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GIACALONE-MADDEN, Jacalyn Rose, 1947-
THE BEHAVIORAL ECOLOGY OF THE SOUTHERN
FLYING SQUIRREL, GLAUCOMYS VOLANS, ON
LONG ISLAND, NEW YORK.

City University of New York, Ph.D., 1976
Biology

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THE BEHAVIORAL ECOLOGY OF THE SOUTHERN FLYING SQUIRREL, GLAUCOMYS VOLANS, ON LONG ISLAND, NEW YORK

by

JACALYN R. GIACALONE - MADDEN

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York.

1976

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

The social organization and the distribution of individuals of Glaucomys volans were found to vary greatly with locality and appeared to be affected by both behavioral and environmental factors. At the Kalbfleisch Field Research Station, Suffolk County, New York, females had home ranges with little overlap and exhibited very aggressive behavior. Males lived in small groups which shared daytime nests and had widely overlapping home ranges. Females appeared in traps in greater proportion than their actual numbers, suggesting that they are socially dominant over males. Flying squirrels at Kalbfleisch occurred in oak-maple forest and did not travel together or feed in large groups, while squirrels on the edge of a cypress swamp in Worcester County, Maryland, had been observed feeding and traveling in a group of 10 or more. Squirrels in a swampy region interdigitating with a dry pine-oak forest in Connetquot River State Park, Suffolk County, New York, were usually found in the ecotonal area and had widely overlapping home ranges.

It was concluded that under some conditions flying squirrel females defend their entire home range. The size, number, and overlap of these female territories at Kalbfleisch varied between years. These parameters seemed related to food supply and population density. In seasons of high density, females had smaller home ranges that overlapped more than in years of lower density. Population rose sharply the year of a bumper acorn crop. It appears that territory does not control absolute numbers of residents, but may act as a buffer system by excluding some young of the year from breeding.

Comparisons of the distribution of squirrel captures with the distribution of tree species did not reveal any correlations, as expected at Kalbfleisch. The distribution of squirrels was not random, nor was the distribution of trees, but they were not related. It had been hoped that a correlation between captures and tree species might give an indication of one of the specific resources which makes a territory beneficial to a defender. Instead, it was suggested that the spatial dispersion of resources (food, water, and nest sites) at Kalbfleisch is uniforn enough to make defense of an entire home range advantageous. Observations of squirrels in patchy habitats indicated that gregarious behavior occurs under circumstances of different resource distributions, Activity of squirrels in localized swamps was marked by a strong preference for ecotonal areas and a lack of territorial defense.

The time of appearance of the first signs of reproductive readiness in the winter breeding season varied from year to year, indicating that the stress formerly placed on photoperiodic control is an oversimplification. Nutrition appears to play a very important role in setting the cycle of this species. In the year of the best acorn crop, when territories were small and numerous, some females bred at an earlier age than had ever been noted before. Also, the annual complete molt was found to occur after the peak of energy expenditure for the breeding effort, which is completed in different seasons by the sexes.

Vocalizations were found to be much more complex than expected from the literature; echolocation is suggested, but experimental data are needed. Learning was found to play a role in the development of gliding skills in the young. Food storage behavior is an important activity, the adaptive significance of which is probably for the preservation of rather than simply the accumulation of food. Activity recordings gave a clear picture of the fallacies behind attempts to make stereotypic statements concerning the onset and lengths of activity periods of free-living flying squirrels.

Behavioral lability is characteristic of this species and is discussed as an evolutionarily advantageous strategy. Suggestions are made for future study.

ACKNOWLEDGEMENTS

An enormous number of people have influenced this work and my [illegible] career in many ways. At the risk of leaving some out, I will mention these. Thanks go to those directly involved in the preparation of the dissertation: Sydney Anderson, Max and Bessie Hecht, Leslie Marcus, Donald Griffin, Brock Fenton, and Wesley Lanyon, who also provided Kalbfleisch facilities. Robert Madden was involved in many aspects of this work and my life. Technical advice from Estelle Geller and Sheldon Feingold was invaluable. Lodgings and information on local flying squirrels were provided by William and Helen Kolinek at Connetquot and Don and Jean Harrold in West Virginia. Paul Conner and Gilbert Bergen generously supplied locality information for Long Island; Gil often dined an insatiable trapper in banquet style. Dick Shook, a fellow squirrelist, thrashed out many ideas, compared notes, and commiserated with me. Helen Giacalone typed and edited much of the manuscript and, along with my father, gave moral support.

Many of my friends at Queens College, my non-biologist friends, the NSF-URP students at Kalbfleisch, and fellow guides at Connetquot often helped me run trap-lines, but more importantly, were always willing to listen, discuss, and offer suggestions or encouragement. To them I owe much: Dave Ewert, Chris Lastinger, Audrey Lefkowitz, Terry Wojtowicz, Jim and Anne Edwards, Mary Guillet, Kathe Geist, Chaim and Bobbie Kropach, Michael Gochfeld, Uldis Roze, Celia Moore, Mike Venuti, Gary Lawton, Pat Detamore, Bill Sampson, Jim Mansky, Allen Furst, Alan Brown, Brian Malone, Barry Koffler, Pearl Waltzer, Rhoda Kullar, Ruth Monson, Lou Werner, Joe Wunderle, Michael Rivlin, and Greg Pence. And special thanks to that crazy crew of grad students who inhabited the top of B building.

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Introduction

The behavioral ecology of the southern flying squirrel, *Glaucomys volans*, was studied both in the field and in the laboratory, from June 1970 to December 1975. Efforts were made to disturb the animals as little as possible, and yet obtain long-term information on the activities of individuals in a single population in an area protected from human interference. The main goal was to obtain information on home range and its ecological significance, particularly with regard to population structure, social structure, and habitat characteristics. Toward this end, movements, behavioral interactions, and territoriality were also studied.

The most intensive part of this study was conducted in 1972 and 1973 at the Kalbfleisch Field Research Station of the American Museum of Natural History in Dix Hills, Suffolk County, Long Island, New York. Most data were obtained by direct observation and live-trapping. Additional information was obtained by a photo-relay-event recorder system, radio-telemetry, and examination of nest boxes. Observations were also made on reproduction, vocalizations, pelage changes, and body weights. Additional field work was conducted at Connetquot River State Park in Oakdale, Suffolk Co., Long Island, New York, and, on a number of occasions, in other states.

Distribution and Relationships

Flying squirrels have long been objects of curiosity both because of their gliding ability and their nocturnal habits. Unfortunately, both characteristics make observation difficult and, consequently, there are few prolonged field studies of the genus *Glaucomys*. On Long Island, where the major part of this study was done, the native flying squirrel is *Glaucomys volans volans* (Linnaeus), family Sciuridae, subfamily Petauristinae. *Glaucomys volans* is the smaller of two species in this genus, the other being *Glaucomys sabrinus*. These are the only gliding mammals in the Western hemisphere. *Glaucomys volans* is one of the smallest members of the family Sciuridae, and has a widespread distribution in North America and Middle America (see range map - Figure 1a). It reaches its northern limit of distribution near Laurentides Park in southern Quebec (Wrigley, 1969). In the west it is limited by the prairies. To the south it is found in apparently isolated populations in mountain-top forests in Guatemala and Honduras (Tomes, 1861; Goodwin, 1961). The larger species, *G. sabrinus*, has a more northern and western distribution (Figure 1b) and is found at higher elevations than *G. volans* in regions of sympatry.

The two species are very similar externally and cranially (Burt, 1960); however, their bacula are quite different. The baculum of *G. sabrinus* resembles that of *Hylopetes*, an Asian genus of small gliders in the subfamily Petauristinae, more than that of *G. volans*. Burt suggested that *G. sabrinus* split off from the Asian stock of Petauristinae much later than did *G. volans*. The more southern distribution of *G. volans* would support this hypothesis.

As Burt (1960) suggested and Muul (1968) elaborated, the ancestral stock of *G. volans* would have spread across Canada, probably during the Miocene and Pliocene, and been pushed southward by the advancing Pleistocene glaciation. This species probably spread into the eastern U. S. and Middle America during the glaciation and remained in the tropics in refugia on forested mountain tops after the retreat of the glaciers. Glaucomys sabrinus would have been found in the boreal forest closer to the receding glaciers, a habitat not suitable for G. volans, but G. sabrinus seems to compete poorly with G. volans in non-boreal forests. Glaucomys sabrinus remained in some mountain refugia in southern California and Utah (Musser, 1961) and in the Appalachians but the main distribution of this species is much more northern. Fossil evidence suggests that G. sabrinus occurred at lower elevations in the late Pleistocene than it does now at the same latitude (Guilday, 1962; Gidley & Gazin, 1938).

Work done by Muul (1968) on the physiology of heat conservation in G. volans suggested that the northernmost boundary of distribution of this species is at the 20°F isotherm of average January temperature. The energy budget of this species probably makes colonization at more northern latitudes very risky. It appears that G. sabrinus, which can be twice as heavy as G. volans, is better adapted to cold climates. In areas of sympatry, G. volans breeds earlier, seems to occupy the best nest cavities, and in breeding season is more aggressive than G. sabrinus. Glaucomys volans seems to have displaced G. sabrinus at lower elevations in more southern parts of the latter's distribution.

