

The Ecology of *Glaucomys volans* (Linnaeus, 1758) in Virginia¹

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The ecology of the southern flying squirrel, *Glaucomys volans* (Linnaeus, 1758) was studied in 2 areas of central Virginia, using artificial tree shelter traps and baited live trapping. Within one year after their installation, 46.9% of the artificial shelters were used for nesting sites, 26.6% as feeding stations, and 17.2% as defecatoria; only 9.4% were without evidence of use. The animals utilized several shelters for nesting in addition to others used for food storage and defecatoria. In habitat selection, availability of bodies of fresh water was important, but the slope of the terrain was not significant. Foraging (average range 126.8 m \pm 14.8 S.E.) was not significantly related to distance from aquatic habitat. Adult males foraged substantially farther than sexually inactive females or juveniles. Most females (94.2%) became pregnant within 6—8 months after birth. Birth of young occurred in early spring, March and April, and in late summer, from August to early October. Removal rate of young squirrels from the population by mortality was 50% within 5.5 months and 67% in 7 months. Population density, estimated by the Petersen index and regression analysis of recapture frequency, varied at different seasons from 4.5 to 10.1 flying squirrels/ha at one of the localities, and from 6.2 to 13.8/ha at the other.

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1. INTRODUCTION

The southern flying squirrel ranges from Ontario and Minnesota (Stormer & Sloan, 1976) southward throughout the eastern and central United States to central Mexico. Despite its wide range and abundance, relatively little is known of the ecology of this highly secretive, nocturnal animal. Perhaps the most extensive investigations

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were those by Muul (1968, 1969, 1970, 1974), who worked with populations in Michigan and Massachusetts, near the northern limit of the range. Other ecologic studies were done by Jordan (1948), Solberger (1943), Moore (1961), Weigl (1974), Goertz *et al.* (1975) and Madden (1974, 1976). Flying squirrel activity rhythms were studied by DeCoursey (1960, 1961, 1972, and 1973) under laboratory conditions.

Recently, Bozeman *et al.* (1975) described a reservoir of epidemic typhus (*Rickettsia prowazeki* in several populations of *G. volans*). In view of the association of the flying squirrel with this important disease organism, the need for detailed information on the ecology of the flying squirrel is increased. Research on the epizootiology of this zoonosis provided an opportunity to study the ecology of the flying squirrel in a limited area, involving capture and examination of almost 400 individuals, during all seasons of a consecutive 4-year period. The results provide new findings on population regulation and habitat utilization of the flying squirrel in central Virginia.

2. MATERIALS AND METHODS

Two study areas were chosen. The Ashland Study Area (Fig. 1) in Hanover County comprised 12.8 ha of mature hardwood forest and was used from 1972 to 1976. The Lorne Study Area (Fig. 2) in Caroline County, approximately 15 miles distant, included 7.8 ha and was used from June, 1974 through April, 1975. Both areas included relatively flat uplands sloping to streams, a lake or a pond. Slopes ranged from 3° to 24° per 100 m at different sections of the 2 areas, excluding occasional steep banks beside the streams. Vegetation at the 2 areas was primarily subclimax deciduous forest, with a small tract of pine (0.9 ha) at the Lorne area; neither area had been recently lumbered. Dominant tree species on the uplands included oaks, hickory and beech; on the lower slopes and in the swamps, additional species found included ironwood, birch and gum.

The areas were sampled by two capture methods, namely 1) artificial shelter traps, and 2) baited live traps. Artificial shelter traps (Sonenshine *et al.*, 1973) were installed on trees at a height of from 3.7 to 4.3 m in a grid system at intervals of 32 m, providing a trap density of 9.9/ha (128 traps at Ashland and 77 at Lorne). Squirrels in the shelter traps were captured by sealing the aperture, opening the door and removing them separately through the screen guard with the gloved hand. The artificial shelter traps were monitored at regular intervals throughout the study period. Baited live trapping was done with Sherman traps (7.6×7.6×25.4 cm) installed on trees at the same sites as the artificial tree shelters. The traps were oriented vertically with the doors facing the ground and positioned at a height of 2.4 m elevation, the highest elevation accessible without tree climbing aids; further increase in height did not improve trap success. Ground trapping was ineffective and was not used. The live traps were baited with peanut butter and set at approximately weekly intervals during the warm months of the year, June through September. Baited live trapping (on trees) was not done during the colder months to avoid loss of animals from cold stress.

