Homing in and Ecology of the Southern Flying Squirrel Glaucomys volans in Southeastern Virginia

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ABSTRACT: A population of the southern flying squirrel *Glaucomys volans* in southeastern Virginia was examined for its homing ability. Nest boxes were used to capture the experimental animals and to evaluate homing. Squirrels returned home with high frequency from distances up to 1000 m. There was a significant association between low temperature and large aggregations of huddling squirrels in nest boxes. Holes used as feeding stations were never converted to primary nests.

INTRODUCTION

The southern flying squirrel *Glaucomys volans* is a small (60-80 g) arboreal nocturnal sciurid distributed in the U.S. E of a line from S-central Texas to central Wisconsin (Hall, 1981). Northern populations have been investigated in Michigan (Muul, 1968, 1969, 1970), Pennsylvania (Sollberger, 1940, 1943) and New York (Madden, 1974), and southern populations in Arkansas (Heidt, 1977), Louisiana (Goertz *et al.*, 1975), Florida (Moore, 1947), and Virginia (Sonenshine *et al.*, 1979). Only the former and latter studies have investigated the ecology of *G. volans*, and none has sought, specifically, to evaluate their homing abilities. The objectives of this study, conducted in southeastern Virginia from September 1978 through March 1981, were to examine the homing capabilities, use of nest boxes, and winter ecology of southern flying squirrels.

STUDY AREA AND METHODS

The study area was located in a 247-ha mixed deciduous-coniferous forest in Southampton Co., 14.5 km NW of Windsor, Virginia. Two parallel traplines, 250 m x 25 m, were established on high ground at the edge of Seacock Swamp (Fig. 1); 30 nest boxes were later hung at 10-25 m intervals along these same lines. Forest structure was determined by using a circular quadrat method to sample vegetation (Lindsey, 1958). Thirty quadrats of 100 m^2 (5.65 m radius) were sampled, using the nest box trees as center points. Within each quadrat, woody vegetation was placed into tree [≥ 10 cm diam at breast height (dbh)], sapling (2.5-9.9 cm dbh) or seedling (<2.5 cm dbh) categories. Estimates were made of the percent of shrub and herbaceous plant cover on each quadrat.

The relative densities of forest overstory trees were 31.6% oaks (*Quercus nigra*, *Q. falcata*, *Q. michauxii*, *Q. laurifolia* and *Q. velutina* in decreasing order), 18.2% sweetgum (*Liquidambar styraciflua*), 13.7% yellow poplar (*Liriodendron tulipifera*), 8.3% red maple (*Acer rubrum*), 7.5% loblolly pine (*Pinus taeda*), 6.1% beech (*Fagus grandifolia*), 2-5% each of black gum (*Nyssa sylvatica*), red mulberry (*Morus rubra*) and hickory (*Carya glabra*), and lesser amounts of six other species of deciduous trees. The midstory consisted of smaller trees, 75% of which were red maple, sweetgum, black gum, beech and water tupelo (*Nyssa aquatica*). The understory was dominated by holly (*Ilex opaca*), flowering dogwood (*Cornus florida*) and ironwood (*Carpinus caroliniana*). Shrub and herbaceous cover values ranged from <10% to nearly 100% in quadrats dominated by Japanese honeysuckle (*Lonicera japonica*).

The 250 m by 25 m study area is typical of the 247-ha forest, except that species such as black gum and water tupelo are more abundant in the low areas nearest the Seacock Swamp, and upland species, such as oaks, sweetgum and hickory, are more numerous on drier sites. The forest is bordered by cultivated fields and roads, except on the E and SE, where it ends at the Blackwater River 1600 m from the study area (Fig. 1).

Live trapping, with Sherman traps placed on the ground, was abandoned as a means of catching squirrels for the homing experiments, because only one squirrel was caught in 528 trapping nights during 12 days in autumn 1978. By contrast, the 17.8 x 17.8 x 42.0 cm nest boxes (Sonenshine *et al.*, 1973), hung on suitably large trees 3.5-4.5 m above ground, yielded 37 flying squirrels in 90 trapping nights between the time of nest box placement on 25 January 1979 and the third check on 25 March. Each squirrel was ear-tagged with a numbered metal tag, and each was weighed and its sex and reproductive condition determined prior to release.

For the homing experiments, squirrels taken from nest boxes on the grids were placed in covered boxes and removed to predetermined release sites (Roman numerals, Fig. 1). The behavior of each released squirrel was recorded, including the immediacy of response and whether more than one squirrel used the same escape route and "flight" path through the trees, all indicators of familiarity with the release site.