Examining the anatomical evidence, Burt (1960) found indications that G. volans has long been separated from its ancestral stock, if it did indeed arise from the Petauristinae. The baculum is not only very different from that of *G. sabrinus*, but from that of other sciurids as well. Wade and Gilbert (1940) concluded that the structure of the baculum of *G. volans* indicates a rather remote relationship with other arboreal North American sciurids. However, not all workers are in agreement. Nadler and Sutton (1967) examined the chromosomes of both species of *Glaucomys* and compared these with chromosomes of members of the genus *Sciurus*. Contrary to bacular structure, chromosomal similarities suggested that the two species of *Glaucomys* may be closely related. Furthermore, similarities to the karyotypes of *Sciurus* support Black's (1963) suggestion that *Glaucomys* arose from a line that would be considered in the Sciurinae rather than Petauristinae. Black had based his conclusions on the anatomical similarities between *Sciurus* and *Glaucomys*, stating that, except for the gliding membrane, the two genera were quite similar.

Program of Study

This study began in 1970 and continued through 1975. The primary effort was directed toward the tagging and monitoring of the *Glaucomys* population on my main study area at the Kalbfleisch Field Research Station. The study area is about 5 hectares of woodlot in the Dix Hills region of Huntington Township, Suffolk County, Long Island, New York (Fig. 2). This woodlot was designated BWFl, black oak-white oak forest, by McCormick, *et al*. (1969), and is the largest of the forested areas on the station. On the northwest and northeast it borders on a public road, a highway, and a residential area. On the southwest it borders on a field. A private wooded residential area lies to the southeast adjacent to a small wooded area within the station, designated BWF2, which is periodically burned. One of the most mature woods on the station is BWF1. Many oaks here exceed 0.3 meter in diameter and 15m in height. The most common tree species are *Quercus velutina*, *Q. alba*, and *Acer rubrum*. Also present are *Castanea dentata*, *Cornus florida*, *Betula lenta*, *Sasafras albidens*, *Quercus prinus*, and *Carya ovalis*. A detailed analysis of tree species abundance and distribution is given in the section Vegetational Analysis at Kalbfleisch. The understory includes *Kalmia latifolia*, *Viburnum acerifolium*, several species of *Vaccinium*, and *Gaylussacia baccata*.

Trapping was begun in 1970 using Havahart No. 1 size live traps and Longworths, in several wooded sections of the Station. Success was very poor with Longworths and in areas outside BWF1, while Havaharts used in BWF1 had immediate and continued success. Traps were set on the ground at the bases of large trees. Some homemade wooden box traps with swinging doors were constructed and wired to the trunks of trees at a height of 2 meters. These readily caught *Peromyscus leucopus*, *Tamias striatus*, and *Glaucomys*, but the *Glaucomys* soon learned how to lift the doors from inside and escape. The use of these traps was discontinued. Several types of baits were tried, including various combinations of fruits, nuts, meats, oatmeal, and peanut butter. The most successful combination was peanut butter and sunflower seeds.

When sufficient Havaharts were acquired in 1971, traps were laid out in a grid system, following the quadrat markers already set up on the Station, at 25 m. intervals. The area covered by the grid was expanded in 1972, when more traps were purchased, until most of BWF1 was covered (see Fig. 2). This trap spacing was wide enough for inclusion of several animals' complete home ranges, yet packed tightly enough so that at least 10 traps were included in each home range.

Trap data were supplemented by several other techniques. At intervals, various models of radio-transmitters were attached to squirrels in different ways, none of which remained on a squirrel and operative for more than 3 days. However, this work did give some valuable data on squirrel activity and movements, which could be compared with trap data. The only other telemetry work on Glaucomys was done on the larger species by Weigl and Osgood (1974). These workers were able to monitor their animals for a maximum of only 6 days. My problems and results are described in the section Social Behavior and Spatial Distribution.

Another valuable technique was direct observation at nest boxes, water holes, and feeding stations, using a flashlight equipped with a red filter. Many hundreds of hours were spent in observation both in the field and in the lab. The most efficient use of observation time was made later in the study, in 1972 and 1973, when an activity recorder was set up. This system monitored activity at several nest sites and so permitted me to predict more accurately where and when squirrels might be observed. The activity recorder gave information on levels of activity in different seasons and an analysis of these data is given in the section on activity. Equipment carried during direct observation often included a Uher 4000 Report-L tape recorder for recording audible squirrel vocalizations and a McCue-Bertolini ultrasonic detector (McCue and Bertolini, 1964) to monitor ultrasonic vocalizations. The results of these observations are in the section Vocalizations.

All of these methods were used to gather information on the population structure, behavior patterns, breeding cycle, and molt, as well as movements.

Although not as much time could be spent in a comparative study area, a one year study (Oct. 1973 - Oct. 1974) was done at Connetquot River State Park, Suffolk Co., on the south shore of Long Island. This area is a large (1800 hectares) tract of _Pinus_ _rigida_ mixed with several species of _Quercus_ and interdigitating with swampy areas lining the river system. The dry, sandy, pine-oak forest was trapped unsuccessfully (except for an occasional _Peromyscus_ _leucopus_) in many sections, but the swampy areas were inhabited by _Glaucomys_. Trapping, marking, and recapture techniques were employed in a section of _Acer_ _rubrum_-_Nyssa_ _sylvatica_ forest. Because of brooks and sphagnum bogs in this area it was not possible to set up a grid system for trapping. Instead, two intersecting trap lines were maintained in order to learn about the home ranges of squirrels in an area comparable in size to that of BWFl. Since this forest is wetter and patchier than that at Kalbfleisch it seemed likely that home range sizes and overlap might reflect the habitat differences.

Several one-day and two-day observation periods (1966, 1971, 1975) were spent at Shad Landing State Park, Worcester Co., in peninsular Maryland in the ecotonal area between cypress swamp and pine-oak forest. Sightings of flying squirrels were infrequent here but of particular interest because of their contrast with observations made at Kalbfleisch.

Lastly, two days of observation and trapping (1974) in hickory-oak-maple-beech forest on the Harrold property near Clarkesburg, Harrison Co., West Virginia, provided additional information on the species in yet another habitat.

Previous Relevant Work

Although several field studies (Blair, 1935; Booth, 1946; Burt, 1940; Goertz, 1965; Goertz, Dawson, and Mowbray, 1975; Jordan, 1948; Muul, 1965; Sollberger, 1940) have provided general information on the natural history of this species, very little is known about the movements, home ranges, and behavioral interactions of individuals. Osgood (1935) suggested the possibility of sexual exclusiveness of home ranges. In a three-year study in deciduous forest in Vermont he found that all adults sharing a single nest cavity were of the same sex. Males formed larger groups than females. Males and females were usually found on separate ridges within his study area. However, he had no information on the movements of individual animals and his sample size was small (apparently 22 animals).

Later work by Burt (1940), Sollberger (1940, 1943), and Jordan (1948, 1956) gave estimates of population densities and ranges of activity, but are not strictly comparable because of differences in methods, season of study, and length of study. Only Burt's study in Michigan used a grid system of traps and maintained a regular schedule of mark and release over a summer. He found a sex ratio heavily in favor of males and a tendency among females to be caught in many different traps rather than repeatedly in the same traps. This suggests some interesting sex-related behavioral differences. Jordan (1956), in contrast, had a sex ratio which favored females (1:2) in Illinois. Because of the limitations of these studies it is not possible to say how much of these results are due to differences in survival or behavior rather than to sampling errors.

One of the more detailed works devoted to Glaucomys volans is Muul's 1968 paper on behavioral and physiological influences on the geographic distribution of this species, based on field work done from 1959-1963 in Michigan and Massachusetts, and on laboratory studies of animals kept in large cages. He was concerned mainly with the role of nesting behavior in the success of the species in the northernmost parts of its range. Of particular interest to me was his observation that females with young can be highly aggressive and territorial. However, he felt that the territory did not extend beyond the tree in which the young were kept. He did not report on home range size or overlap.

In the areas which Muul studied, individuals were found to have severals nests used as primary nests, emergency retreats, feeding shelters, food storage sites, and defecatoria. Muul felt that the availability of suitable nest sites might limit the population size of flying squirrels since nearly everything that is important to the survival of the species has some connection with the various types of nest sites. Most nests (82 out of 88) were located in sheltered positions within tree cavities or under the root systems of trees, while only 6 were "outside nests" composed of twigs, bark, and leaves. There seemed to be considerable variation in the desirability of different nest sites. When the more favorable nest sites were cleared of their inhabitants, they were quickly occupied by new individuals. Nest cavities became unsuitable for a variety of reasons, including the rotting away of the tree trunk, and the build-up of large populations of mites and fleas. These observations suggest that there is probably strong competition for the best nest sites, and that this competition would be interspecific with other rodents as well as intraspecific.