All animals captured were brought to the field laboratory for processing. Ear tags (Salt Lake City Stamp Company, Salt Lake City, Utah) were used to tag each individual. Weight, sex, estimated age (according to Solberger, 1943) and reproductive condition were recorded at each capture. In addition, blood samples ca. 0.2–0.3 ml were taken by orbital bleeding (Riley, 1960) at no less than two week intervals; nursing juveniles, pregnant or nursing females and animals showing signs of stress were not bled.

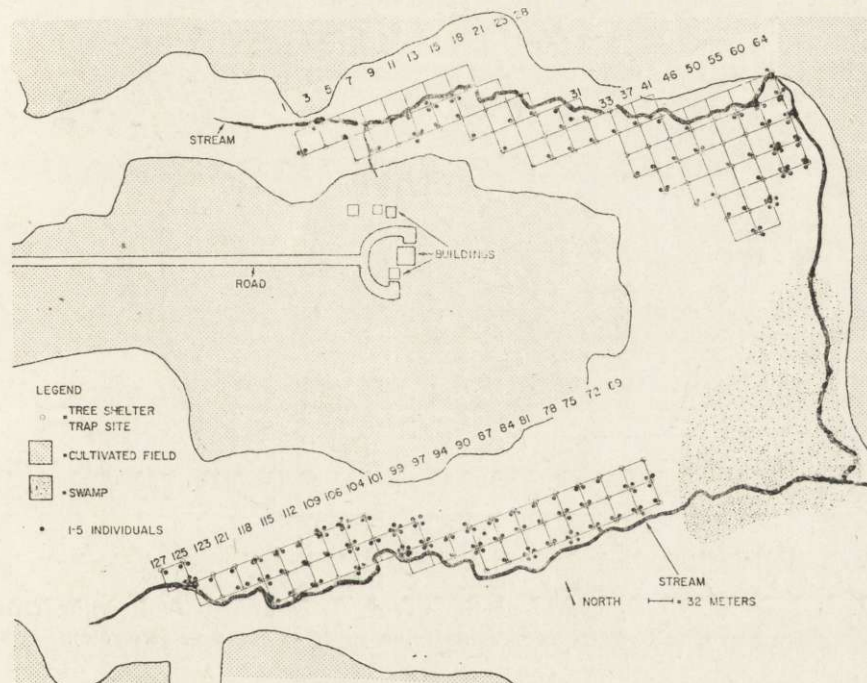


Fig. 1. Map of the trapping grid at the Ashland study area, Ashland, Virginia. Black circles represent flying squirrel captures (5/circle).

Estimates of population size were made using the Petersen index (Davis, 1963) and the regression analysis of recapture frequency (Edwards & Eberhardt, 1967). We modified Edwards and Eberhardt's technique by comparing the log of the number of individuals in each capture class (dependent variable) with individual capture frequency (independent variable). No estimates were prepared for periods when pregnancy, parturition and rearing of young might bias the results. Corrections for mortality were made, using the results of a survival study.

3. RESULTS

3.1. Shelter Trap Utilization

Flying squirrels commenced using the artificial shelter traps within a few days after installation and continued using them extensively from

October through May in each year, but only sporadically during the intervening warmer months. Over the 4-year study period, 1,111 captures were made in the 128 artificial tree shelters at Ashland, 280 at Lorne. Flying squirrel use of the shelters at the different available sites