RESULTS AND DISCUSSION

Homing. — Because the term "homing" is usually restricted to the ability of an animal to return to its area of familiarity after being released at a distant point, the analysis of homing ultimately requires an understanding of home range. The familiar area, or home range, of an animal, which includes its nest and places where it forages or escapes from predators, can be determined by an examination of trapping or nest-box locations, or more recently for some species, using radiotelemetry. The published trap or nest box-revealed home ranges for southern flying squirrels vary greatly, from 0.41 ha

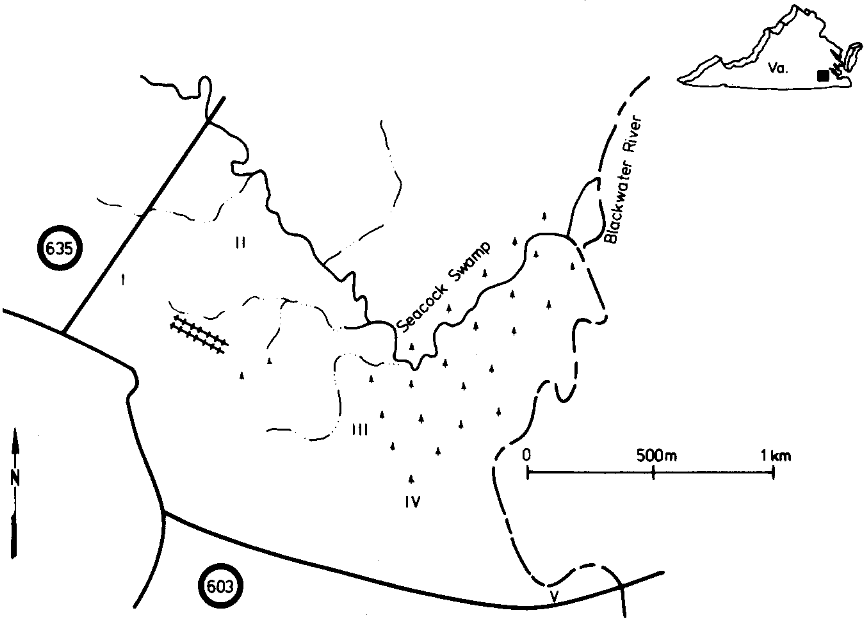

Fig 1. — Map of study area showing the location of the study grid, represented by lines with cross bars, in relation to the release sites used in the homing experiments (Roman numerals)

for females and 0.53 ha for males (Madden, 1974) to 1.6 and 2.0 ha (Schwartz and Schwartz, 1959). If these estimates are valid for our population, then all squirrels would have been released well beyond their home ranges.

However, Sonenshine *et al.* (1979), who reported instances of Virginia squirrels traveling as much as 560 m and 792 m in 1 night while moving from one study area to another, calculated the average radius of movement to be 157 ± 39.2 m for males and 103.1 ± 11.4 m for nonreproductive females. Assuming circular home ranges, these radii give home range values of ca. 7.7 ha for males and 3.3 ha for females, suggesting that Virginia flying squirrels may have larger home ranges than previously estimated. If the squirrels in our study have similarly large home ranges, they probably were familiar with most of the area up to 500 m from the study area.

Squirrels were considered to have returned home if they subsequently were captured in any nest box on the grid; this seemed valid because individual squirrels used several nest boxes scattered across the 30 stations on the grid. Of the 13 males and eight females released at distances ≤ 700 m (Table 1), the males showed a higher return success rate (11 of 13) than females (four of eight). Sexual maturity and stage in the estrous cycle seemed to affect females, because four of five subadult females returned home but none of three adult, estrous females did so. In this small sample, subadult females returned home at approximately the same rate as males, at ≤ 700 m. The two squirrels released at 1000 m returned home, but it took 18 and 25 days, respectively. None of the six squirrels returned from 1600 m, the farthest release site. Previous homing experience did not appear to give any of five male squirrels that participated in more than one homing trial an advantage over naive squirrels.

Squirrels released at ≤ 500 m, after only a few seconds for orientation, immediately glided toward a specific tree. This behavior, repeated by subsequently released squirrels, often required two or three glides to reach the target tree. By contrast, squirrels released at ≥ 700 m climbed the nearest large hardwood tree and remained there. These contrasting behaviors suggested that squirrels released at ≤ 500 m were familiar with both the terrain and the location of trees with secondary nests or feeding stations. The behavior of squirrels upon release and the high percentage of returns to the grid from ≤ 500 m distances support our contention that squirrels were familiar with most of the area up to 500 m.