Muul conducted laboratory studies of competition for nest sites between the larger sympatric *Glaucomys sabrinus* and *G. volans*. The latter seemed the more aggressive species, but the results were not clear-cut. Resident *G. volans* were always aggressive toward introduced *G. sabrinus*, while resident *G. sabrinus* were usually tolerant toward introduced *G. volans*. In one case, a female *G. volans* drove a pair of resident *G. sabrinus* from their nest box. When individuals of both species were introduced to new nest boxes simultaneously, *G. sabrinus* individuals occupied the nests in two cages, while *G. volans* occupied the third. When the nests were repeatedly disturbed, both species came to occupy two boxes as mixed pairs, and sometimes all three boxes had mixed pairs. In another series of trials with new animals, all three boxes were occupied the first night by both species. It had previously been observed that female *G. volans* with litters were extremely aggressive toward adults of the same species. When females of both species with litters were placed in competition for a single nest box, *G. volans* excluded *G. sabrinus* in three out of four matches. No reversals were observed when the experiment was prolonged for three to four days. Similar experiments by Weigl (1968) also indicated that *G. volans* has a slight advantage over *G. sabrinus* in competition for nest sites. Muul and Weigl were concerned mainly with interspecific competition and did not experiment with paired conspecifics.

Muul did, however, report his observations on the aggregative tendencies of *G. volans*. He observed that while adults of this species in the wild are usually solitary in the warm months, from November 1962 to March 1963 in Michigan and Massachusetts they were found in aggregations averaging from 4.5 per nest in December to 8.5 in February (maximum 19). The composite four year average for November - March nests was 5.7 adults per nest, while the April - October average was 1.3. Monthly winter averages in minimum temperature ranged from approximately 30°F (-1°C) to less than 10°F (-12°C) in Michigan in 1962 - 1963.

As part of his effort to investigate the relationship between ambient temperature and aggregation, Muul housed 30 non-breeding adult animals in a large (5 x 4 x 2.5m) cage in Michigan and provided 10 to 15 nest boxes. Aggregations were recorded from June 1962 to July 1964. Pregnant females were removed and replaced with non-breeding females because pregnant females defended their nest boxes from all other adults, thus interfering with aggregation. Sizes of aggregations were found to be inversely related to ambient temperature in the laboratory, as well as in the wild. However, captive aggregations were much larger than natural aggregations. Captives averaged approximately 7 - 15 per nest in warm months and 9 - 24 in cold months. I would expect that this effect is the result of the abnormal crowding to which captive animals were subjected, as well as an insufficient number of nest boxes.

An environmental chamber was used by Muul to estimate the lowest ambient temperature at which an average aggregation of six adults is able to maintain a microclimate suitable for homeothermy with only a basal expenditure of energy. He measured the cumulative insulative value of wood enclosing the nest cavity, of nesting material, and of members of the aggregation. The savings through insulation, when compared with expenditures necessary in excess of basal metabolic demands at the same ambient temperature without such insulation, indicated that an average aggregation could tolerate temperatures down to 10°C without an increase in heat production. Thus it appears that aggregation is an important behavioral adaptation to winter conditions in the northern sections of this species' range.

Muul's study also indicated that the species has an emergency physiological adaptation to the stresses of severe cold and insufficient food supplies. On a few occasions, captive and wild animals were found in a torpid condition. These individuals occurred in both small and large aggregations and had rectal temperatures of 22°C to 29.4°C (normal body temperature 39°C). When disturbed, torpid squirrels returned to normal activity and body temperature within 20 - 40 minutes. Attempts to induce torpidity in the laboratory were unsuccessful, even when food was withheld. When some captive animals which were housed outdoors all winter were found torpid, the ambient temperature the previous night had reached a low of -12°C, and the food supply had been depleted, perhaps as long as 36 hours. Only five of the 30 animals were torpid and these became fully active within 20 minutes of disturbance.

Muul's study indicates that nest-building, winter aggregations, and possibly food-storage and torpidity, contribute to the ability of G. volans to succeed in the northern parts of its range. Farther north it is replaced by G. sabrinus, which has the energetic advantage of larger size. In areas of sympatry, *G. sabrinus* seems to be confined to higher elevations than *G. volans* or to those habitats where outside nests are sufficient shelter for *G. sabrinus*. Breeding females of *G. volans* seem to occupy the more favorable tree cavity nests both because they breed earlier in the year than *G. sabrinus* and so establish residency first, and because they are somewhat more aggressive than *G. sabrinus*. Muul (1968) speculated that as climates became warmer since the Wisconsin glaciation, *G. volans* invaded areas previously occupied by *G. sabrinus* and replaced the latter at low altitudes. The limitations of its energy budget, although ameliorated considerably by behavioral adaptations, may be the determining factor in the northern boundary of distribution of *G. volans*.

Weigl (1968) examined limiting factors and concluded that *G. volans* is dependent upon hickories and oaks. The northern limits of *G. volans* and these mast trees roughly coincide. *Glaucomys sabrinus*, however, feeds mainly on lichens, a food source used by few species. Weigl felt that competition for food resources between the two flying squirrel species was insignificant.

The results of these studies that were most pertinent to my work were the indications that oaks, hickories, and nest sites are the most important resources to *G. volans*.

Social Behavior and Spatial Distribution

Methods

Trap sites were first spaced (in 1970) at approximately four-meter intervals in lines laid out along already existing trails. In some cases traps were clustered in groups of 3 or 4. Although trap-success was high (on some nights catching six animals in twelve traps), this type of arrangement did little to reveal the home ranges of the animals. More traps were acquired in 1971 and laid out in a grid system with 25-meter intervals.

Squirrels were marked with individually numbered fingerling tags (originally for fish) attached to the ear. They were also marked with patterns of notches clipped in the tail fur so that they could be identified in the field without examination of ear tags. This provided a back-up identification system when animals lost their tags. I decided in favor of tags in spite of their frequency of loss (30% at Kalbfleisch and Connetquot) because both ear-punching and toe-clipping seemed even less satisfactory. Holes punched in ears with a standard poultry punch often healed over completely and notches became partially obliterated and difficult to read. Toe-clipping seemed undesirable because it might place individuals at a disadvantage. Only one animal in the total of 118 handled had a part of one toe missing from natural causes. It should also be noted that one animal temporarily lost the use of one leg yet was able to survive for at least a day in the wild.

Since I was not completely satisfied with trap results, and since it was obvious that not all animals were trapped with equal frequency, I attempted more direct methods of observation. Feeding stations were set up at sites A & B in the woods at Kalbfleisch, and also in the laboratory window (site C) (see Fig. 2). These were used as observation sites, where I could situate myself before the squirrels became active and wait for them to arrive. A & B were both located at natural water holes where squirrels had previously been seen drinking. I used a flashlight with red filter because, although visible to the squirrels, it was less disturbing than a white light. Flying squirrels' retinas are nearly pure rod, but do contain some cones (Walls, 1942). Consequently, one would have expected their apparent awareness of the red observation light. It is interesting to note that R. Shook's attempts to induce breeding in captive _G. volans_ were successful and synchronous one year when he used a white light, but when he used the same white light regime with a constant red light background, estrus and parturition dates were delayed and spread in time (pers. comm.).

Animals were also marked with fluorescent dyes and paints (watercolors, alcohol bases, acrylics), and followed with a portable ultra-violet light. Unfortunately, these were suitable only at close range (7 meters) and the animals quickly removed the substances from their fur.

In an attempt to check the accuracy of trap data as a reflection of actual squirrel movements, radio-telemetry equipment was tested in various ways. First, two 1.5 gram transmitters attached to thick wire loops which doubled as collars and antennae were fitted to two females. One female was lost and never found again. The other was followed, as shown in map (Fig. 3a), was lost apparently because of equipment malfunction (she was observed in the area, at a feeding site) and was recovered in a trap. Her left foreleg was caught inside the collar. She had attempted to remove the collar and in so doing, had slipped a leg inside the collar. The styliform cartilage on her wrist hooked on the collar and prevented withdrawal of the foot. The leg became swollen and the skin around the neck became irritated where the collar rubbed. Loose folds of skin adhered to the transmitter and collar, making removal very difficult. The animal completely recovered in a few days and was released again without transmitter. A different type of collar was tried later, one made of a soft, flexible plastic strip. Animals chewed through this collar in a matter of minutes. Transmitters were glued to the fur on the backs of their heads. These animals immediately took shelter and worked at the transmitter, breaking and pulling out hairs until the unit had been dislodged. Positioning the transmitter on the rump or across the shoulders was no less annoying to the animals and no more successful. Another, but not final attempt to attach a transmitter was made by implanting subcutaneously, under the very voluminous ventral skin. The transmitter was embedded in a surgical grade of silicon rubber, which did not cause any discernable tissue reaction when implanted in laboratory rats and mice.