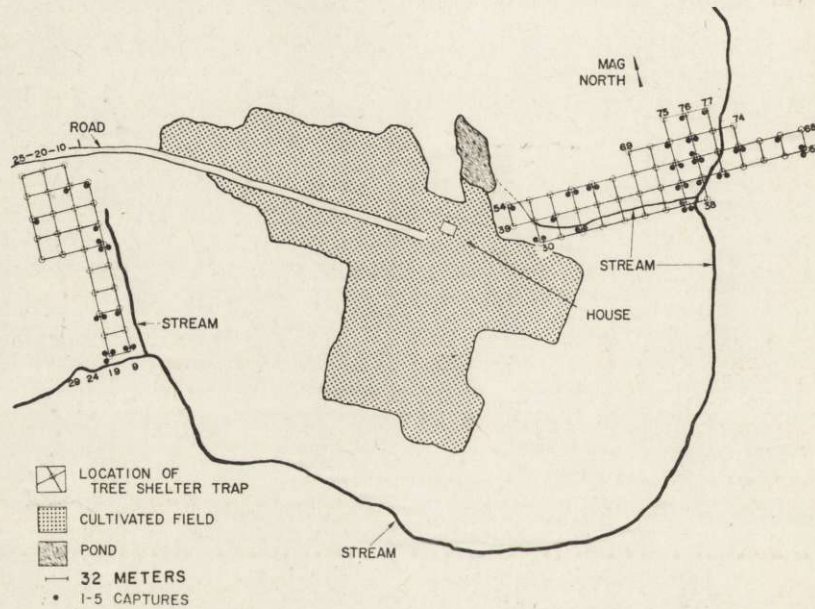


Fig. 2. Map of the trapping grid at the Lorne study area near Bowling Green, Virginia. Black circles represent flying squirrel captures (5/circle).

Table 1

Frequency of capture of flying squirrels in artificial tree shelter traps at the Ashland study area, June 1972 — April 1976.

Total No. Captures in the same shelter	No. Shelter Traps
0	27
1—5	42
6—10	20
11—15	14
16—20	8
21—25	10
26—30	6
>30	1

was selective. During the 4-year study period at Ashland, no animals were caught in 21.1% of the shelters and only 1—5 individuals were found in 35.9% other shelters. The remainder were heavily used (Table

1). Maximum usage of a single box was indicated by 36 captures, representing 24 individuals.

A distinct seasonal trend in shelter use was noted, with aggregation more frequent in winter. The number of flying squirrels simultaneously caught in a single box varied from 1 to 13. Monthly averages of aggregation size were minimal in November (2.3), maximal in January (3.5) at Ashland. A similar pattern was found over the 8-month study period at Lorne. Aggregation size declined in February prior to the spring peak of parturition. The shelter traps were rarely used during the summer months.

The 4-year observation period at Ashland revealed multipurpose use of the tree shelter system. Flying squirrel use could be distinguished from that of other species by their characteristic nests, fecal droppings, and their method of opening acorns or nuts. Approximately 90% of the shelters showed evidence of some type of use by flying squirrels within 1 year after their installation. Almost half of the tree shelters had nests in them. The large number of nests, several times the number of aggregations, suggested that the flying squirrels used more than 1 nest during the cold weather period. The winter nests were made almost entirely of cedar bark, and ranged in weight from 24.8 to 171.7 grams (average 62.9 grams); they were used either for aggregations or for a single female and her offspring. Nests were also constructed in summer (June through August) of fresh leaves and cedar bark and were lighter in weight, from 5.1 to 87.5 grams (average 30.9 grams). Other shelters were used by the flying squirrels as food caches (26.6%) or as defecatoria (17.2%).

3.2. Association with Aquatic Habitat and Terrain Characteristics

Flying squirrels tended to nest in shelters near bodies of water more frequently than elsewhere (Table 2). The distribution of captures in the tree shelters indicated a highly significant deviation from random, with a strong bias against those shelters farthest from aquatic habitat ($\chi^2=43.16$, 3 d.f., $p<0.001$ at Ashland; $\chi^2=60.58$, 3 d.f., $p<0.001$ at Lorne). However, the distribution of flying squirrel captures in baited live traps was not significantly related to distance from aquatic habitat ($\chi^2=0.30$, 3 d.f., $p<0.90$, not significant). Presumably, the foraging needs of these animals are not as affected as their sheltering requirements by the availability of aquatic habitat. Slope of the terrain was also considered; several different categories of terrain slope were present, ranging from 6° or less to as much as 24°. However, no clearly defined relationship was found in this case; more captures than expected were

found in areas with the least slope and with the greatest slope, while fewer than expected were found in areas with intermediate slope. The influence of terrain slope, therefore, is not regarded as an important factor influencing flying squirrel distribution.

Table 2

Summary of flying squirrel occurrence in relation to aquatic habitat at two study areas in Virginia.

