9	19	2	4	6	28
Total: No.:	20	28	48		7	15	22	
%:	42	58		100	32	68		100
			Winter Displacement					
Adult	1**	2***	3	33	0	0	0	0
Subadult	4	0	4	45	0	0	0	0
Juvenile	1	1	2	22	0	1	1	100
Total: No.:	6	3	9		0	1	1	
%:	67	33		100	0	100		100

* This includes one squirrel which was displaced a second time after homing. It was not known to home a second time.

** This squirrel was displaced a second time after homing in the fall. It was not known to home a second time.

*** Both of these squirrels had previously been displaced in the fall and both homed. Neither was known to home a second time.

(Table 3). Only 1 out of 3 females and none of 6 males released during the winter established residence. Of the 22 squirrels released during the fall that established residence, 7 (32%) were male, and 15 (68%) were female.

Eight (36%) of 22 displaced adult squirrels, 8 (33%) of 24 displaced subadult squirrels, and 7 (64%) of 11 displaced juvenile squirrels established residence where they were released (Table 3). One juvenile of 2 released in the winter established residence. None of the adults or subadults released in the winter established residence. Of the 22 squirrels released in the fall that established residence, 8 (36%) were adults, 8 (36%) were subadults and 6 (28%) were juveniles.

Squirrels Which Homed

A total of 53 gray squirrels was displaced, 9 (17%) of which returned home. Of the 9 squirrels which returned, 4 were displaced a second time to a different woodlot; none of these were known to return home a second time.

Influence of Displacement Distance, Time, and Size of Woodlot Where Released

No squirrel was known to have homed from a woodlot which was more than 3,624 feet from the home woodlot (Table 4).

The time required to return home did not seem to be influenced by distance since all squirrels that homed did so from similar distances. Both squirrels that were followed home (Figs. 5 and 6) returned the same day that they were released. The time required

Table 4. Relationship between displacement distance and the number of displaced gray squirrels which returned home; VPI College Farm, Sept. 1971-Feb. 1972

Woodlot where released*	Shortest distance of return using available cover	Number released**	Homing- No.	Homing- %
Turkey Pen	3250 ft.	18	7	39
Price's Fork	3624 ft.	16	2	13
North Crumpacker	4622 ft.	2	0	0
Trailer Camp	5000 ft.	1	0	0
Crumpacker	6124 ft.	16	0	0
Center	7120 ft.	4	0	0

* Home woodlot for all squirrels was President's Hill Woods.

** This includes four squirrels which were displaced a second time after homing. Each was displaced to a different woodlot: two in Crumpacker, one in Price's Fork, and one in Trailer Camp. None were known to have homed a second time.

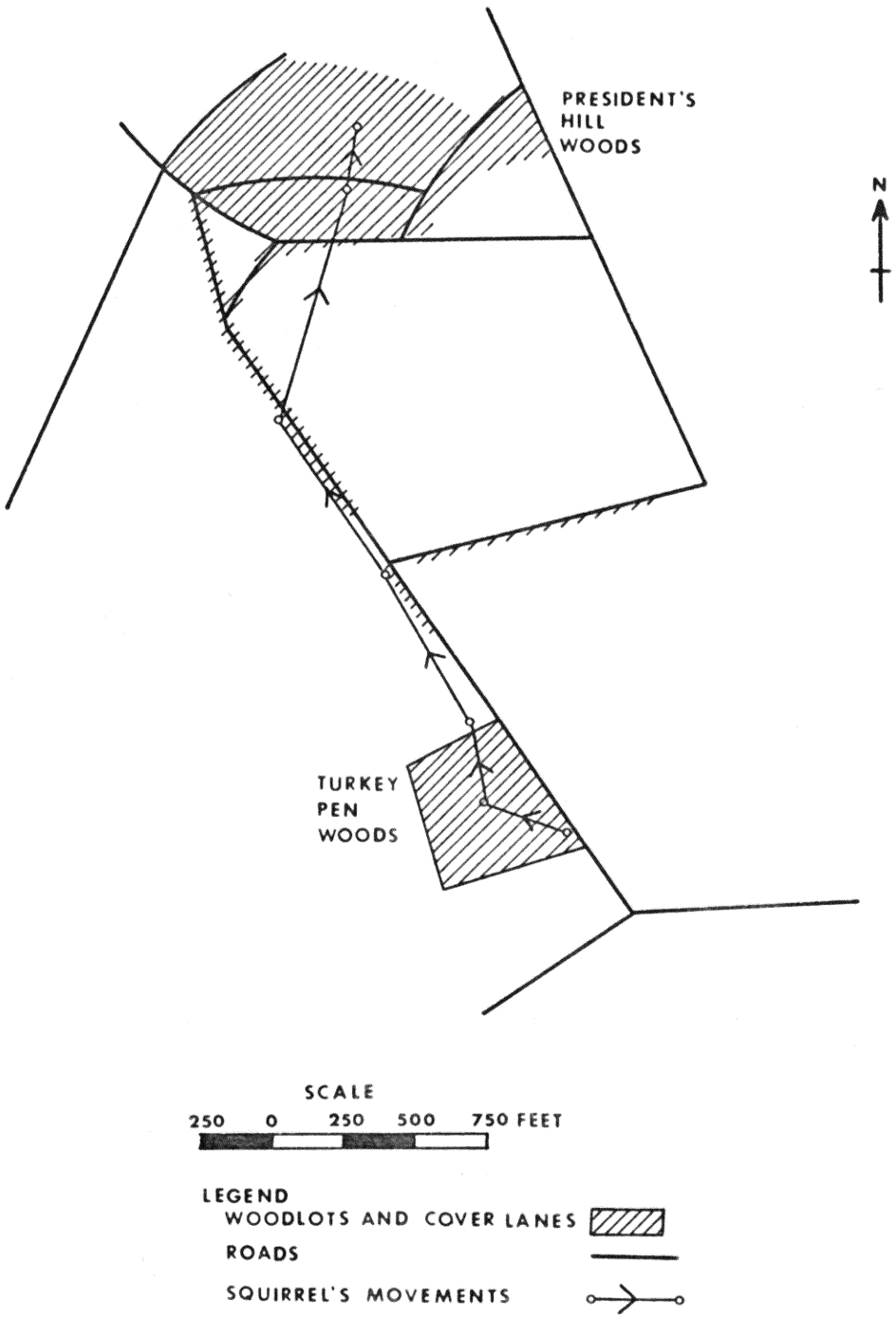

Fig. 5. Movements of a subadult male, #753-754, following release in Turkey Pen Woods at 2:00 p.m. until the squirrel reached its home area in President's Hill Woods at 6:45 p.m. on September 24, 1971.

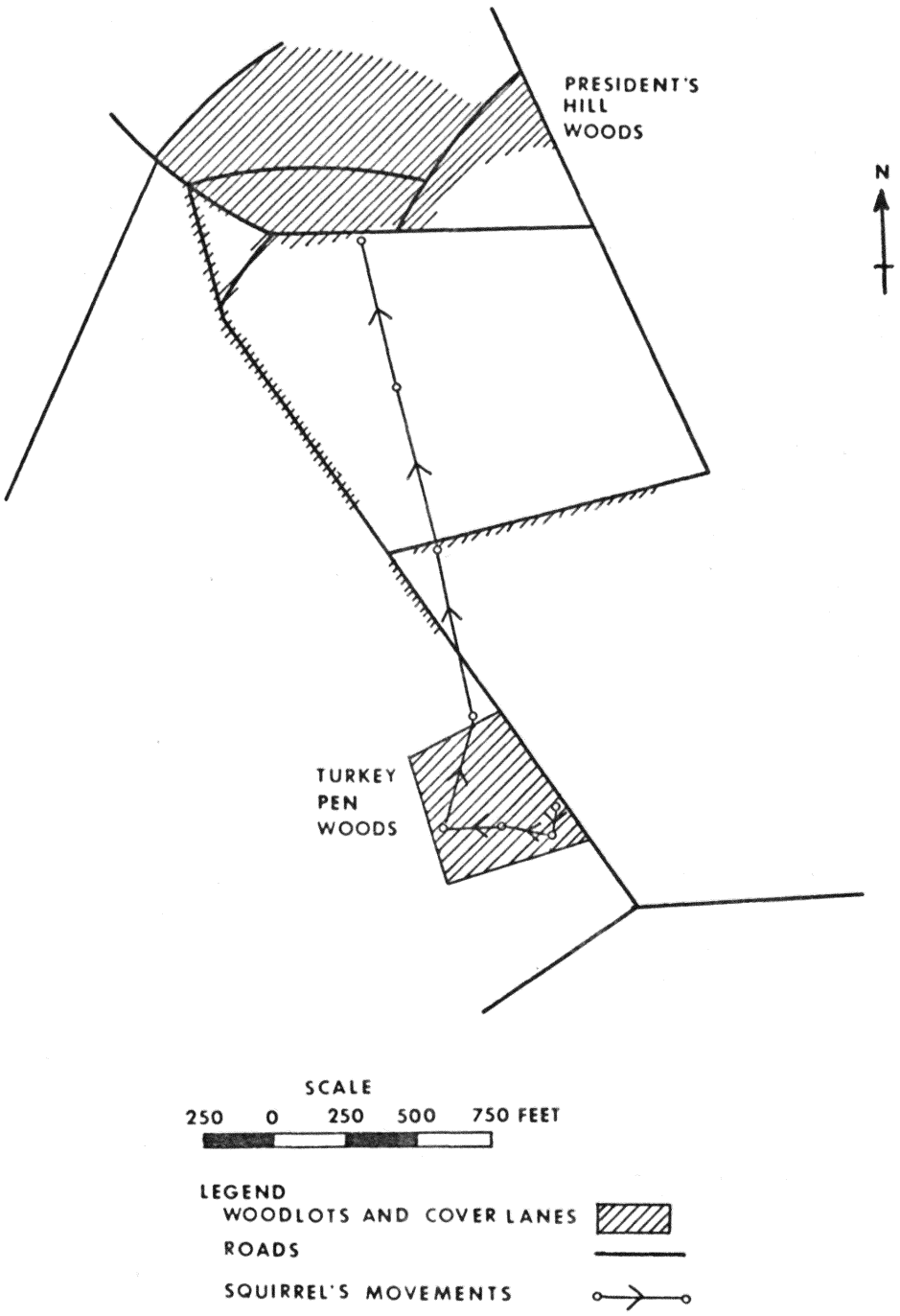

Fig. 6. Movements of a subadult male, #2151-2152, following release in Turkey Pen Woods at 4:15 p.m. until the squirrel reached its home area in President's Hill Woods at 6:15 p.m. on February 9, 1972.

to home for the other 7 squirrels that returned is not known. Table 5 presents the time after release when the squirrels that homed were known to be in the home woodlot. The 2 squirrels that took more than 22 days to home were known to be in the home woodlot 43 days and 60 days after release.