Squirrel no. 41, a male which appeared to live mainly off the study area, was chosen for implantation because his possible demise would be of less consequence than the loss of an animal from the center of the area. He was anesthetized with a total of .54 cc. of 20% Diabutal given over a one-hour period. The necessary dose was larger than I would have expected from my experience with lab rats.

The transmitter was implanted in the evening and he appeared to be fully recovered from the anesthesia the next day. The sutures were secure and there were no signs of inflammation. I decided to release him that evening. He was followed for several hours that night, but could not be located the next morning. He was recovered fourteen months later in a trap. Careful palpation under anesthesia disclosed that the transmitter had indeed been rejected. No scar was visible and the animal was in excellent health. It appears that on the night of his release he travelled to his area of usual activity outside the field station, in a narrow strip of trees along the Northern State Parkway, and chewed off the numerous sutures which closed the incision. Furthermore, it appears that he destroyed the transmitter, since its signal could not be picked up again. Later work showed that squirrels do indeed destroy transmitters.

In November 1975, male No. 105 was equipped with a transmitter collar, released near his trap site, and followed for two evenings. On the third day his signal was lost. When the squirrel was again trapped 13 days later, he was without collar. This squirrel was kept indoors with two captives and equipped with a new transmitter collar. This transmitter was potted in fiberglas-reinforced epoxy since it was suspected that squirrels were chewing open the transmitter packages. Indeed, three days after attachment, the transmitter was found, separated from its collar and inoperative because the potting compound had been chewed through and the battery lead disconnected.

A third type of package, which was considered squirrel-proof, was attached to this squirrel and he was released at his nest tree on December 7. This transmitter was enclosed in a glass tube and attached to a metal band collar covered with and fastened by electrical tape. His signal was lost 20 minutes after he left his nest that evening. Figure 3b shows the area used by this squirrel.

Data were also obtained by using a portable multi-channel event recorder fitted with a system of photo-relays positioned at the entrances of nest boxes, at natural cavities, and at a waterhole. Each photo-relay unit had a lightbulb with a red filter (Wrattan 89B) focused by small lenses on a photocell (system designed by R. C. Madden). Interruption of the light beam resulted in movement of the pen of one channel on the recorder. The pen did not return to its original position until the light again shone on the photocell. This system gave useful data on activity patterns and allowed me to predict where it would be most profitable to make observations at a particular time, thus providing information on movements.

Twelve nest boxes were built along the design of Barkalow and Soots' (1965) gray squirrel nest box, but scaled down to dimensions more suitable for flying squirrels (30 x 15 x 15 cm). These were installed in BWF1 on tree trunks over 15 cm in diameter and at heights from two to four meters above ground. I already ascertained that it would be difficult to obtain information from squirrels nesting in natural cavities without undue disturbance to the animals and destruction of the nests. It was difficult to dislodge squirrels from tree cavities without destroying the cavity; furthermore, it was difficult merely to verify whether or not a cavity was occupied. When nest boxes were in use by squirrels it was learned that even rough banging on the boxes did not usually cause the animals to look out of the entrance. A relatively small number of nest boxes made possible some interesting observations.

I built my boxes with 38 mm holes placed in the front for maximum observability. The smoothness of the wood may explain the apparent reluctance of the squirrels to nest in boxes until crossbars had been placed beneath the entrance holes. I retained the wire mesh bottom and removable top of Barkalow's box. Sonenshine's group (1973) changed to a solid bottom, which might explain why use of their boxes declined in August and stopped in September, since the screen bottoms seem to allow some ventilation in the hot months. As Sonenshine _et al._ point out, however, the wire bottoms become disadvantageous in winter because of their poor insulative properties.

Home Range

Kalbfleisch Field Research Station was deemed ideal for a long-term study of animal movements because it was well-protected from the depradations of human neighbors, yet easily accessible from my home 32 miles to the west in Queens, N.Y.C. The species chosen was small enough to have a large population on the 40-hectare field station, yet large enough to be observed directly and even capable of carrying a radio transmitter if trap data proved insufficient. Past publications on Glaucomys volans indicated that the species' social organization may vary seasonally. It was reported that large social aggregations formed in the winter and dispersed in the spring when breeding females became aggressive toward other adults (Muul, 1968; Sollberger, 1943). The actual social arrangement at Kalbfleisch proved even more unusual and suggested the necessity of obtaining comparative data at another locality with different habitats. Data from past work on home ranges would not be strictly comparable because none of the workers published home range maps, nor did they trap in grid systems, nor did they continue capture-recapture studies for more than a few months (Muul, 1968; Jordan, 1948; Sollberger, 1943; Burt, 1940). For purposes of comparison, a one-year study was conducted at Connetquot River State Park on the south shore of Long Island, from Oct. 1973 - Oct. 1974. The park was not as well-suited to a study as was Kalbfleisch. Security on the 1400-hectare area was difficult to maintain, so traps left out from one day to the next were often stolen. The distribution of squirrels in the park was patchy, corresponding with the distribution of red maple-black gum swamps (see Figure 4). Both this patchiness and the presence of localized spagnum bogs made it infeasible to trap in a grid system. However, an area roughly equivalent in size to the study area at Kalbfleisch was trapped with several intersecting trap lines and gave data sufficient for my purposes.

Kalbfleisch home range data for 1971 and 1972 were reported in Madden (1974:648-9):

> Field data on a free-living group in Dix Hills were obtained by capture-recapture live-trapping and by direct observation. The trapped area was approximately 150 by 250 meters(m), 3.75 hectare (ha), in 1971 and was expanded to 175 by 300 m (5.25 ha) in 1972.
>
> In Dix Hills, the number of recaptures per resident adult squirrel ranged from five to 29 per year, mean 15.0±1.34 (N=12). Four males with fewer than three captures each in two years were considered transients and not included for the purposes of this report. The home ranges of all adults known to reside mainly on the study area during 1971 and 1972 are shown in Figs. 5 (females), and 6 (males). The minimum home range or polygon method (Hayne, 1949) was used to determine home range size. The averages are 0.41 ha for females and 0.53 for males. The adult females' home ranges show little or no overlap, whereas the males' ranges are heavily overlapped and concentrated in areas unoccupied by females. The lack of overlap of female home ranges in conjunction with behavioral observations reported below indicate that females defend their home ranges. Two adult females that appeared in 1972 (A and F in Fig. 5) and lived mainly outside the study area occasionally invaded their neighbors' territories. Invasions may have been possible only when residents were confined to traps. Female A was caught on the western edge of female B's territory 13 times. Nine of these invasions occurred on the same night the resident was caught. The outsider may have found the bait attractive enough to risk intruding on another female's territory, particularly when that resident was unable to respond because she was already in a trap. When on three occasions both intruder and resident were released simultaneously on the same tree inside the resident's territory, the intruder twice left the territory immediately and once was chased off by the resident.

It was quite clear from these results (figures 5 & 6) that females were not behaving the same as males. The 1973 results were more complicated because two very young females of the April brood remained on the area and bred that summer, much earlier than expected. The female ranges are presented separately for January through June and July through December (Fig. 7). This divides the year between the two breeding seasons. Note that broad overlap occurred between females 57 and 45, but these females did not breed in the spring and may not have been territorial. Females 26 and 25 did have young and maintained nearly exclusive home ranges. Female 26 had a large portion of her home range off the study area although two of her brood nests were located in the area in nest boxes which were monitored by the activity recorder (x's on map). During the summer breeding season, female 61 was one of the young females that had a litter. Her home range shows substantial overlap with that of female 25. Number 26 moved farther south and almost completely off the area, so is not included in the summer map. Number 62 did not breed but did seem to have established a territory. Number 45 shifted to the east and remained separate, having a litter that season. Number 57 disappeared from the area. The two female offspring born to No. 26 in the spring disappeared before the summer breeding season. That fall there was a tremendous acorn crop and more juveniles were captured than in any other year (Fig. 11).

In the spring of 1974 there were large quantities of acorns on the ground (as in no other year) and the home range picture was rather different (Fig. 9). There were nine breeding females whose home ranges were mainly on the study area. All of these females had young in the spring, but none bred in the summer, so all data for the year were put on one map (Fig. 9). Some ranges were quite small, while others were a more usual size. The small size of some ranges was partly due to a small number of captures for those individuals. The main peculiarity of this year was the high degree of overlap in the western portion of the study area. In the summer of 1974 breeding ceased to occur, the population decreased, and by 1975 there was a return to the pre-1974 situation. No breeding occurred in the spring of 1975, but some did take place in the summer.

The situation among the males stayed fairly constant throughout the study. In each year there were six breeding-age resident males, except in 1975 when there were eight. Male ranges tended to be clumped in the eastern end of the study area and overlapped broadly. Males were frequently found nesting in groups, sometimes accompanied by a subadult female. For example, males 27, 82, 88, 89, 90, and 91 all nested in the box marked by the x on the map for 1974 (Fig. 9) during the spring. Males 27, 82, and 91 were rarely trapped on the area, although they nested there. Observation showed that their main activity areas were south of the trapped area, so their ranges are not included on the map. This case points out some of the difficulties of interpreting capture-recapture data, although the data seem truly representative of areas of activity. Squirrel activity is usually away from the vicinity of nests used as daytime retreats.