Distance, m	Ashland				Lorne		
	No. locations	% of total	No. animals in: tree live shelters traps		No. locations	% of total	No. animals in tree shelters
<32	56	43.8	492	147	36	46.7	151
>32, <64	42	32.8	375	104	23	29.9	115
>64, <96	24	18.8	111	71	11	14.3	7
>96, <128	6	4.7	50	15	7	9.1	7
	128	—	1028	337	77	—	280

3.3. Foraging activity

Foraging range of individuals was determined by comparing consecutive captures in baited live traps. The mean range was $126.8 \text{ m} \pm 14.8 \text{ m}$ ($N=23$). The analysis was repeated using the individual's last known nesting site as the point of origin between successive captures in the baited traps. The new mean range, $158.1 \text{ m} \pm 16.7 \text{ m}$ ($N=26$), was not significantly different from the preceding estimate ($t=1.37$, 66 d.f.). Great variation in individual foraging ranges was observed. A total of 46.5% of all instances involved a foraging range of 92 m; 2 animals traveled 566 m and 800 m, respectively, in a single night. Calculated ranges of 16 flying squirrels captured in baited live traps 5 or more times are illustrated in Fig. 3. Adult males had a mean range radius of $157.8 \pm 39.2 \text{ m}$ ($N=5$), non-reproductive females, $103.1 \pm 11.4 \text{ m}$, ($N=5$) and juveniles only $102.8 \pm 19.3 \text{ m}$ ($N=5$); the one lactating female had a range radius of 76.8 m.

3.4. Reproduction

Two major peaks in reproduction occurred, one in the late summer and early fall, the second in the spring. This is summarized in Table 3, showing the rise in percent adult males with enlarged scrotal testes and percent of estrous or pregnant females. The data suggests that most males reached reproductive condition in advance of females. Some of this lag by females represents the 40-day gestation period, but the

actual anticipation in males exceeded 40 days. Reproduction peaks are confirmed by the April and September peaks in lactating females at Ashland, where the largest sample was observed. Weight changes of

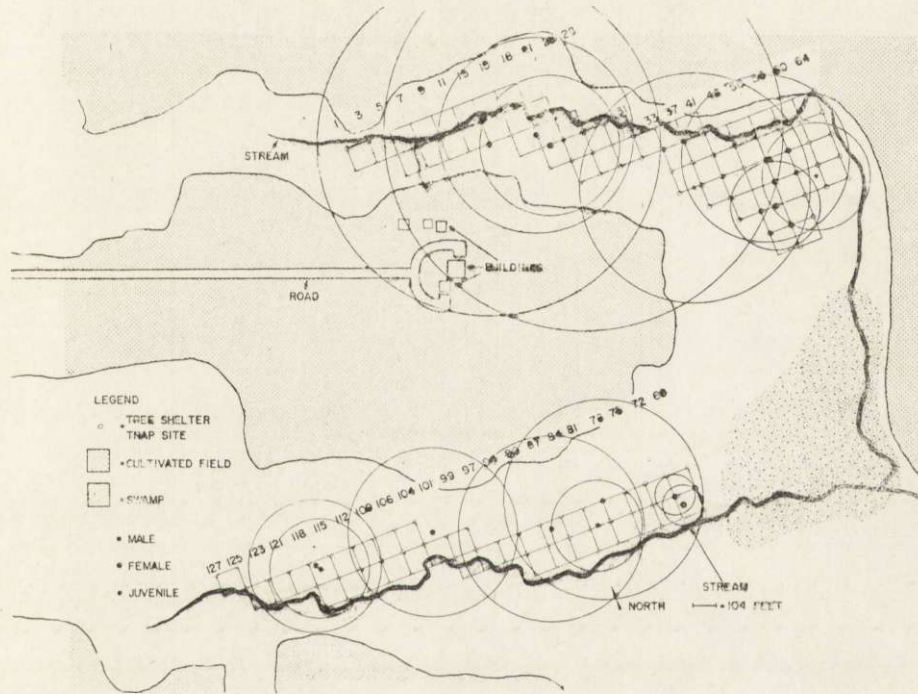


Fig. 3. Range of selected individual flying squirrels at the Ashland study area during the spring-summer trapping period as determined by the distance between successive recaptures.

adult flying squirrels also appeared to be correlated with the reproductive cycles (Fig. 4). Two sharp increases in female weight occurred at the time of the two breeding periods, April and August. The precipitous declines observed following these peaks probably reflects weight loss following parturition. In contrast, male body weight declined during periods of sexual activity, gradually during the winter months January—March, precipitously during the summer period June—August.