The size of the woodlots where squirrels were released, and the number of displaced squirrels known to have moved from these woodlots is shown in Table 6.

The home woodlot, President's Hill, was 18.0 acres in size. A total of 54 squirrels were removed from this woodlot: 53 were displaced and 1 died in a trap. Nine of the 53 displaced squirrels returned, and 4 of the 9 were displaced a second time, none of which were known to return. A population estimate made after the completion of this study indicated that 35 squirrels remained in President's Hill Woods.

Influence of Season of Release, Sex, and Age

Displaced gray squirrels seem more likely to home when released in the winter than in the fall (Table 7). Five (10%) of 48 squirrels released in the fall (September 24 to December 3, 1971) homed, and 4 (44%) of 9 squirrels released in the winter (January 19 to February 15, 1972) homed. Three of the individuals released in the fall and 1 released in the winter were known to have moved from the release site to non-home woodlots.

Six (23%) of 26 displaced males and 3 (10%) of 31 displaced females homed (Table 7). Of the squirrels that homed in the fall,

Table 5. Relationship between the number of displaced gray squirrels which returned home and time to return home; VPI College Farm, Sept. 1971-Feb. 1972*

Time to return home (days)**	Squirrels which homed- No.	% of total	Accumulative (%)
1 or less	2	22	22
2 to 7	3	33	56
8 to 14	1	11	67
15 to 21	1	11	78
22 or more	2	22	100

* The shortest distances of return using available cover are 3250 feet and 3624 feet.

** Time to return home was the number of days between the time of release and the time that the squirrel was known to be in the home woodlot.

Table 6. Relationship between the size of the woodlot where released and the number of displaced gray squirrels leaving (including homing and moving to woodlots other than home) the woodlot where released; VPI College Farm, Sept. 1971-Feb. 1972

Woodlot where released[#]	Size of woodlot (acres)	Number released	Squirrels leaving woodlot where released- Homing No.	Homing %	Other than home No.	Other than home %	Total No.	Total %
Turkey Pen	4.8	18	7	39	1*	6	8	45
North Crumpacker	7.9	2	0	0	0	0	0	0
Trailer Camp	15.8	1	0	0	0	0	0	0
Crumpacker	17.9	16	0	0	3**	19	3	19
Price's Fork (east of U.S. 460 bypass)	31.2	16	2	13	0	0	2	13
Center	46.5	4	0	0	0	0	0	0

[#] Home woodlot was President's Hill Woods

* Moved to Trailer Camp Woods.

** One squirrel moved to Turkey Pen Woods and 2 squirrels moved to Trailer Camp Woods.

Table 7. The influence of season of release, sex, and age on movements between woodlots of displaced gray squirrels: VPI College Farm, Sept. 1971-Feb. 1972

Age Class	Squirrels released				Squirrels homing				Squirrels moving from release site to non-home woodlots			
	Male	Female	Total No.	%	Male	Female	Total No.	%	Male	Female	Total No.	%
Fall Displacement												
Adult	7	12*	19	39	1	3	4	80	1	1	2	67
Subadult	10	10	20	42	1	0	1	20	0	1	1	33
Juvenile	3	6	9	19	0	0	0	0	0	0	0	0
Total: No.:	20	28	48		2	3	5		1	2	3	
%:	42	58		100	40	60		100	33	67		100
Winter Displacement												
Adult	1**	2**	3	33	0	0	0	0	0	0	0	0
Subadult	4	0	4	45	3	0	3	75	1	0	1	100

Table 7. (Continued)

Age Class	Squirrels released				Squirrels homing				Squirrels moving from release site to non-home woodlot			
	Male	Female	Total No.	%	Male	Female	Total No.	%	Male	Female	Total No.	%
Juvenile	1	1	2	22	1	0	1	25	0	0	0	0
Total: No.:	6	3	9		4	0	4		1	0	1	
%:	67	33		100	100	0		100	100	0		100

* This includes one squirrel which was displaced a second time after homing. It was not known to home a second time.

** This squirrel was displaced a second time after homing in the fall. It was not known to home a second time.

*** Both of these squirrels had previously been displaced in the fall and both homed. Neither were known to home a second time.

2 (40%) were males and 3 (60%) were females. The 4 squirrels that homed in the winter were all males.

Four (18%) of 22 displaced adults, 4 (17%) of 24 displaced subadults, and 1 (9%) of 11 displaced juveniles homed (Table 7). Of the 5 squirrels that homed in the fall, 4 (80%) were adults, 1 (20%) was subadult, and none was juvenile. Of the 4 squirrels that homed in the winter, 3 (75%) were subadults, 1 (25%) was juvenile, and none were adults.

Influence of Random Wandering and Cover Lanes

Table 8 seems to indicate that the movements of displaced squirrels (including those that homed) between woodlots is more than random wandering. An exception to this statement might be the one squirrel that moved from Turkey Pen Woods to Trailer Camp Woods.

The two squirrels that were followed (1 by radiotracking) from the release site back to the home woodlot (Figs. 5 and 6) did not appear to be randomly wandering. The squirrels did not follow the available cover lanes exclusively; they both crossed a large treeless area despite the fact that they could have followed a line of trees. The route followed was more direct than if they had followed the available cover lanes exclusively.

Table 8. Observed between-woodlot movements of displaced gray squirrels and the probability that such movements resulted from random wandering; VPI College Farm, Sept. 1971-Feb. 1972

Woodlot involved		Distance	Squirrels	Squirrels which moved between woodlots		
Moved from	Moved to	(ft.)	released	No.	Observed (%)	Maximum[#] Expected (%)
Turkey Pen	President's Hill*	3250	18	6	33	7
Price's Fork	President's Hill*	3624	16	2	13	4
Turkey Pen	Trailer Camp	2874	18	1	6	11
Crumpacker	Turkey Pen	3000	16	1	6	3
Crumpacker	Trailer Camp	4374	16	2	13	5

[#] The maximum probability that a squirrel would move to another woodlot by random movements was calculated by dividing by 360, the angle subtended by the other woodlot at the point of release (See Chapman 1971:688).

* President's Hill was the home woodlot.

Behavior of Displaced Squirrels

Initial Movements

Each squirrel, when released, ran to and climbed a nearby tree. The tree chosen was not necessarily the nearest one, but was always one of the larger trees available.

Fig. 5 and Fig. 6 show the movements of the two displaced squirrels which were followed home the same day that they were released.

Figures 7, 8, and 9 show the movements of 3 displaced squirrels during the first day of displacement. These squirrels later returned home.

Figure 10 shows the movements of a displaced squirrel during the first day of displacement. This squirrel later moved from Crumpacker Woods to Turkey Pen Woods.

Figure 11 shows the movements of a displaced squirred during the first day of displacement. This individual was known to remain in the woodlot where released for at least 14 days.

Figures 12 and 13 show the route taken by 2 displaced squirrels during the first day of displacement; the fate of these individuals is unknown.

Social Encounters With Resident Squirrels

Proportionally more females (61%) than males (39%) were observed in agonistic social encounters (Table 9). Observations of agonistic behavior indicates that female squirrels had more agonistic social