The male data for the summer of 1973 were peculiar in that none of the resident adult males was captured on the study area from mid-August until mid-October, the most active nesting season of the study. This may be a result of exclusion by the breeding females.

The comparative study area trapped at Connetquot was approximately 150 x 200 m (3 ha). Trap success within the trap area was very patchy. Squirrels were caught most often in the ecotonal area between the dry pine-oak forest and the very boggy red maple-black gum swamp (Fig. 12). Weigl (1968) states that G. volans is invariably associated with hardwood forests and does not frequent pine forests unless mast trees, particularly oaks and hickories, are nearby in abundance. Since not all of the study area at Connetquot was used by Glaucomys, it is difficult to give a meaningful estimate of population density. In contrast, the Kalbfleisch area is quite uniform. Therefore, comparison between even these two areas is difficult.

At Connetquot there were broad areas of overlap between female home ranges, but the two older females (1 and 2) seemed to have one large area each that was exclusive of other females (Fig. 13). Females 3 and 4 were caught as young in the fall. Female 4 disappeared in the following spring, while the remaining three females bred. It should be noted that while the range of No. 1 is shown as covering a large section of sphagnum bog, this squirrel was never caught in the traps laid out through the middle of the bog. The lines connect all the traps at which she was caught and these were all situated on slightly higher ground than the center of her "home range". The adult females at Connetquot were the first ones captured and were caught more frequently than any other animals. Adult females: 24 captures each; young females: 14 and 3 captures; males: 9 captures, 2 captures, and four squirrels with 1 capture each. Two of these males were caught just prior to the breeding season and were very likely transients seeking females in estrus. All four females were caught before any males. These trapping data indicate a possible social dominance of females over males at Connetquot as well as at Kalbfleisch, but it appears that they did not maintain exclusive territories at Connetquot, as they did at Kalbfleisch in most years.

The best estimate of population density that I can give is 8 squirrels resident on the area, that is, 2.7/ha. This is comparable with the density at Kalbfleisch, which ranged from about 2.5 adults/ ha in 1971 to 3.7 in 1974.

It seems unprofitable to attempt to compare home range size between the two habitats because the trapping systems were laid out differently, the physical characteristics of the habitat were different, and sample size at Connetquot was poor. Furthermore, it should be kept in mind that the animals at Connetquot did not seem to utilize the entire trap area, but only certain strips of forest, since many traps never caught animals.

The data from telemetered Glaucomys at Kalbfleisch were gathered in order to check the reliability of trap data. All that can be concluded from the data thus far obtained (Fig. 3) is that home range sizes estimated by trapping are not very different from those obtained by telemetry, as long as the squirrel has its entire range on the trap area. Obviously, telemetry is a much quicker way of gathering home range data, but better methods will have to be devised for protecting the transmitter package.

FACTORS AFFECTING MOVEMENTS OF INDIVIDUALS

I. Behavioral Interactions: the effects of dominance and territoriality

Since it was apparent from Muul's work that females will defend their nests, and since Osgood (1935), Burt (1940), and Jordan (1956) found sex-related differences in distribution and trap-response, I began to suspect that the non-overlapping nature of my Kalbfleisch females' home ranges was an expression of territoriality. This was borne out by my behavioral observations, which contradicted some observations in the literature. Several authors (Audubon and Bachman, 1849; Evermann and Clark, 1911; Howell, 1918) described flying squirrels as highly gregarious, living together in groups of 10 or more and feeding and traveling together in even larger groups. Animals from these gregarious populations were docile and did not bite handlers. As stated in Madden (1974:647), "Burt stressed the sociable nature of G. volans in Michigan, writing, 'Never have I seen any indication of antagonism between individuals, either in captivity or in the wild.' However, adult females in Dix Hills are markedly aggressive and were observed to initiate agonistic encounters in a variety of situations.... These conflicting observations seem to be a consequence of variations in social organization between populations of this species."

Observations were made both in the wild and in the laboratory. Feeding stations in BWF1 and in the lab window were very useful. Some observations were (1974:649-650):

Each feeding station seemed to "belong" to one breeding-age female who tolerated use of the station by males and females only when she herself was satiated. Twenty-two out of 25 observed aggressive encounters were initiated by adult females. In the three other cases the quick movements of the animals made it impossible to be certain of their sex. The aggressors usually stamped their feet rapidly and lunged at the intruder, who quickly fled. Several times intruders were slapped in the face and once a resident female jumped on the back of an invading lactating female. Often, an approaching animal would flee if the resident female merely looked up from her feeding.

In July 1972 in 13 hours of observation at the nest tree of a female with young, only one intruder was observed to approach the nest and this animal was chased off the territory so quickly it could not be identified. When a newly caught female was introduced to a captive nonbreeding female housed in a room 9 by 12 by 18 feet, the new female was harassed all night by the resident. The intruder was pursued, repeatedly slapped in the face, and frequently knocked off perches. The chases were accompanied by loud squeals and churring noises similar to those heard during encounters in the wild. By dawn the captives resolved their conflict; the intruder retreated to a nest box on the floor while the resident retained four nest boxes near the ceiling.

The males are more docile than females when handled and are quite tolerant of other males. In all seasons males may be found living in pairs or trios, sometimes accompanied by a subadult female. Unlike a group of about 10 squirrels which I observed traveling and feeding together in Maryland (June 1966), the Dix Hills males do not travel together and even leave the nest separately at different times, usually taking different glide paths. Although small "evening parties" (two to four individuals) were seen in November 1960 at the edge of a southern white cedar (Chamaecyparis thyoides) swamp near Riverhead, Long Island, by Conner (1971 and personal communication), I have never seen such gatherings in Dix Hills. Here, even families tend to travel as individuals as soon as the young are proficient gliders. Groups of from seven to nine individuals were encountered by Gilbert Bergen (personal communication) living in two stumps in pine-oak forest near red maple-lined brooks in Connetquot River State Park (formerly the Southside Sportsmen's Club) in Oakdale, Long Island. They were observed several times from November to January of 1958 to 1961. These may represent winter aggregations, but no groups of comparable size were found in Dix Hills.

When one sex of a species is socially dominant over the other or highly territorial, the members of the dominant sex tend to be larger. This is the case among European rabbits (Lepus europaeus), in which the females are larger and hold territories from which males are excluded (Etkin, 1964), and among territorial female duikers (Cephalopus; Jarman, 1974). One would expect holders of prime territories to be the heaviest animals in the population, as was disclosed by several studies of birds discussed by Crook (1970a). In Glaucomys volans I found that (Madden, 1974:650) "...males generally weigh less than the females, as one would expect if the females are territorial and dominant over the males. The mean weight of 13 adult males in 1971 and 1972 was 68.2 grams ± 1.45, while that of eight adult females was 79.1±1.84. The difference between the means was significant by Student's t-test ($P<.001$). Weights used were those taken when the females were neither pregnant nor lactating."

Likewise, the data for Kalbfleisch in 1973 were 72.9g ± 1.6 (males) and 81.3 g ± 3.1 (significant difference at .05 level). The results at Connetquot are suggestive: females not pregnant or lactating had a mean weight of 73.0 g ± 1.2 ($N=4$) while males were 73.5 ± 3.7 ($N=6$). The difference between the means is not significant ($P>.7$). This lends some support to my impression that Connetquot females are less territorial than the Kalbfleisch females.

Interestingly, the Kalbfleisch weights in 1974 were 69.9 g ± 1.1 (males) and 68.8 g ± 4.2, which are not significantly different ($P>.7$). This was a year when the population density was high, home range overlap was increased, and breeding ceased in the summer. It is reminiscent of Odum's (1955) 11-year study of a Sigmodon hispidus population, in which he found that when numbers of individuals were high the average weight and age decreased. Total biomass fluctuated less than total numbers.

It is now clear that the social behavior of this species varies between habitats and probably with changes in population density. Such lability of behavior would be highly adaptive because it would enable a species to expand into a variety of habitats and to respond quickly to annual variations in resources. Social lability has been observed in some of the more intensively studied diurnal animals, particularly primates (Crook, 1970a; Struhsaker, 1967; Dunbar and Dunbar, 1976), and is not unexpected. Although more difficult to observe in small, nocturnal species, social lability has been found in some, such as Mus musculus (Anderson, 1961; Lloyd, 1975; Crowcroft, 1955).

It has been noted (Davis and Emlen, 1956; Kikkawa, 1964; Summerlin and Wolf, 1971 and 1973) that, among small rodents, dominant animals are more active than subordinants and are captured more frequently. Dominants appear to exclude subordinants from traps either actively by aggression or by leaving a scent mark or more indirectly by causing reduced exploratory behavior in subordinants. Examination of sex ratios might give some indications of differences in activity resulting from behavioral differences between the sexes.