The periods of reproduction are also evidenced by the discovery of sucklings as early as March and October and the frequency of occurrence of juveniles from March to August and October to January. Development of young was studied in the field and in a laboratory colony as a means of aging the animals. Flying squirrels acquired a fine coat of fur ap-

Table 3
Monthly reproductive status of flying squirrels and occurrence of juveniles at two study areas in Virginia.

Month	ASHLAND Females					LORNE Females				
	Reproducing Males ¹ %	Estrous/ Pregnant %	Nursing %	Juveniles %	Total Captures, 4 yrs	Reproducing Males ¹ %	Estrous/ Pregnant %	Nursing %	Juveniles %	Total Captures, 10 mths
Jan.	69.8	23.2	0.0	7.0	168	93.1	16.0	0.0	3.6	56
Feb.	60.1	61.3	0.0	0.0	80	76.5	77.8	0.0	0.0	26
Mar.	9.1	30.8	23.1	18.6	199	9.1	0.0	33.3	0.0	20
Apr.	2.9	17.8	33.6	27.0	162	25.0	75.0	25.0	28.0	25
May	100.0	12.8	16.2	26.3	76	—	—	—	—	—
June	89.6	16.5	4.3	27.8	98	100.0	33.3	0.0	25.7	39
July	88.6	46.1	0.0	26.5	178	100.0	73.7	0.0	19.5	46
Aug.	59.8	45.9	7.4	37.3	157	90.0	66.7	33.3	37.1	35
Sept.	60.0	15.8	26.3	0.0 ²⁾	21	—	—	—	—	—
Oct.	3.0	6.4	21.9	32.2	132	0.0	0.0	33.3	59.2	27
Nov.	37.2	0.0	11.0	33.8	178	22.2	0.0	0.0	41.4	58
Dec.	78.3	2.5	0.0	12.5	87	93.6	0.0	0.0	6.5	62
Total					1536					280

¹⁾ Testes descended. ²⁾ Small sample.

proximately 2½ weeks after birth; the eyes were opened fully at the middle of the fourth week. Weight gains of laboratory reared young increased approximately logarithmically during an 11-week period and resembled the growth pattern described by Sollberger (1943). In nature, nursing terminated after approximately 44 days. Juveniles began foraging and appearing in baited traps 60 to 80 days after birth. Weaned juveniles were recognized as individuals weighing less than approximately 60 grams, with a drab pelage. Adult features were acquired after

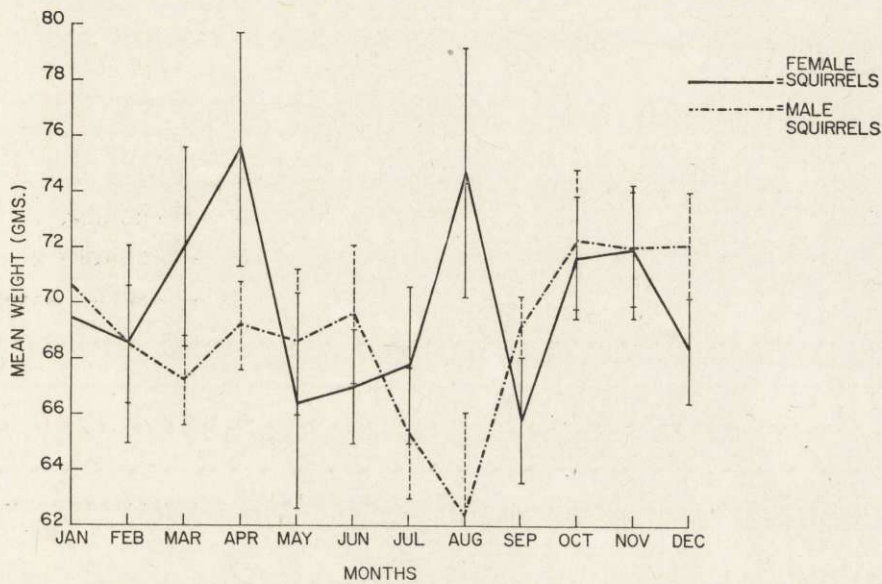


Fig. 4. Mean monthly weights of wild flying squirrels, *Glaucomys volans*, in a natural area near Ashland, Virginia. Vertical bars represent ± 2 S.E.

approximately 4 months. Young flying squirrels tended to remain together in family groups, even after weaning, and usually with the mother.