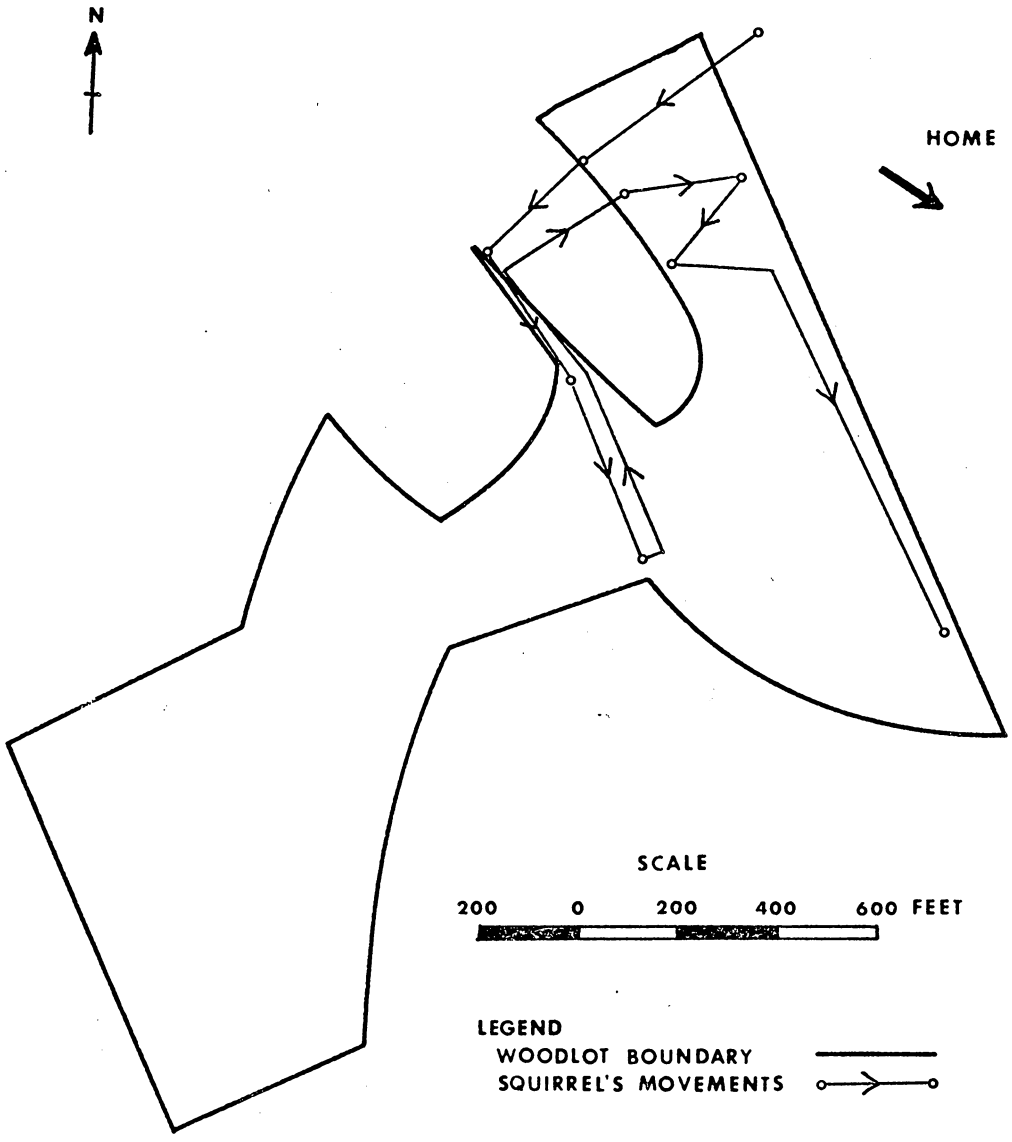

Fig. 7. Movements of a subadult male, #2145-2146, following release in Price's Fork Woods at 1:15 p.m. until 5:40 p.m. January 19, 1972. Squirrel was found dead, apparently killed by a car, in President's Hill Woods on January 24, 1972.

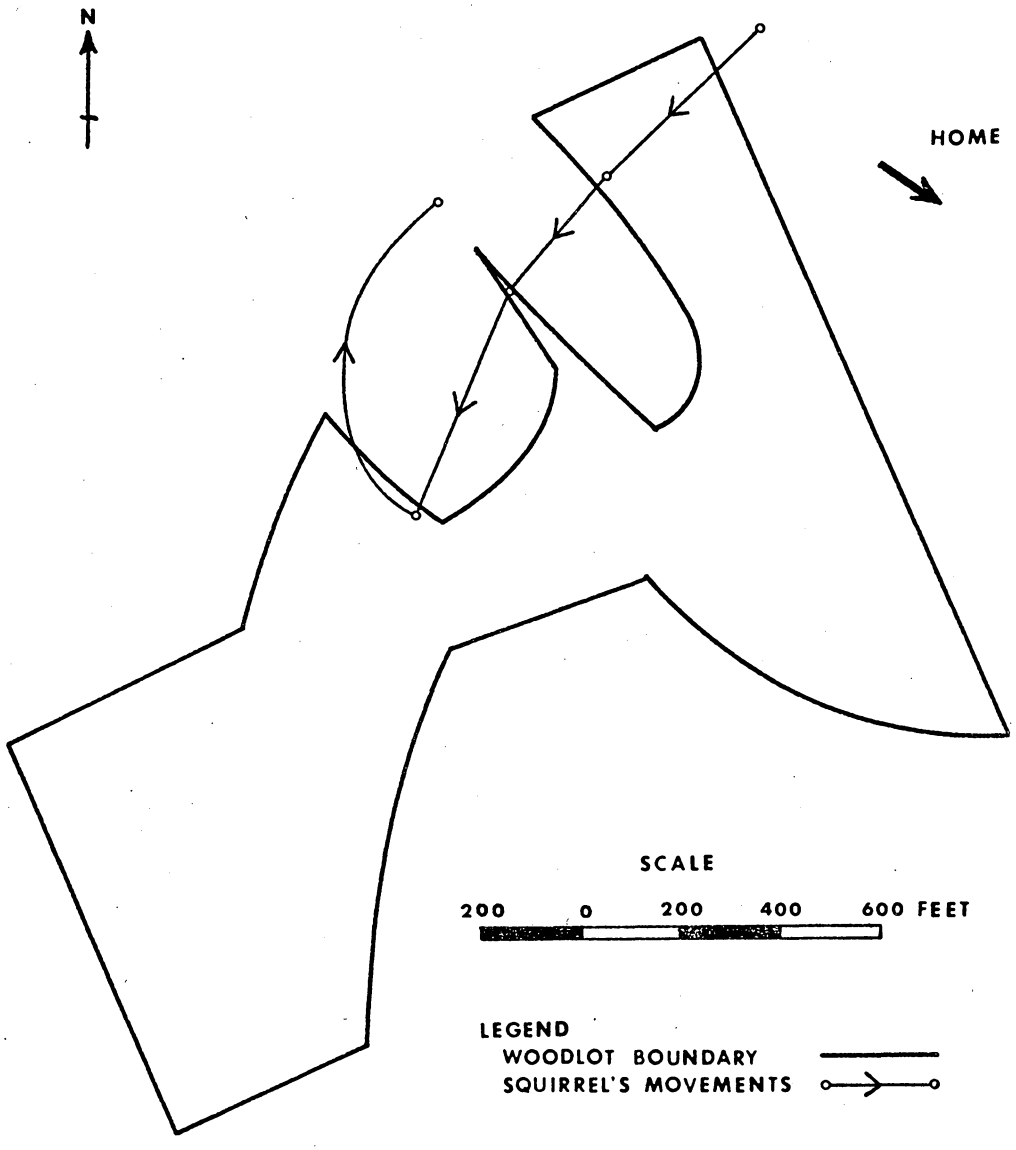

Fig. 8. Movements of a subadult male, #2147-2148, following release in Price's Fork Woods at 3:55 p.m. until 5:30 p.m. on January 27, 1972. The squirrel was last sighted in Price's Fork Woods on February 11, 1972, and was trapped in President's Hill Woods on March 10, 1972.

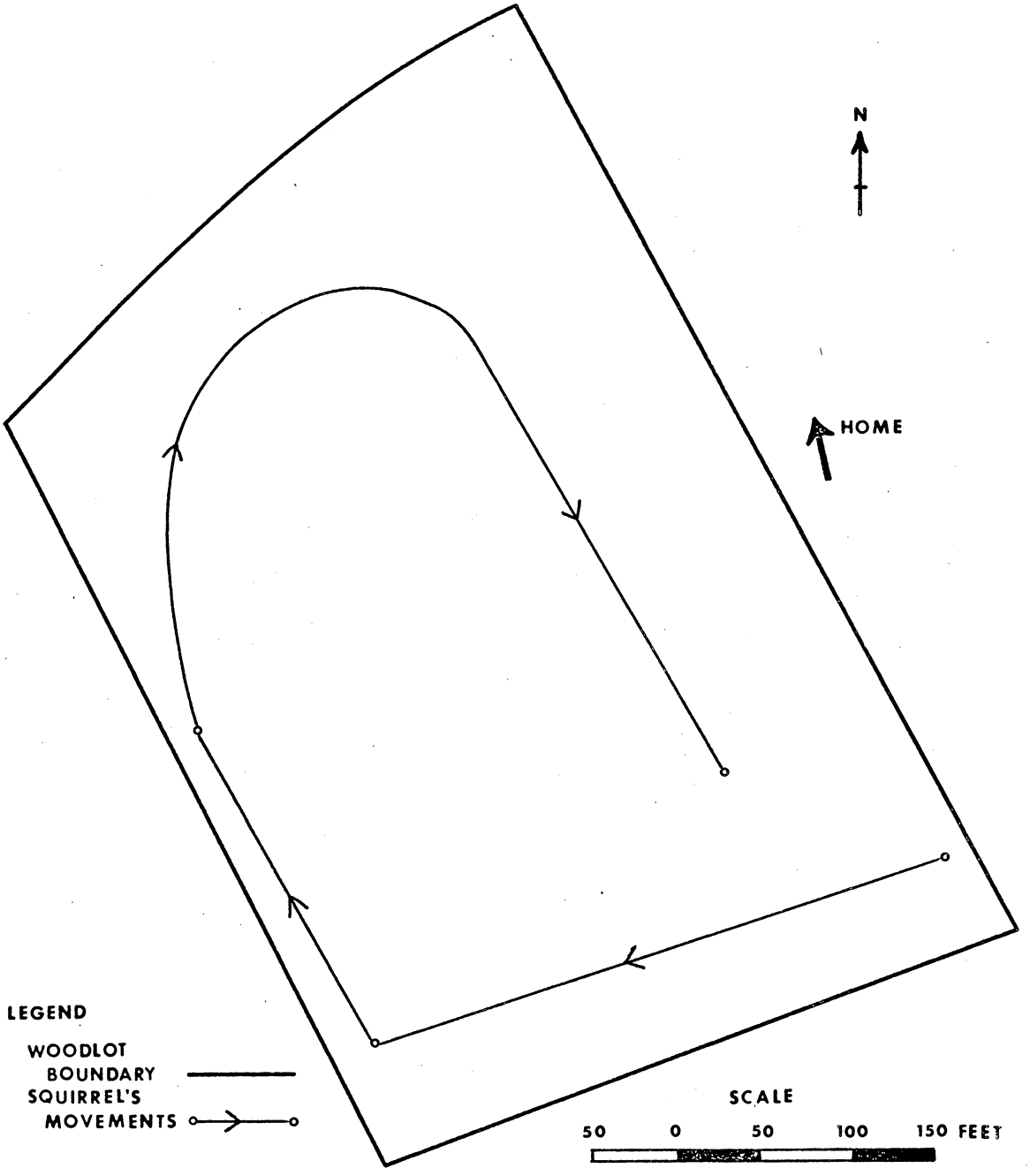

Fig. 9. Movements of a juvenile male, #2153-2154, in Turkey Pen Woods following release at 4:05 p.m. until 6:40 p.m. on February 11, 1972. The squirrel was last sighted in Turkey Pen Woods on March 1, 1972, and was trapped in President's Hill Woods on April 11, 1972.