We conclude that the squirrels were not homing from distances up to 500 m, but were simply travelling through familiar terrain. Beyond these distances, squirrels may have found their way home by random wandering until familiar surroundings were entered, as proposed by Griffo (1961) and Murie (1963) for other rodents. They probably also used certain landforms, such as Seacock Creek, to aid in finding the homesite. A major motivation to return to the homesite appeared to be the quality of the habitat at the release site. The habitat of the release sites at 700 m and 100 m, but not at 1600 m, was of poorer quality than what Sonenshine and Levy (1981) believe to be prime forest conditions for southern flying squirrels in Virginia.

Ecology. — Use of nest boxes. Shortly after nest boxes were erected in January 1979,

TABLE 1. — Results of homing experiments for male (M) and female (F) southern flying squirrels released at 250-1600 m distances in southeastern Virginia

Distance released	No./sex	Date released	Days to recapture
250 m	3 M, 2 F	3/16/80	2 M, 2 F in 1 day
500 m	2 M, 2 F	3/16/80	2 M, 1 F in 1 day
425 m	5 M, 2 F	1/12/81	5 M in 1, 8, 9, 11, 34 days 1 F in 9 days
700 m	3 M, 2 F	1/20/81	2 M in 1, 17 days
1000 m	2 M	1/28/81	2 M in 18, 25 days
1600 m	5 M, 1 F	2/22/81	No returns

flying squirrels began using them. Later, several boxes were occupied as early as October, usage gradually increased throughout late autumn, reached a peak during the coldest weeks, and then declined to near zero by the end of March. Few squirrels, including only one female, remained on the grid for more than 1 year, indicating a high rate of disappearance (dispersal?) from the study grid.

The number of squirrels per nest box increased toward midwinter; on very cold nights, the squirrels often huddled in two or three boxes. For example, on 5 January 1981, two boxes contained six and 11 squirrels, the latter being the largest aggregation. In order to determine if size of the aggregations was dependent on temperature, a regression analysis was performed, using the minimum daily temperature of the trapping night as the independent variable and the number of squirrels found in each box as the dependent variable. Temperatures were obtained from the nearest NOAA weather station. There was a significant ($p < .05$) relationship ($F = 13.753$, df $= 1, 68$) between size of the aggregation and cold temperature, substantiating Muul's (1969) viewpoint that flying squirrels form aggregations for the purpose of thermoregulation.

Torpor has not been reported in the literature for flying squirrels in the southern states, nor was torpor observed in this study, conducted primarily in the winter months. Instead of becoming torpid to conserve energy, the flying squirrels in our study formed progressively larger aggregations in response to low ambient temperatures, *i.e.*, individuals formed communal groups and jointly shared the cost of warming the nest.

Boxes, classified according to Muul (1968), sometimes were used differently from year to year. Overall, at one time during the study 13 boxes were used as primary nests, 14 as secondary or escape nests and 13 as feeding stations. (Three boxes were used as primary nests in all 3 years, six were used only as secondary or escape nests, nine were used only as feeding stations, and two were visited but unused.) A primary nest was used more or less continuously for winter aggregation during periods of inactivity. Nesting material was fashioned either into a cuplike depression (5-15 cm deep; $\bar{X} = 3.97$ squirrels; $N = 8$) or into a looser or deeper nest (16-20 cm deep; $\bar{X} = 5.46$ squirrels; $N = 5$). The cuplike nest did not evolve into a deeper nest.

Secondary nests, which had little or no nesting material except in those previously used as primary nests, were used only briefly during a year and were inhabited by an average of two squirrels. With two exceptions, secondary nests were used only in late autumn or early spring, *i.e.*, they tended to be abandoned in midwinter. One box was used by four squirrels as an escape nest in January 1980, and another was used in late February 1981 by a female who was probably pregnant. Five boxes were used as escape nests when the primary nest was disturbed. Escape nests differed from secondary nests by having deeper nesting material and they were always the closest box to the primary nest not used as a feeding station. Each primary nest had associated escape nests, both natural tree holes and other nest boxes. After removal from nest boxes for tagging and weighing, released squirrels would either climb and wait for the nest box to be returned, or else they would glide to an escape nest in a nearby tree. Not all squirrels disturbed from the same primary nest retreated to the same escape nest, but those that did followed the same glide path, even in cases where reaching the escape nest required several glides.