Reproduction may be expected to occur in female flying squirrels during their first year. Data was accumulated for 27 females of known history, or which could be traced for extended periods. Most females (94.2%) became pregnant within 6—8 months after birth, at the next breeding season following their birth. The remainder became pregnant in the next breeding season 12—15 months after birth. Eight of these females were observed to become pregnant again, 5 within 6 months *post-partum*, the others within 12 months *post-partum*. One individual became pregnant again in the following year, but aborted. The oldest

female to bear young was 3 years and 8 months old when it was found with a litter of 4.

3.5. Mortality

Disappearance of individuals from the populations was believed to be due almost entirely to mortality, since the relatively isolated nature of the woodlots studied minimized emigration. At Ashland, tree shelter traps were deployed in nearby woodlots to intercept emigrating resident

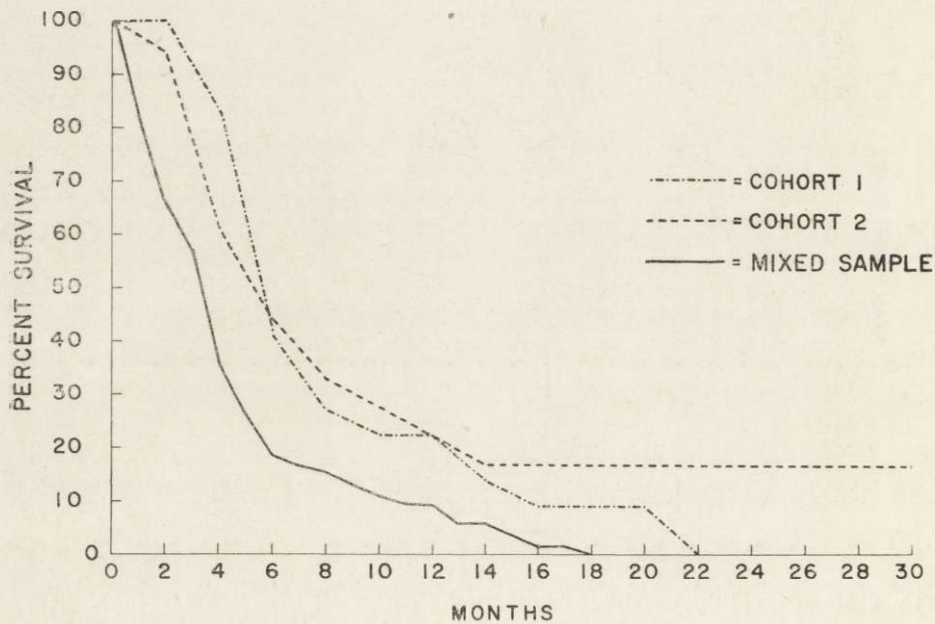


Fig. 5. Survival curves for flying squirrels at the Ashland Study Area. Cohort 1=22 individuals born in the spring of 1973; Cohort 2=18 individuals born in the fall of 1973; Mixed Sample=53 individuals of unknown age, captured for the first time in May or June of 1973, and monitored thereafter.

individuals; no captures or visitations were observed. Mortality was estimated by determining recapture rates over 2 years for specific population cohorts, namely, a spring born juvenile cohort and a fall born juvenile cohort. Finally, a mixed group of all ages, but captured at a specific time, was analyzed (Fig. 5). Disappearance of individuals in the juvenile cohorts during the first 2 months after they commenced foraging was negligible. More than half of the spring-born squirrels

disappeared from the population within 5½ months, and two-thirds within 7 months. For the fall born squirrels, the same rate of disappearance values occurred within 5 and 8 months. The mixed population sample exhibited a more rapid rate of disappearance of individuals, with 50% absent after only 3½ months and 67% absent by 4 month after their first capture.