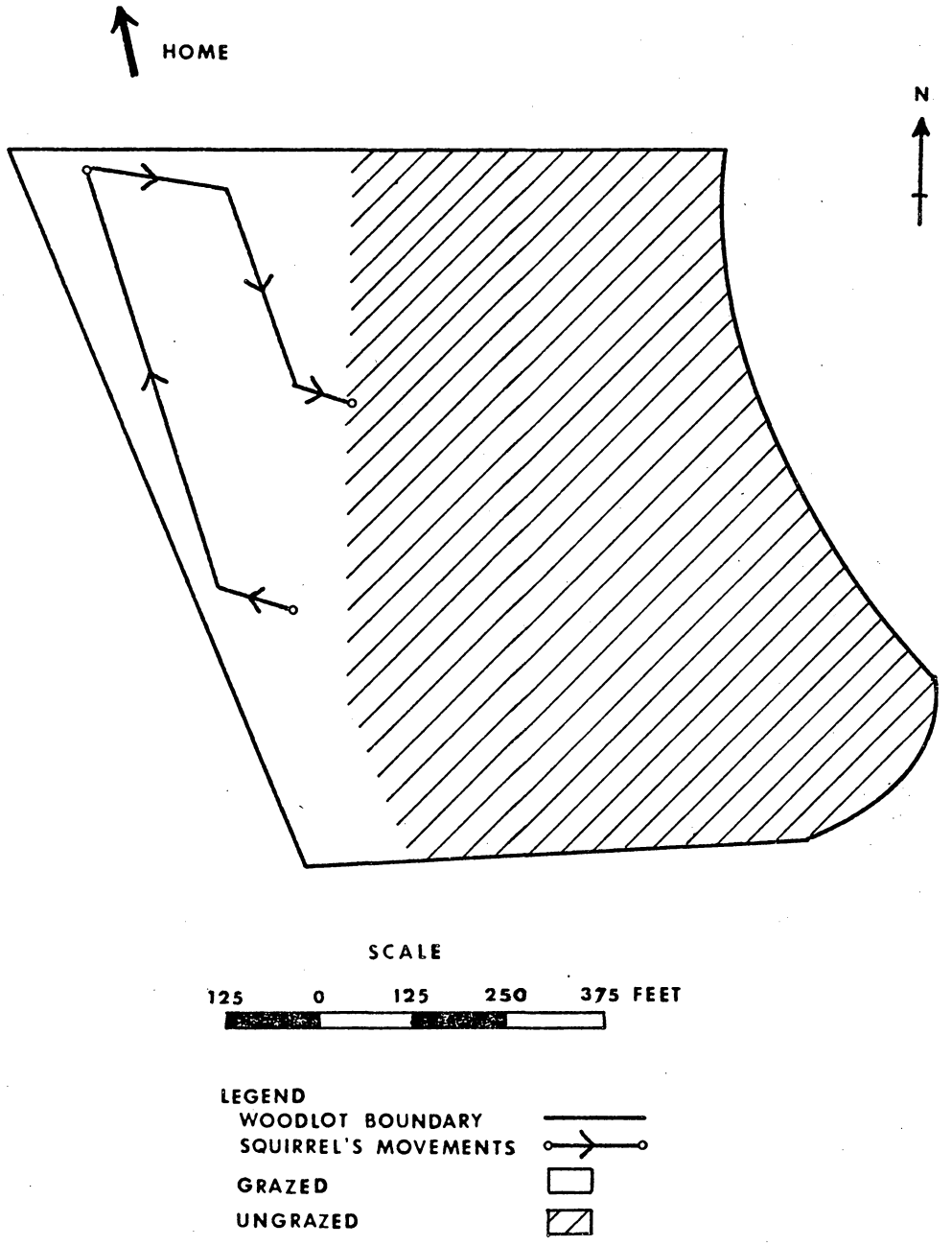

Fig. 10. Movements of a subadult male, #2149-2150, in Crumpacker Woods following release at 4:10 p.m. until squirrel disappeared into ungrazed woods at 4:40 p.m. on January 31, 1972. Squirrel moved to Turkey Pen Woods by February 12, 1972.

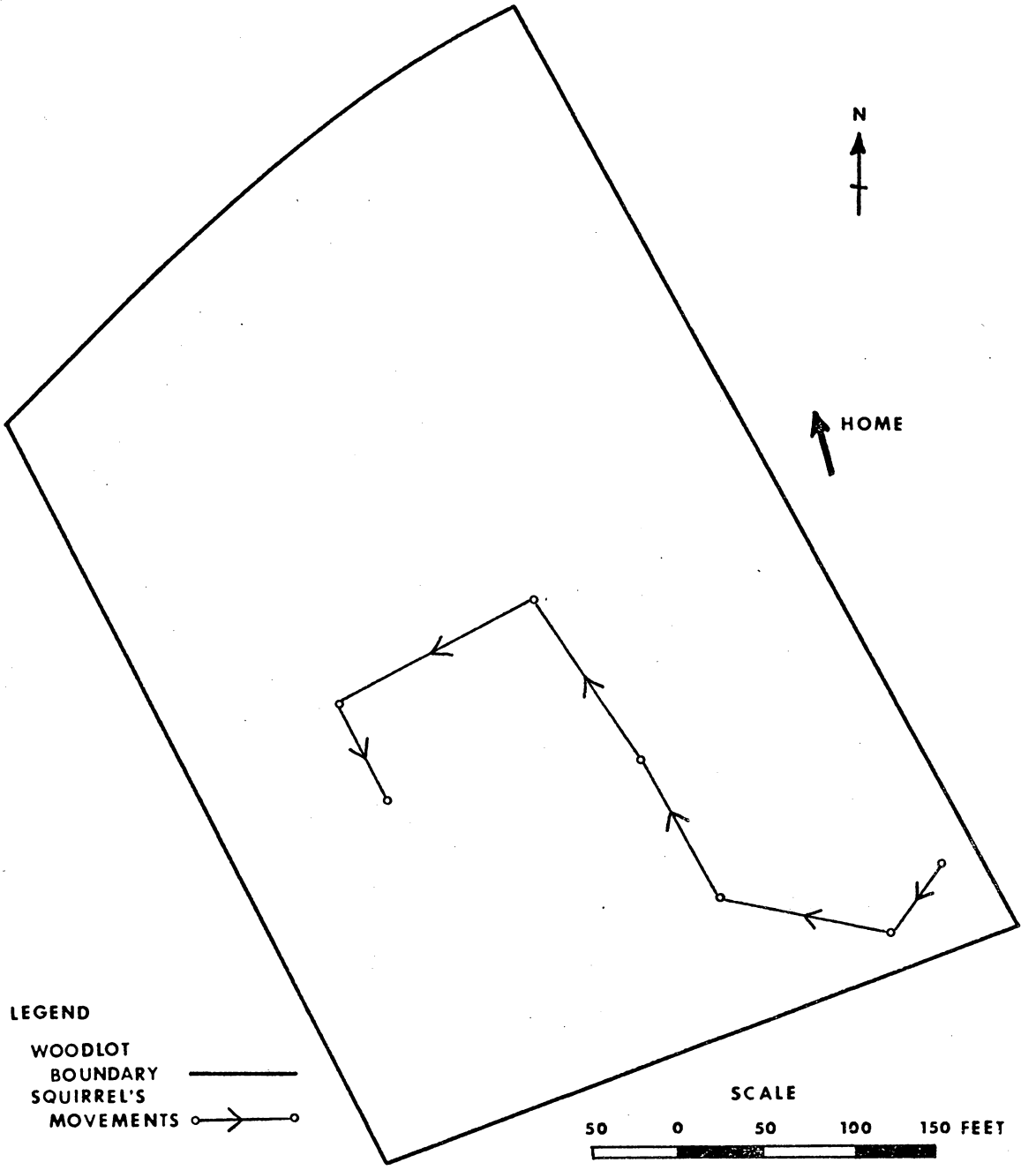

Fig. 11. Movements of a juvenile female, #2155-2156, in Turkey Pen Woods following release at 4:10 p.m. until 6:15 p.m. on February 15, 1972. Squirrel was last sighted in Turkey Pen Woods on February 29, 1972.