The presence of acorn and hickory nut middens indicated a nest box being used as a feeding station. No caches of food were found in any of the boxes. Of the 13 nest boxes used as feeding stations, two had prior use as secondary nests, one as an escape nest, and a fourth had been a primary nest which was occupied by wasps, and later cleaned out (by the senior author) prior to its use as a feeding station. In no other case was an old primary nest ever converted to a feeding station, nor was a feeding station ever converted into a primary nest. This suggests to us that the availability of natural tree holes, or open nest boxes, may significantly affect the density of squirrels in a forest study plot. Specifically, if feeding stations cannot be converted into primary nests (where, for example, young are born), then squirrels immigrating into an area may have difficulty establishing residency because of a scarcity of open, unused tree holes. The placement of nest boxes on a forest plot, therefore, potentially increases density by increasing available cavities for primary nests. Support for this contention that unused tree holes are needed for the establishment of new primary (maternity) nests was seen in spring of 1979, when three females used the (new) nest boxes for parturition. None was used in the following two autumn and two spring breeding periods, when estrous and pregnant females disappeared from the nest boxes well in advance of parturition, perhaps to find unused tree holes elsewhere to build their maternity nests. Because no reproductive female lived 2 years on the grid, we must discount learning as an explanation for this pattern. The situation differed in later breeding periods in that the nest boxes had a prior use; only in the 1st spring were they available to pregnant females as sites for maternity nests.

Density.—In this study, 58 tagged squirrels (37 males: 21 females) were captured 248 times from 11 February 1979 to 27 March 1981. Of these, 24 males and 10 females were considered to be transients, because they were captured <3 times. One male was caught 16 times in 3 years and one female nine times in 2 years. Resident males were captured an average of 7.09 times, and resident females 5.27 times.

Population densities were estimated using the Lincoln-Peterson Index for spring 1979, and using the Jolly (1965) estimator for the next 2 years. Peak densities were achieved in March 1979 (38.4 squirrels/ha) and in January 1980 and 1981 (36.09 and 31.49 squirrels/ha, respectively).

Reproduction.—The main differences between northern and southern populations of *Glaucomys volans* relate to the timing of the breeding seasons and to litter sizes. Two peaks of parturition are known to occur in northern populations of *G. volans* (Muul, 1969; Sollberger, 1943), one in spring (April-May) and another in late summer (August).

In southeastern Virginia, adult males were sexually active (descended testes) by late December (except 2 weeks later in January 1981), and females were coming into estrus by mid-January, based on perforate vaginae. Matings apparently occurred in mid- to late January, for young were born in late February and early March, after a 40-day gestation period. Other studies in southern states (Goertz *et al.*, 1975; Heidt, 1977; Linzey and Linzey, 1979; Sonenshine *et al.*, 1979) have reported first litters a month earlier in southern populations than in northern populations, starting in late February. One advantage of an early breeding season is that it permits young squirrels from the spring cohort to breed in the autumn, for young males may be capable of maturing by 108 days (Hatt, 1931), and young females probably breed at about the same age if conditions for body growth are favorable for the populations. By contrast, squirrels from northern populations cannot breed until the spring following their birth, when they are 8-11 months old.

The observation that populations from higher latitudes have more young per litter than populations of the species at lower latitudes (*e.g.*, Smith and McGinnis, 1968, for *Peromyscus*) appears to be true for the southern flying squirrel as well. In the spring of 1979 three litters (averaging 1.7 per litter) were found in the nest boxes. Average litter sizes for other southern populations were 2.0 in Arkansas (Heidt, 1977), 2.1 in Louisiana (Goertz *et al.*, 1975) and 2.8 in North Carolina (Brimley, 1923) and in Kentucky (Hibbard, 1935). By contrast, litters in northern populations averaged 3.0 in Pennsylvania (Sollberger, 1943), 3.3 in Illinois (Jordan, 1956) and 3.5 in Missouri (Schwartz and Schwartz, 1959). Linzey and Linzey (1979), who studied 12 wild and 12 captive-born litters from Alabama, reported a mean litter size of 3.17 (±0.36). However, autumn litters averaged 4.0 and spring litters 2.8 young. Here the relationship between geographic location and litter size has been complicated both by analysis of seasonal samples and possibly by effects of laboratory rearing.

Southern flying squirrels (1) were able to return home when displaced up to 1000 m; (2) readily used nest boxes placed in a mixed deciduous-coniferous forest; (3) used the nest boxes as primary nests, secondary or escape nests, or as feeding stations; (4) achieved estimated densities of 31-38/ha; (5) produced small litters in March and September-October, and (6) did not enter torpor on cold days but instead formed significantly larger aggregations on colder days as a means to conserve heat and energy. Southern populations of *Glaucomys volans* appear to differ in a number of parameters from northern populations, indicating that this small nocturnal sciurid is adaptable to local environmental conditions, which no doubt contributes to its widespread distribution and successful coexistence with man.

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