3.6. Population Size

The results of the two different methods of analysis suggest that population size at both study areas was lowest during the summer period,

Table 4

Summary of estimates and census values of the population of the southern flying squirrel, *Glaucomys volans* at the 2 Virginia study areas.

Seasonal Period	Census	Petersen index N ± 2 S.E. (Dates)	Regression of recapture frequencies N	Conf. Limits	R ²	(dates)	Range of both est. (avg/ha)
A. Ashland study area (12.8 ha)							
Summer, 1972,	61	85 ± 18 (19—26 June)	85	83—87 [P<0.005]	0.99	(19 June—21 Aug.)	6.7
Fall, 1972	55	71.5 ± 17.0 (16—31 Oct.)	93	91—95 [P<0.005]	0.91	(31 Oct.—31 Dec.)	5.7—7.4
Spring-Summer, 1973	56	56 ± 22 (5 June—18 July)	87	75—94 [P<0.025]	0.88	(5 June—28 Aug.)	4.5—6.9
Fall, 1973	43	71 ± 50 (22 Oct.—6 Nov.)	129	124—138 [P<0.005]	0.92	(5 June—15 Dec.)	5.7—10.1
Spring-Summer, 1974	36	48 ± 21 (26 June—3 July)	38	35—40 [P<0.25]	0.22	(28 May—21 Aug.)	3.0—3.7
Fall, 1974	56	86.1 ± 30.2 (15 Oct.—11 Nov.)	98	95—101 [P<0.005]	0.60	(28 May—9 Dec.)	6.7—7.7
B. Lorne study area (7.8 ha)							
Summer, 1974	43	48 ± 4 (17 June—3 July)	60	57—63 [P<0.005]	0.81	(2 June—21 Aug.)	6.2—7.7
Fall, 1974	56	72 ± 15.9 (21 Oct.—6 Nov.)	108	103—114 [P<0.005]	0.87	(2 June—19 Dec.)	9.1—13.8

from as low as 3.7 flying squirrels/ha at Ashland in 1974 to as high as 7.4 flying squirrels/ha at Lorne (Table 4). Major expansion of the population was found to occur in late summer and early fall in most years. This expansion was most pronounced in 1974 at Ashland, when the fall population increased to a size approximately 1.8 to 2.5 times as great as that of the preceding summer. An increase of similar proportions occurred in the same year at the Lorne study area (Table 4).

4. DISCUSSION

The peak of reproduction in Virginia occurred one month earlier in spring than reported by Muul (1969) for flying squirrels in Massachusetts and Michigan, or by Sollberger (1943) for Ohio and Pennsylvania. However, the results are similar to those of Goertz *et al.* (1975) for northern Louisiana.

Jordan (1948) and Madden (1974) reported that standing fresh water was not a necessary component of flying squirrel habitat. Muul (1968), however, noted that nearly all nests were less than 100 m from water. The Virginia populations were clearly influenced by nearness to available ground water for their shelter sites, in agreement with Muul's findings.

Foraging ranges of adult males were significantly larger than those of adult females or juveniles, in contrast to Madden's (1974) observations for Long Island, New York. Furthermore, no defense of territory by females against other females as reported by Madden for Long Island squirrels was ever observed at Ashland.

The data for population regulation indicates a range of densities throughout the year, correlated with peaks of reproduction and periods of high attrition. The assumptions of the Petersen index may be met most readily during brief, nonreproductive periods of the year. Mortality corrections were available also (Fig. 5). Horizontal population exchanges were minimized by the relatively isolated nature of the habitats studied. Consequently, the Petersen index estimates may approximate the natural population numbers, though with relatively large margins of error. Regression analysis of recapture frequency was used as an alternative to the Petersen index calculations for estimating flying squirrel abundance. This method was used by Edwards & Eberhardt (1967) to estimate a known experimental cottontail rabbit population; with the exception of the Lincoln index, other methods tended to over or underestimate the number of individuals present. Nixon *et al.* (1967) working with two species of tree squirrels, also found that linear regression estimates closely approximated those obtained with the Lincoln index, whereas other methods produced poor fits and much lower values. The assumptions of the regression method are similar to those for the Petersen index, as described previously. In addition, the method assumes consistency of behavior by the animals with respect to the traps, an untested assumption. However, the high R^2 values and narrow confidence limits suggest a close fit between the regression estimates and the data (except for the spring-summer period, 1974, at

Ashland), consistent with the hypothesis of relatively constant trap susceptibility.