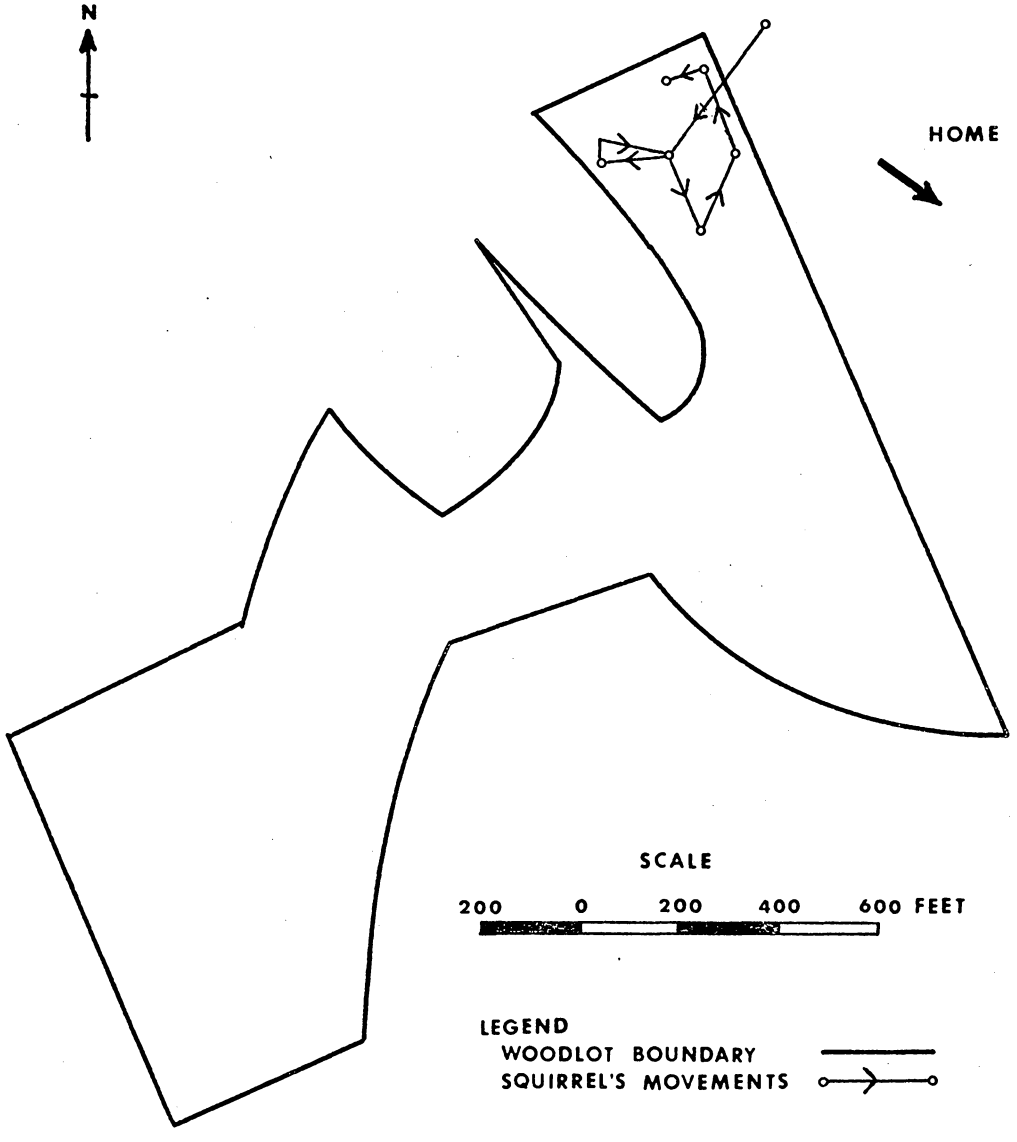

Fig. 12. Movements of an adult female, #2139-2140, following release in Price's Fork Woods at 2:40 p.m. until 5:30 p.m. on January 24, 1972. Squirrel was observed in woodlot for 4 days following release.

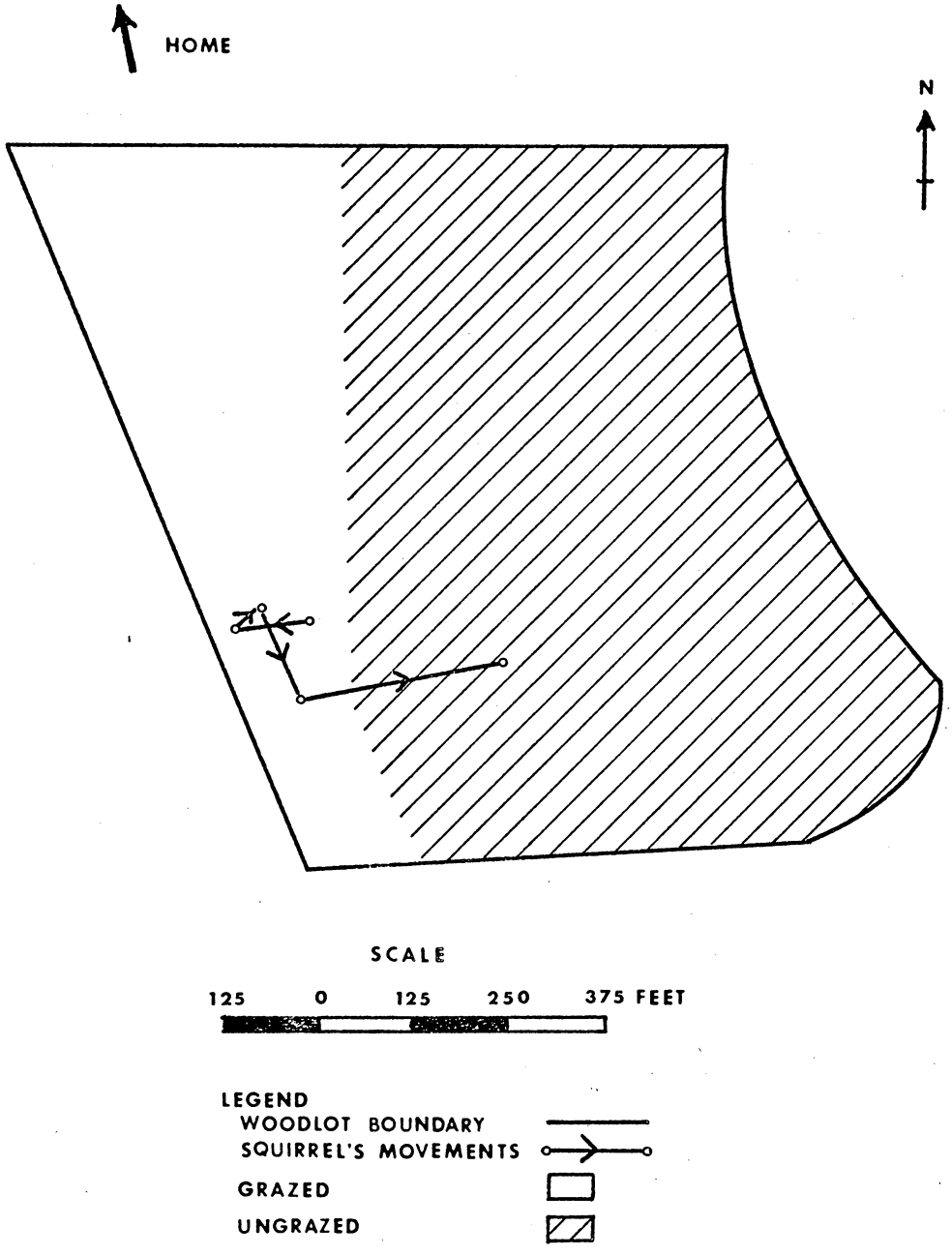

Fig. 13. Movements of an adult male, #2114-2115, in Crumpacker Woods following release at 5:10 p.m. until squirrel disappeared into ungrazed woods at 5:20 p.m. on February 4, 1972. Squirrel was never seen again.

Table 9. The influence of sex on the agonistic behavior of displaced gray squirrels; VPI College Farm, Sept. 1971-Feb. 1972

Sex of squirrel	Squirrels observed[#]	Squirrels observed in agonistic encounters No.	%	No.	No. per squirrel	No. Won	% Won
Male	13	5	39	12	2.4	2	17
Female	18	11	61	42	3.8	15	36
Total/ave.	31	16	52	54	3.4	17	32

[#] This includes any displaced squirrel observed at least once at the release site after being displaced.

encounters per squirrel than did the males. Female squirrels also won a greater proportion of agonistic social encounters (36%) than did the males (17%).

The proportion of juveniles (71%) that engaged in agonistic social encounters was greater than either the proportion of adults (42%) or subadults (50%) (Table 10). In addition, juveniles averaged more (4.8) agonistic social encounters than either adults (3.4) or subadults (2.2). However, the three age classes seemed to win similar percentages of these encounters.

Eleven of 27 displaced squirrels observed less than 30 days following release took part in 25 agonistic social encounters and won 4 (16%) (Table 11). Eleven of 22 displaced squirrels observed more than 30 days after release took part in 29 encounters and won 13 (45%).

Of the 11 displaced squirrels observed in agonistic encounters less than 30 days after release, 4 (36%) were males, and 7 (74%) were females. The 4 males had 8 encounters, and won 1 (12%). The 7 females had 17 encounters and won 3 (18%).

Of the 11 displaced squirrels observed in agonistic encounters more than 30 days after release, 3 (27%) were males, and 8 (73%) were females. The 3 males had 3 encounters and won 1 (33%). The 8 females had 26 encounters and won 12 (46%).

Of the 11 displaced squirrels observed in agonistic encounters less than 30 days after displacement, 4 (36%) were adults, 4 (36%) were subadults and 3 (28%) were juveniles. The 4 adults had 7

Table 10. The influence of age on the agonistic behavior of displaced gray squirrels; VPI College Farm, Sept. 1971-Feb. 1972

Age Class	Squirrels observed[#]	Squirrels observed in agonistic encounters No.	%	Agonistic encounters No.	No. per squirrel	No. Won	% Won
Adult	12	5	42	17	3.4	6	35
Subadult	12	6	50	13	2.2	4	31
Juvenile	7	5	71	24	4.8	7	29
Total/ave.	31	11	52	54	3.4	17	32

[#] This includes any displaced squirrel observed at least once at the release site after being displaced.