Of 107 individuals caught at Kalbfleisch from 1970 to 1975, 65 (61%) were males and 42 (39%) were females. This ratio differs significantly from the expected 50:50 ratio (Chi-square test; $P<.05$). If only those animals first caught as adults are considered, the ratio is even more heavily skewed in favor of males (71%). Of those animals caught as juveniles, 28 were males (50.9%), 27 were females (41.9%). This is almost exactly as expected. At Connetquot 10 animals were caught in one year and 60% were males.

A preponderance of males is actually a fairly common occurrence, at least among rodents. Layne's 1954 survey of a Tamiasciurus (red squirrel) population disclosed a sex ratio heavily in favor of males. He also found the same to be true of his adult Sigmodon hispidus (1974).

It is probably true that survivorship is poorer among female Glaucomys, not simply that females are more difficult to capture. Female Glaucomys may be limited by their ability to carve out a suitable territory, while males may range more freely, overlapping activity areas with other males as well as with females. Behavioral differences would show up as differences in trappability. Individual resident females were caught more frequently than individual males (females: 16.4; males 11.4 mean number of captures per animal). Also, there were seasonal differences in trappability. While a certain number of males might be resident on the area at a given time, they are not captured in proportion to their numbers, nor are the proportions the same every month. Figures 14 through 19 show the percentages of individual males present as well as the percentage of captures in which they resulted each month of this study, from 1970 to 1975, at Kalbfleisch. These graphs show that males are sometimes not caught as frequently as one might expect from their absolute numbers in the population. The times of lowest capture success coincided with times when females have young in the nest and might be expected to be very aggressive and territorial (April to May, and August to September). The behavior of territorial females probably depresses the activity of males. At other times of the year, or in years when breeding did not occur (e.g.: summer 1974), male captures were in proportion to male numbers or exceeded male numbers. High proportions of male captures occurred during times of estrus: February, June, July. This would be expected if males are most active and investigative at this time.

It should be kept in mind that the sample size is small, so it is difficult to say how much of these variations is due to sampling error rather than activity levels. The frequently occurring drop in males in September (1971, 1972, 1973, and 1975) is probably related to poor data for that month. This is a season when squirrels are busy gathering and storing nuts and do not concern themselves with traps. However, the discrepancies between percentages of individuals and percentages of captures in other months are probably real.

Layne (1974) found seasonal changes in the sex ratio of _Sigmodon hispidus_ and attributed them to changes in the behavioral interactions between males and females. This would influence their relative trappability. Layne noted that females were most readily caught when juveniles were on the area. Otherwise, it was more common to catch males. As expected, it was the adult age class in which this seasonal variation was most pronounced. Furthermore, males actually had reduced movements and less home range overlap with females during peak periods of juvenile abundance. Female home ranges overlapped each other less than male home ranges overlapped each other. It had already been demonstrated in the laboratory that pregnant and nursing _Sigmodon hispidus_ are highly aggressive and that subordinant individuals are less exploratory than dominants

(Summerlin and Wolf, 1973). At Kalbfleisch during the summer nesting season of 1973 no male *Glaucomys* of breeding age were captured on the study area. It appears that social structure in *S. hispidus* and *G. volans* may have strong similarities.

Jordan (1956) trapped 48 *G. volans* in black oak-hickory woods in Illinois in February and March. In his first 5-day trapping period 20 of the 22 captures were females. The overall sex ratio was 16 males to 32 females. Jordan suggested (p. 294): "The preponderance of females in the traps indicated that there was a sex-related difference in the activity of flying squirrels at that time of the year. This may have been related either to a dispersal of females from the usual winter concentrations of these animals following breeding, or to an increased demand for food as a result of pregnancy."

Likewise, my trap records show that resident females appear in the traps before males do. At Connetquot, all 4 females were trapped before any of the six males were. At Kalbfleisch, in the central portion of BWF1, 3 females were trapped, then six males. As the trapped area was expanded, six more females were caught, then a mixed series of squirrels having a more random sex ratio.

These results all indicate that female *G. volans* are more exploratory than and socially dominant over males.

II. Habitat and Social Organization

In a review article on the relationship between social organization and the environment, Crook (1970a) discussed the status of research in this area and suggested some generalizations. Of particular interest is his statement that close correlations exist between the social organization and the ecological niche of a population. He discussed the work of Jarman on the range of social structures found in ungulates and stressed its importance in demonstrating the involvement of a social factor in population dynamics. Jarman (1974) argued that the dispersion of ungulates is related to the spatial and temporal distribution of food plants. The duikers and dik-diks of the forest and forest ecotonal areas have territories, live in pairs or alone and show little sexual dimorphism. The relevant part here seems to be that the resources are scattered and the animals maintain a similar dispersion pattern. Concerning the Kalbfleisch squirrels, one could hypothesize that the females are dispersed on the best parts of the habitat, as far as food resources are concerned, while the male groups with associated subadult females are on the periphery of and also overlap female territories. In that case, one would expect to be able to demonstrate differences in the habitat used by the territorial and non-territorial animals.

As in the tropical rain forest, the temperate forest food supply is scattered both spatially and temporally; and, if resources other than food can be limiting, then the picture becomes even more complex. Although flying squirrels sometimes use leaf nests, rearing of young and overwintering normally take place in tree holes. The availability of tree holes might be limiting at the peak of the breeding season or during a severe cold spell. Likewise, water supplies in the form of rainwater collected in tree holes might limit the population in long periods of dry weather on woodlots where no ponds or streams occur. Examination of disappearance rates for males versus females might give some indication of differential mortality, but this is difficult to assess because it appears that subadult females may be subjected to some of the same stresses (or advantages) of peripheral living which affect the non-territorial males. Furthermore, in very good years there may be no difference in survival between the two groups, while in very poor years young females could adopt a strategy of delayed first breeding and perhaps achieve an advantage over those females which breed unsuccessfully.

The approach taken in the following section was to examine the relationships between resources and social behavior.

Vegetational Analysis at Kalbfleisch

As mentioned above in the section on home ranges, I thought that there might be a relationship between the distribution of home ranges and variations in the habitat in BWF1 at Kalbfleisch. Some areas were utilized mainly by females, other areas mainly by males (Figs. 5-10). Different sections of this forest differed slightly in species composition, elevation, moisture, exposure, and undoubtedly many other factors. Yet, compared with squirrel habitat in other localities, this trap area was relatively uniform, composed of dry oak-maple woods uninterrupted by bodies of water. At Connetquot, the squirrels were found where pine-oak woods interdigitated with red maple-black gum swamp. At Riverhead, Long Island, squirrels occur near the interface of pine-oak forest and isolated white cedar swamps (personal observation and Conner, 1971). In Shad Landing State Park, Maryland, squirrels were observed along the edge of the narrow bald cypress swamp bordering Corker Creek, which runs through pine-oak forest.

I felt that the relative uniformity of the habitat probably influenced the degree of territoriality, since territories were observed only at Kalbfleisch and "evening parties" only at ecotonal localities. On the other hand, small local variations in the forest at Kalbfleisch probably influenced which sites were used by breeding females. The actual positioning of home ranges could be a reflection of those factors which are important for rearing young. With this possibility in mind, I did a survey of all trees in my trap area having a diameter at breast height greater than three inches.

The forest in BWF1 is approximately 51% *Quercus velutina*, 28% *Acer rubrum*, 18% *Quercus alba*, 0.5% *Carya ovalis*, and the remaining 2.5% composed of *Castanea dentata*, *Cornus florida*, *Betula lenta*, *B. populifolia*, *Sassafras albidum*, and *Quercus prinus*. Judging from the remains found in nest boxes, the few *Carya* on the area are a major source of food in the autumn and winter. It was thought that the few scattered hickories might play a role in the shapes and positioning of the squirrels ranges. However, mapping of the tree species did not disclose a relationship between the distribution of any tree species and the positions of home ranges. The resultant map was first compared by overlaying maps of squirrels' home ranges. No consistent differences could be found between the tree distributions on male and female home ranges; at least, not by mere inspection of the maps.

Next, a statistical analysis was done. The trap area was divided into quadrats, each centered around a trap location. The data on all adult squirrels captured from 1970 through 1974 were tallied for each quadrat. As shown in Table 1, I listed the number of captures of males at each trap location, the number of different males caught, the same information for females, the total number of nights each trap location was used, and the numbers of each species of tree in the 25 by 25 m quadrat surrounding each trap location. This information was compiled for 34 quadrats, those which were trapped most often. The total number of trap-nights was used to compensate for differences in the data that might be due to differences in trapping effort between locations. A stepwise multiple regression was run on an IBM 370 computer using a program modified by R. C. Madden. Tests were made for correlations between the occurrence of squirrels and the occurrence of tree species. There were six dependent variables for each trap-quadrat: total captures, total individuals, male captures only, individual males, female captures only, and individual females. The independent variables were the numbers of each of the nine species of trees. No significant correlation was found by this method. The highest correlation coefficient was .319, still not significant at the .05 level.

The distributions of captures at the various trap sites were compared with a Poisson distribution. Neither male captures nor female captures showed a random distribution, but instead were clumped. There was no significant correlation between the occurrence of males and females at traps (correlation coefficient .30), and neither did they exhibit repulsion.