The reliability of the population estimates is also influenced by the extent to which the sampling methods are capturing all classes in the population, e.g., new animals, recaptures, juveniles, adults, ... etc. However, comparison of the proportion of adults vs. juveniles at the two study areas did not reveal substantial differences (e.g., adults constituted 70.3% of the sample at Ashland, 76.2% at Lorne). Similar observations were noted in comparing males vs. females. No discernable bias was found which excluded any class of the population, and comparison of the estimates obtained at the two study areas as well as with the two sampling methods appears to be justified.

Census values were also determined for the different populations in each period to provide a comparison between the number of individuals known present and the numbers in each estimate. With one exception (spring-summer, 1973), census values were lower than the estimated total population.

Other workers reported flying squirrel densities ranging from 2.5 to 12.4/ha (Burt, 1940; Sollberger, 1943; Jordan, 1948, 1956; Muul, 1968; Madden, 1974). However, their figures represent minimum densities in terms of the observed number of individuals per unit area rather than population estimates. Moreover, Burt's & Jordan's (1948) studies were done in mid-summer, before the second litters of the year. Sollberger's (1943) values of 4.6 and 12.4 animals/ha at two different localities were based on removal trapping. He recognized the inaccuracy of his estimates, noting that the area was not trapped to extinction. Census figures for flying squirrels at the two Virginia study areas are comparable to those reported by other workers in the eastern U.S. However, the actual numbers present are probably much greater, as suggested by the population estimates.

This study demonstrated that *Glaucomys volans* can attain relatively high densities in favorable habitat, with cyclical expansion and contraction of the population each year.

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EKOLOGIA *GLAUCOMYS VOLANS* W WIRGINII

Streszczenie

Assapan *Glaucomys volans* (Linnaeus, 1758) reaguje pozytywnie na sztuczne schrony i pułapki umieszczone na drzewach. Możliwe, że powodem tego jest ograniczona dostępność schronień naturalnych. Przedstawiono dowody, że zwierzątka używają system schronień przy czym różne z nich służą różnym celom (gniazdowanie, defekacja, gromadzenie pokarmu). Zimą gniazda zbudowane były wyłącznie z kory *Juniperus virginiana* L. a podczas lata z różnych materiałów.

Assapany wykazywały istotną tendencję do zasiedlania kryjówek w pobliżu wody (Tabela 2). Rodzaj terenu, (górzysty lub równinny) czy też odległość od wody nie miały wpływu na zasięg penetracji terenu w celu zdobywania pokarmu. Zasięg ten obejmował $126.8 \text{ m} \pm 14.8 \text{ S.E.}$, i był znacznie większy u dorosłych samców niż u nieaktywnych samic lub osobników młodocianych (Ryc. 3).

Aktywność seksualna ma charakter sezonowy (Tabela 3). Porody ograniczone były do 2 wyraźnie określonych okresów: wiosną i na przełomie lata i jesieni. Zmiany ciężaru ciała specjalnie u samic były związane z cyklem płciowym (Ryc. 4). Większość samic (94.2%) zachodziło w ciążę w ciągu 6—8 miesięcy po urodzeniu. Najstarsza samica zdolna do rozrodu była w wieku 3 lat i 8 miesięcy. Porody miały miejsce na początku wiosny (marzec, kwiecień) i pod koniec lata lub z początkiem jesieni. Młodociane assapany zjawiły się w pułapkach około 60 do 80 dni po urodzeniu.

Ubywanie assapanów z populacji prawie wyłącznie było spowodowane śmiertelnością. Z kohorty wiosennej 50% osobników przeżywało $5\frac{1}{2}$ miesiąca a 67% — 7 miesięcy. Analogicznie w kohorcie jesiennej wartości te wynosiły 5 i 8 miesięcy (Ryc. 5).

Zagęszczenie liczone wg indeksu Petersena i metodą analizy regresji zmieniały się zależnie od sezonu od 4.5 do 10.1 assapanów/ha w jednej miejscowości i od 6.2 do 13.8 w drugiej miejscowości (Tabela 4).