Table 11. The influence of time, sex and age on the agonistic behavior of displaced gray squirrels; VPI College Farm, Sept. 1971-Feb. 1972

Age Class	All squirrels observed				Squirrels observed in agonistic social encounters				Agonistic social encounters observed						
									Male		Female		Total		
	Male	Female	Total No.	%	Male	Female	Total No.	%	Won	Lost	Won	Lost	No.	% Won	% Lost
Less Than 30 Days After Displacement															
Adult	1	7	8	30	0	4	4	36	0	0	2	5	7	29	71
Subadult	6	6	12	44	3	1	4	36	1	4	0	1	6	17	83
Juvenile	3	4	7	26	1	2	3	28	0	3	1	8	12	8	92
Total: No.:	10	17	27		4	7	11		1	7	3	14	25		
%:	37	63		100	36	64		100	12	88	18	82		16	84
More Than 30 Days After Displacement															
Adult	2	6	8	36	1	4	5	46	1	0	3	7	11	36	64
Subadult	3	6	9	41	1	2	3	27	0	1	3	2	6	50	50
Juvenile	2	3	5	23	1	2	3	27	0	1	6	5	12		
Total: No.:	7	15	22		3	8	11		1	2	12	14	29		
%:	32	68		100	27	73		100	33	67	46	54		45	55

encounters and won 2 (29%); the 4 subadults had 6 encounters and won 1 (17%); and the 3 juveniles had 12 encounters and won 1 (8%).

Of the 11 displaced squirrels observed in agonistic encounters more than 30 days after release, 5 (46%) were adults, 3 (27%) were subadults, and 3 (27%) were juveniles. The 5 adults had 11 encounters and won 4 (36%); the 3 subadults had 6 encounters and won 3 (50%); and the 3 juveniles had 12 encounters and won 6 (50%).

Of the 27 displaced squirrels observed between January 1 and February 29, 1972, 6 were observed in sexual encounters (Table 12). Two (33%) of the 6 squirrels were males, and 4 (67%) were females. Two (33%) of the 6 squirrels were adults, 3 (50%) were subadults, and 1 (17%) was a juvenile.

DISCUSSION

Squirrels Which Remained Where Released

A total of 23 (44%) of the 53 displaced squirrels stayed in the woodlot where they were released, including 21 of the 23 which were known to be in the woodlot for more than 50 days following release. Wilson (1967:23) reported that 5 (10.9%) of the 46 squirrels which he displaced remained in the woodlot where they were released. One possible explanation of the difference between the present study and Wilson's was the difference in available food between the two study years. The fall of 1971 produced an excellent mast crop in southwest Virginia. Mast was seen on the ground for most of the winter. Perhaps if a squirrel found enough food in the woods where it was displaced, the motivation to either try to find home or to move to another woodlot would not be as great as it would be if food were scarce. The mast crop in 1970, the year preceding the present study, was very poor. This may have reduced the squirrel populations in the experimental woodlots thereby reducing social pressure and making den sites available to the squirrels which were released in these woodlots. This combination of poor mast crop followed by a good mast crop may account, at least in part, for the success of many displaced squirrels in establishing themselves in the alien woodlots.

Other studies involving displacement indicate that displaced squirrels usually don't stay where they are released. Only 1 of 16 gray squirrels released by Flyger (1955:387-8) remained in the woodlot

where released, and only 3 of 58 fox squirrels displaced by Johnson (1957:45-47) were known to have established residence at the release site.

Homing

In the present study, 9 (17%) of the 53 individual gray squirrels displaced, demonstrated the ability to home. This was a lower proportion than was reported in other homing experiments using gray squirrels. Wilson (1967:21) displaced 46 squirrels, 14 (30.4%) of which returned; Shipley (1941:124-141) reported that 16 (55.2%) of the 29 gray squirrels that were displaced returned home; and Hungerford and Wilder (1941:460) reported that 6 (40.0%) of 15 displaced gray squirrels returned.

Possibly the homing ability of gray squirrels is not the same even among genetically related individuals, since the present experiment, as well as Wilson's and Shipley's was done using squirrels from the same woodlots. Matthews (1968:55) found that different stocks of pigeons had different homing abilities, and this may be true for gray squirrels.

If homing ability was genetically based, at least as great a proportion of squirrels should have homed in the present study as homed in Wilson's study. Wilson tested for homing ability by removing 33 squirrels from President's Hill Woods, 13 of which returned (Wilson 1967:22). If homing ability was genetically determined, and if there were no other factors selecting against it, a greater porportion of the squirrels on President's Hill should have possessed homing ability after Wilson's study than before it. Either homing

ability for the gray squirrels on President's Hill is not genetically determined, or it has been selected against during the time between Wilson's study and the present study.

Another indication that homing is not genetically determined is the failure of any of the 4 squirrels that homed and were displaced a second time in another woodlot, to return again. One of these 4 squirrels was known to have become a resident of the woodlot where it was released the second time. None of these squirrels was displaced a distance greater than gray squirrels have been known to home in previous experiments.

Effect of Displacement Distance

Rather than demonstrating an inverse relationship between homing and distance of displacement as Wilson (1967:31) found, Table 4 seems to indicate a cut off point of about 3,600 feet, beyond which no squirrel was known to have home. Gray squirrels have homed from much greater distances: 11,700 ft. (Wilson 1967:32), 14,800 ft. (Hungerford and Wilder 1941:460), and 17,140 ft. (Shipley 1941:141).

A possible explanation of homing in the present study could be that the squirrels that homed had previously been in the woodlots where they were displaced. The direct route taken by the two squirrels which were followed (Figs. 5 and 6) indicates that they knew where they were going. Both Turkey Pen Woods and Price's Fork Woods, were the woodlots nearest to President's Hill. Mosby (1969:66) reported that there was movement of squirrels between the experimental woodlots; out of 812 squirrels tagged between 1947 and 1966, there were 45

(5.5%) records of between-woods movements with an average distance of movement of 2,449 ft. Johnson (1957:14) and Goodrum (1940:25) report gray squirrels moving up to 5 miles from where they were first captured. On the other hand, Flyger (1960:368) found no evidence that any squirrel ever crossed the one-third mile that separated the two woodlots in his study area.

Fox squirrels have been known to move over one mile from their den trees while foraging (Allen 1943:141; Johnson 1957:15), and a flying squirrel homed over a distance of at least a mile (McCabe 1947:404).

In homing experiments with some other small mammals, an inverse relationship between displacement distance and homing success has been indicated: western harvest mice (Fisler 1966:55); white-footed mice (Murie 1963:338); and meadow voles (Robinson and Falls 1965:188). Chapman (1971:686) found a distinct break-off point of 540 feet, beyond which no brush rabbits were known to home.

Effect of the Size of the Woodlot Where Displaced

Table 6 indicates that displaced squirrels are more likely to leave a smaller woodlot than a large one. However, Table 2 gives no clear indication that displaced squirrels are more likely to remain in a large woodlot than a smaller woodlot. The differences between the number of squirrels which were observed to remain in the three woodlots which had the largest number of displaced squirrels (Turkey Pen, Crumpacker, and Price's Fork) could be due to the size and composition of the woodlots, since a larger woodlot, other factors

being equal, would be expected to support more squirrels. Turkey Pen Woods was both the smallest and, being grazed and relatively flat, the easiest in which to observe squirrels; the entire woodlot could be seen from one spot. Crumpacker Woods was ungrazed in about two-thirds of its area, and the understory in this ungrazed area made visibility difficult. Price's Fork Woods was the largest of these three woodlots and its topography consisted of rolling hills which decreased the range of observation.

Effect of the Season of Displacement, Sex and Age

When taken together, Tables 3 and 7 indicate that displaced squirrels are more likely to remain in the woodlots where released when displaced in the fall, and are more likely to home or to move from the woodlots where released when displaced in winter. This may be explained by the availability of food. In the fall, when food is in abundance, squirrels may have a tendency to stay where released. As the winter progresses and food becomes scarce, the displaced squirrels may move either in an attempt to return to their home woodlot where they may have a better chance finding food since they are more familiar with the area, or they may just move in any direction to look for food.

Wilson (1967:39-41) and Shipley (1941:129-141) who both had a greater proportion of squirrels home than the present experiment, displaced squirrels during the winter and spring (January 14 thru December 14 thru March 16, respectively). Allen (1943:141) and Sharp (1959:386) also believe that squirrels are more likely to

to wander from their home areas in the late winter in search of food.

Another phenomenon which may have influenced this experiment is the so called fall shuffle or fall dispersal when squirrels have been known to leave their home areas. This dispersal has been documented for gray squirrels by Sharp (1959:383) and Cordes (1965: 25-27), and for fox squirrels by Allen (1943:152) and Johnson (1957: 9). Flyger (1960:369) doubted if gray squirrels traveled very far during the fall while Cordes (1965:25-27) reported gray squirrels moving up to 2 miles. Barkalow (1970:489) calculated an average annual dispersal rate of 14.5% for gray squirrels. Perhaps a greater proportion of displaced squirrels remained in the woodlots where they were released when released in the fall because they would have left their home woodlot anyway, and the displacement of squirrels was merely aiding the dispersal.

The biological reasons for dispersal or emmigration are: (1) to extend or restock the range, (2) to promote a limited interchange of genes, and (3) to provide relief from overpopulation (Wynne-Edwards 1962:480). The most common explanation used for the dispersal of squirrels is food shortage and overpopulation (Johnson 1957:5). The most recent theory of dispersal is given by Flyger (1969:75). He believes that during the late summer and early fall, when squirrels are burying nuts for use during the winter, if they don't find enough nuts in their home area, they move elsewhere until they find an adequate supply and remain there. This may help explain

why so many of the squirrels which were displaced in the fall, stayed where they were released since the mast crop was excellent.

Another explanation of the greater proportion of the squirrels homing in the winter than in the fall could be that the population level on President's Hill was lower after more than 40 squirrels had been removed. The squirrels may have been motivated to return to an area when the population pressure was less in the area.