Habitat Differences between Kalbfleisch and Other Localities

Since the distribution of tree species did not yield a significant correlation with squirrel captures, other resources were examined, as described in Madden (1974: 651-652):

> The question arises as to why the Dix Hills population differs from other populations. It is possible that the distribution of resources on an area influences the degree of territoriality of a population. Resources on the Kalbfleisch study area seem uniformly distributed. If a female in a uniform habitat were to defend an area large enough to insure that she and her young have adequate nest sites, food, and watering places, then her chances for reproductive success would be enhanced. A survey of these resources was conducted on the study area.
>
> Females in the wild and in captivity were observed to move their young frequently, apparently because the nests foul quickly and become flea-ridden. Muul (1968) emphasized the necessity for a large number of nests per individual, and suggested that the availability of nest sites may be limiting for the species. A survey of tree holes on the Dix Hills study area revealed an average of 4.8 cavities per .25 ha, or 7.7 per average territory. This is a minimum density since it is not possible to locate all tree holes from the ground. Twelve nest boxes were put up early in 1971, but squirrels did not use them as nest sites until spring of 1972. Then, only three boxes were regularly used as daytime retreats. Most of the boxes had been used as temporary hiding places and some as feeding sites. It would seem that if nest sites were in demand, there would have been heavier use of artificial nest boxes.
>
> Watering places at Kalbfleisch may be another factor influencing the social organization of this population. Muul (1968) has noted that this species was never found more than 100 yards from a pond, stream, or swamp. My squirrels are at least 200 m from the nearest pond. Jordan (1948) assumed that this species does not require surface water in midsummer because all streams on his study area dried up at that time. There never are any streams or ponds on my study area, and I found that the squirrels drink at small tree holes which retain rain water all year. Many tree holes were found and no doubt many remained unnoticed. Only on one day at the end of a prolonged rainless period were all observable holes dry. At all other times during these two years a majority of holes contained water. Squirrels were frequently observed drinking at these holes and a survey showed that there is at least one waterhole in every squirrel's home range.

It is here suggested that the concentration of any one of these resources should lead to a reduction in territoriality. Perhaps this is the situation near localized wet forests of cypress, cedar, and red maple where groups of squirrels have been reported. These swampy areas may be exploited by numerous squirrels living mainly in surrounding pine-oak woods. As long as all resources are evenly distributed over an area, as they are at Kalbfleisch, it will be advantageous for females to stake out territories large enough to insure reproductive success.

Variations in Social Organization Between Populations

In reference to my resource analysis at Kalbfleisch, I stated that one would expect territorial defense of a home range to be advantageous when resources necessary for reproduction are evenly distributed over the area, while clumping of resources might make gregarious behavior more advantageous (Madden, 1974). Wilson (1975: 52) discussed factors which result in different social organizations: "Theoretically, the prime factor for colonial roosting or nesting ... is that the food supply must be considerably variable in space and time. That is, food must appear in unpredictable, irregular patches in the environment. If it occurs in patches but is available in certain spots permanently or at predictable intervals, individuals will simply roost or nest as closely as possible around those spots, and fly singly to them. But if the food is evenly distributed through the environment and concentrated enough to more than repay the energy expended in its defense, the individuals will stake out separate territories from which they exclude other birds."

Wilson refers to this idea as the "Horn principle" (p.525), which was explicitly stated in Horn (1968). Horn particularly emphasized that colonial nesting or other aggregative behavior did not occur simply because of a lack of territoriality. Rather, there are positive pressures favoring aggregation. The most important of these selective pressures seems to be the need for efficient foraging methods in an area having unpredictable resources. Thus one lucky individual can signal the group as to the presence of a new food source.

Smith (1968) emphasized the function of territorial behavior in Tamiasciurus (red and Douglas squirrels) as the defense of food that is stored for winter. This stored food included cones stored in damp places so that seeds are not shed and fungi that have been cut and dried, as well as alder and birch catkins. The only two occasions on which territory broke down were when Douglas fir trees were producing pollen. This is a very rich source of food which cannot be stored and is present in patchy locations superabundantly for only two or three weeks in the spring. More than one squirrel may feed in a producing tree, with little evidence of aggression. Smith noted that there is an advantage for squirrels feeding in groups when food is highly concentrated and superabundant. They can give each other warning against avian predators, which are especially likely to pick off squirrels feeding at the tips of branches.

Likewise, in Shad Landing, Maryland, a "party" (term used in reference to a group of uncertain composition: Crook, 1970b) of flying squirrels fed together at what seemed to be a localized food source. Glaucomys home ranges at Kalbfleisch contain predictable, usually dependable resource supplies, while those at Connetquot or Shad Landing appear not to. In the swamp areas the squirrels probably feed on a variety of buds, fruits, seeds, and insects whenever and wherever they become locally abundant. This corresponds to the type of situation in a tropical rain forest. The flower buds, and later the seeds, of red maples are particularly favored when available. Pine seeds are eaten when available, as are moths, blueberries, and, of course acorns. At Connetquot, nesting is easiest in the red maples, where cavities are abundant. The nearby pine-oak forest is very poor in nest cavities; indeed, I could not find any in several acres bordering the maple-gum swamp in my study area. Weigl (1968) notes that deciduous trees have more hollows than coniferous trees, a result of the different ways in which the two types of tree decay. The mixed forest at Kalbfleisch with its scattering of hickories and abundance of red maples and oaks may provide adequate food and nesting resources all year.

Goertz _et_ _al_.(1975) in a study of _G_. _volans_, installed over 100 nest boxes in different woodlots and noted a correlation between nest box usage and habitat. In immature pine-oak-hickory forest in Louisiana, nest box occupancy was 20% and squirrels were observed living in groups of up to 10. In nearby mature oak-hickory-red maple forest occupancy was only 1% of boxes and groups were smaller (1-3). The authors felt that the difference in box occupancy between habitats was a reflection of the scarcity of natural nest cavities in the pine-hardwood forest and not a measure of differences in flying squirrel numbers.

Rowell (1969) observed that mangabeys (_Cercocebus_) were more aggressive when feeding on large single fruits than when the food was dispersed as small fruits evenly spaced and abundant. When feeding on sprouts growing in piles of elephant dung, they defended the food as do Tamiasciusus at their cone caches. The food source, in order to be profitably defended, must be either quite predictable in its occurrence or gathered into a supply that will obviously last for awhile.

That one species can be adapted to respond to either situation is apparent from the literature (Anderson, 1961; Lloyd, 1975), although examples of regionally comparative studies of variations in behavior are few. That the same animal can alter its behavior depending upon seasonal resources or other circumstances can be seen in oilbirds (Steatornis caripensis). These cave-dwelling birds defend small nesting territories on ledges but feed in evening flocks which increase their chances of locating food supplies in scattered trees (Snow, 1961).

Lack (1968) devoted a large portion of his book to the discussion of the relationship between habitat, nesting dispersion, and type of pair-bonding. Although the comparisons were made mainly at the subfamily level, the data do indicate a close relationship between the dispersion of resources and the dispersion of nesting birds. The best indicators should be those species whose behavior varies from habitat to habitat, yet there is little discussion of this variation, probably because detailed studies of this nature are rare. However, Lack does mention Skutch's observation that Eumomota superciliosa (Momotidae) may be colonial if nesting holes are sparse where food is plentiful. This species normally nests solitarily, as do the other motmots.

The relationship between the dispersion of resources and animals has been more explicitly demonstrated by Wolf and Hainsworth (1971) and Gill and Wolf (1975). Work on sunbirds and hummingbirds has demonstrated a relationship between the density of nectar supply and the degree of territoriality in a population. When nectar is very sparsely distributed or extremely dense, no territories are set up. When it is intermediate in density and evenly distributed, territoriality occurs. Likewise, the yellow-faced grassquit (Tiaris olivacea) is territorial on Jamaica, but social on the Central American mainland (Pulliam, et al., 1972). On Jamaica, grassquit habitat is evenly distributed, but on the mainland it is very patchy.

In Tamiasciurus both sexes can be territorial and defend separate territories. Smith (1968) felt that the resource being defended in his study area was food. He felt that shelter was not limiting because these squirrels could and often did use outside nests of leaves and holes in the ground. Water was often obtainable from succulent vegetation, and seemed usually abundant. In Smith's area territories were non-overlapping, closely packed, and advertised by vocalizations. Kemp and Keith (1970), working with Tamiasciurus hudsonicus in mixed forest habitats in Alberta found that many adults, mostly males and non-breeding females, lived in suboptimal habitats and were not territorial. Those animals living in prime habitat, spruce forest, were territorial and did not usually intrude on other territories. The non-territorial portion of the population was a surplus that constantly intruded in search of recently vacated territories.

It appears that prime habitat for Glaucomys volans exists on the western part of my study area. The limits of crowding were reached in 1974 after a peak of abundance of an important resource.