Tables 3 and 7 indicate that males had a greater tendency to home than females, while females had a greater tendency to remain where displaced than males. Hungerford and Wilder (1941:460) and Wilson (1967:23) both reported that more males homed than females. Similar results were reported for cotton mice (Giffo 1961:257), while no significant difference in homing ability between sexes was noted for either chipmunks (Layne 1957:520) or California voles (Fisler 1967:261). All the females which homed in the present study were adult. Both of the females that homed in Wilson's study (Wilson 1967:32) were also adult; one was pregnant and one was lactating. Wilson believed that a maternal instinct may have motivated these females to home, and the same may have been true for the present study, although it was not determined if the homing females were pregnant, and none was lactating when released. Matthews (1968:56) found that pigeons homed best when they were incubating or feeding young.

All the females that homed, did so in the fall. Of the 3 females released in the winter, 2 had previously homed in the fall.

This may indicate, as was mentioned earlier in this section, that homing ability is not genetically determined. It is doubtful, however, that any conclusions can be drawn, since 28 females were released in the fall, and only 3 were released in the winter. Of the 3 females released in the winter, the fate after release was unknown for 2 of them, and these 2 had previously homed in the fall.

Another explanation of the superior homing success of males is that they are known to travel more and over greater areas than females. This was reported for gray squirrels by Mosby (1969:66) and by Cordes (1965:40-41) and for fox squirrels by Allen (1943:142).

A greater proportion of the females were observed to take part in agonistic social encounters, (Table 9) and each female had more encounters per individual than the males. This may indicate that displaced males avoid social encounters, which may have attributed to their greater homing performance. The males also lost proportionally more agonistic social encounters than females, which may have motivated them to home. Since males have been found to be more dominant than females (Pack 1966:26-30), it may have been easier for a female to assume a subordinate role in an alien woodlot than a male. Flyger (1955:384) described a displaced female feeding with resident squirrels without hostility. He believed that the female had assumed a low rank.

All squirrels won proportionally more agonistic encounters after they had remained in the woodlot where released for at least 30 days (Table 11). Both males and females won similar proportions of their

agonistic encounters (12% vs. 18%) less than 30 days after release. It is difficult to draw conclusions about the proportion of agonistic encounters won by males and by females more than 30 days following release since only 3 males were observed in 3 agonistic encounters. It appears, however, that displaced squirrels become more successful in their agonistic encounters the longer they remain in the woodlot where released.

Although only six displaced squirrels were observed in sexual encounters (Table 12), more females were observed than males. If participating in sexual activity is a measure of establishing residence, this may indicate that displaced females are more likely to establish residence where released than are males.

Table 7 indicates that juveniles are less likely to home than either adults or subadults, and Table 3 indicates that juveniles are more likely to remain in the woodlot where released than either adults or subadults. Wilson (1967:23) had no juveniles home.

The one squirrel that established residence where released in the winter was a juvenile female (Table 3). No juvenile homed in the fall, and one juvenile, a male, homed in the winter (Table 7). This seems to agree with the trends that juveniles are more likely to establish residence than either adults or subadults, that males are more likely to home than females, that females are more likely to establish residence than males, and that displaced squirrels are more likely to home when released in the winter and establish residence where released when released in the fall. Although less juveniles (11) were released in this study than either adults (22) or subadults

(24), proportionally more juveniles (8 of 11 or 73%) could be accounted for than either adults (13 of 22 or 60%) or subadults 14 of 24 or 58%).

A greater proportion of juveniles were observed in agonistic social encounters (Table 10), and each juvenile observed in agonistic encounters averaged more encounters per individual than did the other age groups. All age classes seemed to win proportionally more agonistic encounters more than 30 days after release (Table 11). Subadults and especially juveniles won proportionally more agonistic encounters more than 30 days after release. Adults did not seem to increase their proportion of wins as much as the other 2 age classes. Since social rank is believed to increase with age (Pack 1966:30), it would be expected that all squirrels, and perhaps, especially younger squirrels, would become more successful in agonistic encounters as time passed.

Juveniles trapped in President's Hill Woods were probably born there and had never been in any of the other woodlots since the young are believed to stay with their mothers for six months (Cordes 1965:35), while adults and subadults may have been born in other woodlots and immigrated to President's Hill, or have visited other woodlots while foraging (all squirrels which homed were displaced in the two woodlots nearest to President's Hill). Cordes (1965:25) found that young squirrels dispersed between the ages of 8 to 11 months, which would mean that juveniles (less than 6 months of age) would not have participated in a dispersal.

The greater proportion of juveniles observed in agonistic social encounters may indicate that they were making an attempt to establish residence. Since the proportion of agonistic social encounters won by juveniles was similar to the proportion won by adults and by subadults more than 30 days after release, the juveniles may have been winning more encounters in the alien woodlot than they would have in their home woodlot.

Effect of Random Wandering and Cover Lanes

Table 8 indicates that the movements of displaced squirrels between woodlots is more than random wandering except for movements between Turkey Pen Woods and Trailer Camp Woods. Cover lanes which partly connect all the woodlots used in this study probably influenced the direction a squirrel took, and the route it followed when it traveled between woodlots, which was indicated by the two squirrels which were followed home (Figs. 5 and 6). The higher proportion of squirrels which traveled from Turkey Pen Woods and from Price's Fork Woods to President's Hill Woods indicates the influence of homing. This is not true for the squirrels which traveled from Crumpacker Woods to Trailer Camp Woods.

Other writers have varying opinions about how small mammals home. Fisler (1966:57) believed that homing in the western harvest mouse was accomplished by non-random movements over known terrain; Robinson and Falls (1965:188) believed the same to be true for meadow mice. Giffo (1961:257) hypothesized that his homing cotton mice wandered randomly until they reached familiar territory, and

then they homed by prior knowledge of the area. Matthews (1968:67-68) reported that random search models have been fitted to many bird homing experiments as well as for salmon (fish). He also concluded that the extremely long homing flights of certain birds (over 3,000 miles) seems to dismiss random wandering.

The two squirrels which were followed home (Figs. 5 and 6) did not utilize cover lanes as much as they could have. They both cut across unwooded areas where they would have been much more subject to predation. Both of these squirrels followed a more direct route home, especially more direct to the area of President's Hill Woods where they were captured. This observer concludes that gray squirrels appear to use cover lanes to some extent when traveling between woodlots.

The use of travel lanes between woods has been reported for gray squirrels by Uhlig (1956:73) and by Johnson (1957:15) and for fox squirrels by Allen (1943:141-144). Doebel (1967:61) reported that a gray squirrel moved .25 mile over grazed land between woodlots. Chapman (1971:686) found brush rabbits to use cover while attempting to home, and Giffo (1961:257) found that cotton mice released in areas without cover had less homing success than those released where cover was available.

Time to Return Home

The two squirrels which were followed home (Figs. 5 and 6) both returned the same day that they were released. Both of these squirrels (both subadult males) gave this writer the impression that they knew where they were going. Unfortunately the actual time to return home

as well as the routes taken are unknown for the other 7 squirrels which homed. Table 5 shows that most of the squirrels (78%) which were known to home did so in less than 21 days and more than 50% returned in less than one week. The two squirrels which returned after 21 days were both males, a subadult and a juvenile. Both were known to have remained where displaced at least 14 days (15 days and 19 days respectively), and to have lost all agonistic social encounters. Both of these squirrels were released in the winter (January 27, 1972 and February 11, 1972) when food was getting scarce.

Wilson (1967:32) reported that the majority of homing squirrels returned in 2 to 4 days with none known to home in more than two weeks. One adult male returned 11,700 feet in 3 days or less. Hungerford and Wilder (1941:460) report a displaced gray squirrel returned 14,800 feet in less than 4 weeks. Chapman (1971:686) found a direct correlation between homing time and distance of displacement for brush rabbits, while Fisler (1962:357) and Robinson and Falls (1965:188) reported respectively that displaced California voles and meadow mice homed in about the same time if they home at all, no matter what the distance of displacement was.

Table 11 indicates that the squirrels which remained where released for more than 30 days were winning a greater proportion of their agonistic encounters than in the first 30 days following release. Perhaps the longer a squirrel remains in an alien woodlot, the more successful it becomes in its social relations, and the less likely it is to return home. This is also indicated by the displaced

squirrels observed in sexual encounters. No displaced squirrel was observed in a sexual encounter before it had remained in the woodlot where displaced at least 28 days.

Movements of Displaced Squirrels

With the exceptions of the two squirrels which were followed home (Figs. 5 and 6), the movements of displaced squirrels immediately following release were erratic (Figs. 7 thru 13), but almost entirely confined to the area of the woodlot where released. Since 3 of these squirrels (Figs. 7, 8, and 9) returned home at a later date, perhaps some squirrels required a period of time to orient themselves, or perhaps these three squirrels randomly wandered home, following the cover lanes between woodlots. Chapman (1971:697) reported that there was no indication that initial movements of brush rabbits influenced their homing success. Rabbits that waited for several days before homing did not exhibit random wandering prior to homing (Chapman 1971: 691). Orientation toward home has been reported for snowshoe hares (Keith and Waring 1956:57) and for some birds (Matthews 1968:93).

The 10 squirrels which were followed on the day of release, were released between 1:15 p.m. (EST) and 5.25 p.m. (EST). The initial reaction of all squirrels was shelter-seeking. They remained hidden in a tree from 5 minutes to 2.5 hours except for one squirrel which disappeared and was never seen again. The squirrel which disappeared was released at 5:25 p.m. and the squirrel which stayed hidden for only 5 minutes was released at 5:10 p.m. The other 8 squirrels were released prior to 4:30 p.m. and remained hidden from

30 minutes to 2.5 hours with a mean time of 79 minutes. The 2 squirrels released after 5:00 p.m. may have been motivated to leave their hiding place and search for shelter for the night before the ones that were released earlier. Shelter seeking was reported as an initial reaction for other displaced animals: brush rabbits (Chapman 1971:686), California voles, and western harvest mice (Fisler 1967:261), and old-field mice (Gentry 1964:276). Wilson (1967:28-29) noticed that displaced immature gray squirrels displayed faster escape movements than adults. The adults would smell the bole of a tree before climbing it. This difference was not evident in the present experiment.

On the day of release, the displaced squirrels were seen to be active when there were no other squirrels in sight, but on following days the displaced squirrels that were seen in the woodlots where displaced seemed to syncronize their activities with the resident squirrels.

Fate of Other Squirrels

One squirrel which was displaced in Price's Fork Woods was found wandering near some buildings about 300 ft. NNW of point of release. The animal was apparently in shock as evidenced by its sluggish movements. It was chased into a small building and died during an attempt to recapture it.

Twenty other squirrels (including three which had homed once before) either were never seen again after release or were seen less than the 14 days necessary to designate them residents of the woods

where they were released. The fate of these squirrels is unknown. It is possible that these squirrels simply were not seen by the observer, or that they moved out of the study area. Another possibility is predation. Dogs and cats were often seen in the study areas and a large hawk, believed to be a red tailed hawk (Buteo jamaiceusis), was also seen during November and December.

SUMMARY

Twenty-three (43%) of 53 displaced gray squirrels became residents of the woodlots where released.

No relationship was found between the number of squirrels which remained in the woodlot where released and the size of this woodlot.

It appeared that displaced squirrels released in the fall were more likely to establish residence at the release site than those released in the winter.

Seven (27%) of 26 displaced male squirrels and 16 (52%) of 31 displaced female squirrels established residence where released.

Eight (36%) of 22 displaced adult squirrels, 6 (33%) of 24 displaced subadult squirrels, and 7 (64%) of 11 displaced juvenile squirrels established residence where released.

Nine (17%) of 53 displaced gray squirrels homed. Four squirrels were displaced a second time after homing and none were known to home again.

No displaced squirrel was known to have homed more than 3,624 feet.

Six (67%) of the 9 squirrels that homed, returned in less than 14 days.

Displaced squirrels seem to leave smaller woodlots.

Displaced squirrels seem more likely to return when displaced in the wirter (44%) than in the fall (10%).

Six (23%) of 26 displaced males and 3 (10%) of 31 displaced females homed.

Four (18%) of 22 displaced adults, 4 (17%) of 24 displaced subadults, and 1 (9%) of 11 displaced juveniles homed.

Movements of displaced squirrels (including homing) between woodlots seems to involve more than random wandering.

The 2 squirrels followed home did not use available cover exclusively. They took a more direct route, crossing open areas.

Upon release, displaced squirrels ran up a large nearby tree.

Five (39%) of the 13 males, and 11 (61%) of the 18 females which were observed in the woodlots where released, engaged in agonistic social encounters. Females won proportionally more agonistic social encounters (36%) than males (17%).

Proportionally more juveniles (71%) engaged in agonistic encounters than either adults (42%) or subadults (50%).

Displaced squirrels won proportionally more agonistic encounters, more than 30 days after release (45%) than before 30 days (16%).

Two displaced male squirrels and 4 displaced female squirrels were observed in sexual encounters. Two were adults, 3 subadults, and 1 a juvenile.

Statistical testing was not applied to the data of this study because the fate of 20 of the 57 displaced squirrels (including 4 squirrels that were displaced a second time after homing) could not be determined. The validity of statistical tests performed on data with this variability would be doubtful.

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Appendix Table I. Summary of data obtained from 57 displacements of gray squirrels from President's Hill Woods to other woodlots; VPI College Farm, Sept. 1971-April 1972.

Tag Number	Sex	Age	Date of original capture and release	woodlot where released	Date when known to be in home area	Date last seen in woodlot where released
754-755	Male	Subadult	Sept. 24	a	Sept. 24	
769-770	Male	Subadult	Sept. 30	b		
771-772	Male	Subadult	Oct. 1	b		
773-774	Male	Subadult	Oct. 1	b		
775-776	Female	Subadult	Oct. 6	b		
777-778	Female	Juvenile	Oct. 8	a		Oct. 28
781-782	Male	Adult	Oct. 12	a		*
783-784	Male	Subadult	Oct. 15	a		
785-786	Female	Juvenile	Oct. 15	a		Mar. 3
787-788	Female	Adult	Oct. 15	a		Mar. 4
767-768	Female	Juvenile	Oct. 18	a		Feb. 12
789-790	Female	Subadult	Oct. 18	c		Oct. 27
791-792	Male	Subadult	Oct. 19	d		Jan. 9
793-794	Female	Juvenile	Oct. 19	d		Oct. 22
796-797	Female	Subadult	Oct. 19	c		Feb. 1
797-798	Male	Juvenile	Oct. 21	e		
800	Female	Adult	Oct. 21	c		Feb. 16
590-591	Male	Adult	Oct. 25	c		Feb. 1
2067-2068	Female	Adult	Oct. 27	c		Mar. 1
2101-2103	Female	Juvenile	Oct. 28	a		Feb. 28
761-762	Female	Adult	Nov. 1	e		
2104-2105	Female	Adult	Nov. 1	e		Nov. 9**
2106-2107	Female	Adult	Nov. 3	c		Mar. 1
2108-2109	Female	Subadult	Nov. 4	e		Feb. 25
2110-2111	Male	Subadult	Nov. 4	e		

Appendix Table I. (Continued)

Tag Number	Sex	Age	Date of original capture and release	Woodlot where released	Date when known to be in home area	Date last seen in woodlot where released
2112-2113	Female	Subadult	Nov. 5	e		
2041-2042	Female	Adult	Nov. 8	a	Nov. 12	
2114-2118	Male	Adult	Nov. 8	a	Nov. 11	
2119-2120	Male	Adult	Nov. 9	e		
2051-2052	Male	Adult	Nov. 9	e		Feb. 28
2121-2122	Female	Subadult	Nov. 10	e		Feb. 10
2057-2058	Female	Adult	Nov. 10	e		Feb. 28
2123-2124	Female	Subadult	Nov. 10	c		Feb. 16
2125-2126	Male	Subadult	Nov. 12	a		Feb. 25
2127-2128	Male	Juvenile	Nov. 16	c		Mar. 1
2129-2130	Male	Juvenile	Nov. 17	c		Jan. 29
2059-2060	Female	Adult	Nov. 17	a	Dec. 5	Nov. 18
756-757	Male	Subadult	Nov. 19	c		
765-766	Male	Subadult	Nov. 19	e		Feb. 28
2131-2132	Female	Subadult	Dec. 1	c		***
2133-2134	Male	Adult	Dec. 1	c		
2041-2042	Female	Adult	Dec. 2	e		Feb. 25
2032-2033#	Female	Adult	Dec. 2	c		
759-760	Female	Subadult	Dec. 2	e		****
2135-2137	Female	Juvenile	Dec. 2	e		
2139-2140	Female	Adult	Dec. 2	a	Dec. 13	
2141-2142	Female	Subadult	Dec. 2	a		Feb. 25
2143-2144	Male	Adult	Dec. 3	a		
2145-2146	Male	Subadult	Jan. 19	c	Jan. 24	Jan. 20
2139-2140#	Female	Adult	Jan. 24	c		Jan. 28
2147-2148	Male	Subadult	Jan. 27	c	Mar. 10	Feb. 11
2149-2150	Male	Subadult	Jan. 31	e		##

Appendix Table I. (Continued)

Tag Number	Sex	Age	Date of original capture and release	Woodlot where released	Date when known to be in home area	Date last seen in woodlot where released
2114-2118#	Male	Adult	Feb. 4	e		
2059-2060#	Female	Adult	Feb. 7	f		
2151-2152	Male	Subadult	Feb. 9	a	Feb. 9	
2153-2154	Male	Juvenile	Feb. 11	a	April 11	Mar. 1
2155-2156	Female	Juvenile	Feb. 15	a		Feb. 29

[a] Turkey Pen Woods

[b] Center Woods

[c] Price's Fork Woods

[d] North Crumpacker Woods

[e] Trailer Camp Woods

* Found dead in a trap in Trailer Camp Woods 11-12-71.

** Observed in Trailer Camp Woods 12-16-71 and 2-23-72.

*** Died, apparently from shock, 300 feet NNW of release point on 12-2-71.

**** Observed in Trailer Camp Woods 12-29-71 and 2-23-72.

Second displacement.

Observed in Turkey Pen Woods from 2-12-72 through 3-3-72.

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THE BEHAVIOR OF DISPLACED GRAY SQUIRRELS

by

John Thomas Brady

(ABSTRACT)

From September 24, 1971, to February 15, 1972, 53 gray squirrels were trapped, marked, and displaced up to 7,120 feet from their home woodlot to other woodlots on the College Farm of Virginia Polytechnic Institute and State University. Twenty-three (43%) remained where released. Nine (17%) homed. Four were displaced a second time; none returned. No squirrel homed more than 3,624 feet. More females (52%) established residence than males (27%). More juveniles (64%) established residence than either adults (36%) or subadults (33%). Most squirrels that homed (67%) took less than 14 days. More squirrels homed when released in the winter (44%) than in the fall. More males (23%) homed than females (10%). More adults (18%) and subadults (17%) homed than juveniles (9%). Movements between woodlots seemed more than random wandering. Traveling squirrels did not use cover lanes exclusively. More females (61%) were observed in more and won more (36%) agonistic encounters than males were observed in (39%) and won (17%). More juveniles (71%) engaged in agonistic encounters than either adults (42%) or subadults (50%). More agonistic encounters (45%) were won more than 30 days after release than before 30 days (16%). One adult male, 1 adult female, 1 subadult male, 2 subadult females, and 1 juvenile female were observed in sexual encounters where released.