Territorial behavior and changing nutritional levels probably resulted in the return to pre-abundance Glaucomys density. In addition, this species is adapted to patchy habitats in ecotonal areas where gregarious behavior is an important response to spatially less predictable resources.

While territory may not control absolute numbers of a population, it does appear to regulate density on optimal habitat with some flexibility allowing for variations in available resources. As in Kluijver and Tinbergen's study (1953) of three species of titmice, territory is compressible, but only to a certain extent, and this is dependent upon the quality of habitat. Bordering suboptimal habitats act as buffers and absorb excess population. Crook (1970a:198) emphasizes that, "...social structure is a dynamic system expressing the interactions of a number of factors within both the ecological and social milieux that influence the spatial dispersion and grouping tendencies of populations within a range of lability allowed by the behavioral tolerance of the species." Thus, lability of social behavior can be a species characteristic just as advantageous as specialization or stereotypy. The importance of understanding the full range of social lability of a species cannot be overstressed. It is only through an understanding of the interplay of ecology and behavior that we will untangle the intricacies of population regulation complicated by spatial and temporal variations in habitat and social structure.

Another important consideration is, what is the energetic cost of territorial defense in Glaucomys? Feasibility of defense is greatest in birds, and Glaucomys shares some of their advantages. As

Wilson says (1975:265), "Absolute feeding territories are more frequently encountered in birds, which have excellent vision, access to vantage points, and the flight speed to scan relatively large forage areas. This difference between the two major vertebrate groups is the reason why territoriality was originally elucidated in birds, and why its general significance in that group has never been in doubt, while in mammals the subject has always been plagued by seemingly inadequate data and semantic confusion." Glaucomys volans has certain advantages over non-gliding mammals in that it is an arboreal species with a very rapid method of locomotion. Flying squirrels can easily seek vantage points and can patrol the entire border of a home range in a matter of minutes. Furthermore, mammals have an advantage over birds in that they can use scent to mark a border through time without the actual presence of the defender or the continuous expenditure of energy.

Time budgets taken by Smith (1968) in summer showed that very little time was spent by Tamiasciurus in territorial defense. A lactating female spent 0.25% to 0.76% of time in defense; an adult male spent 0.3% of his activity time in territorial defense. Smith felt that these figures were at a maximum for established adults since the observations were made at a time when young were attempting to set up their own territories. Most of the squirrels' defense activities were vocal (76%); the rest was time spent in chases. It seems likely that territorial defense is not especially burdensome for flying squirrels either.

III. Population Characteristics

In a study of a living population it is not usually possible to determine the age structure, mortality and natality rates, or even causes of mortality. Yet, information can be culled from long-term trapping records that gives an approximation of population structure and changes.

Causes of Mortality

Causes of mortality are difficult to pinpoint. Predation on the Kalbfleisch population did not appear to be severe, but then one does not expect to observe predation as it occurs. Only one case of predation was noted: a squirrel caught in a trap was released, killed, and partially eaten by a predator, probably a domestic cat. The owls which commonly occurred here were screech owls, which probably do not take prey as large as *Glaucomys*. A great horned owl was present on the area for a week or two. Examination of six owl pellets of small and large sizes revealed a variety of prey (one *Blarina brevicauda*, one *Rattus novegicus*, and an indeterminate number of small *Sylvilagus floridanus*), but no *Glaucomys*. Indeed, *Glaucomys* are rarely found in owl pellets (Pearson and Pearson, 1947; Moore, 1945).

No *Glaucomys* were caught that appeared to be in poor health, although many were heavily infested with mites and fleas. Several young of the very numerous 1973 brood had pink swellings on the head and shoulders that appeared to have been caused by parasitic fly larvae. This was the only year that such swellings were seen, and they occurred only in the young. No traces of the swellings were observed in those young which were re-examined the following spring.

Disappearance Rates and Longevity Estimates

Figure 10 shows the appearance and disappearance dates of all flying squirrels examined at least three times at Kalbfleisch. Actual and estimated birth dates are given, as well as time of first capture. Juveniles could be recognized as such up until about four months of age. The grayer pelage, low body weight, small nipples, and fully-furred scrotum of juveniles were all used to distinguish from adults. There is no way of aging living adult squirrels, so estimates of age are to the most recent breeding season for those animals first caught as adults. Therefore, age estimates are a minimum.

This type of data might give indications of differences in longevity and mortality between the sexes and suggest differential selective pressures. The sex ratio, which is nearly 50:50 in juveniles but is 71:29 (males:females) in adults, suggests that mortality is greater in the territorial sex, the same sex that bears the energetic cost of raising the young. Since trap data reveal only appearances and disappearances from trap records, which are affected by social factors, these may not be true estimates of longevity; however, in a large sample over a long period of time the relative estimates might be suitable for comparison. The mean minimum estimated age for females was 14 months ± 1.9 (maximum 48) and

12.2 ± 1.5 (maximum 51) for males. Although the mean longevity for females is slightly greater than for males, the difference is not significant by Student's t-test (P=.5). These data do seem to indicate that although juvenile females disappear from the population at a higher rare than males, those females that establish territories have the same life expectancy as males.

It would probably be misleading to construct a life table based on these data, especially since the sample size is not great and the population varied. However, the cohort for which I have the most data might be examined in more detail, if we keep in mind the fact that this cohort (summer, 1973) was the largest and was raised at a time of a bumper crop of acorns. Twenty-two animals were handled which could definitely be classified as juveniles born in late summer of 1973. Half were females, four of which established territories and survived until 1976. Other females of this cohort disappeared by their first breeding season. All four resident females of this cohort had litters their first breeding season (Fig. 21), did not appear to have litters the summer of 1974 although two had shown signs of estrus, definitely did not breed in the spring of 1975, and all showed signs of estrus and some were lactating in the summer of 1975. The males of this cohort had four survivors into 1974 but only two continued into 1975. However, the total male population remained high because there were males of undetermined age living on the area. These data should not be interpreted as actual indications of mortality since some young are likely to disperse and survive in other areas. It appears that once a female establishes residency, she is likely to remain on her territory quite awhile, whereas a male is likely to move around. The appearance of six unmarked males of unknown age (Fig. 20, squirrels 88-93) at the time of estrus of resident females suggests that males are especially mobile when searching for estrous females.

A time-specific adult mortality rate can be calculated as did Kemp and Keith (1970), for the period summer 1973 to summer 1974: adult mortality rate = adult population in summer 1974 x percentage of adults two years or older in summer 1974/ adult population in summer 1973 = 75%. This is much larger than Kemp and Keith's 21% mortality from 1967 to 1968 in a territorial Tamiasciurus hudsonicus population. Of course, these are actually disappearance rates since nothing is known of dispersal in G. volans. However, Kemp and Keith's mean annual mortality rate of 48% for adults suggested that there were large year to year variations in mortality, although this discrepancy could be due to errors associated with the different types of estimates they used. When my data were used to calculate time-specific yearly mortality rates of adults, very large year to year variations were evident: 1971-1972, 51%; 1972-1973, 25%; 1973-1974, 75%; 1974-1975, 46%. It appears that although 1973-1974 was a good year in terms of food resources and young produced, adult survivorship was poor relative to other years. The population was stabilized by heavy losses of adults as well as juveniles.

That population density in squirrels responds quickly to acorn crop has been observed before in fox and gray squirrels (Sciurus niger and S. carolinensis). Baker (1944) did not give a quantitative estimate of acorn crop, but did state that in the fall and winter of an exceptionally good acorn crop the numbers of these species of squirrels in Texas rose very high but returned to normal levels the following spring and remained stable in the following years, which were poor in acorns.

An examination of the reproductive cycle is in order before consideration of a possible mechanism by which populations might quickly respond to yearly resource variations.

Reproduction

Muul (1969) presented the results of experiments which indicated that photoperiod alone is sufficient to induce breeding in flying squirrels. He speculated that "the annual minimal photoperiod triggers reproductive activities and photoperiods equivalent to the annual maximum influence the post reproductive regression of gonads." Reversal of the natural photoperiodic regime was associated with a reproductive cycle that was six months out of phase with that of animals on a natural cycle. Speeding the decrease and then increase of photoperiod so that minimum photoperiod occurred two months earlier than the natural minimum was associated with descent of testes two months earlier than in those experimental groups exposed to a natural light regime.

Muul's conclusions were based mainly on the pattern of testicular descent and also on the time of birth of litters, and not at all on the estrus cycle. Most workers gauge the onset of breeding in a population by the descent of testes, and take no indication of the readiness of a population from the condition of the females' vulva. Yet, male Glaucomys may actually make poor indicators of the breeding status of a population since their period of sexual readiness is so much longer than that of females. Individual females (in this study) in the wild were observed to be in estrus for a few short periods in a year, while males had scrotal testes for six months or longer each year. Females were considered to be in estrus when they had swollen, reddened vulva, as described by Sollberger (1943). This criterion is supported by the observed dates of litter appearance, both in this study and in Sollberger's. Vulva will swell to five times their usual size during estrus and remain this way for five days if the animal is not mated. The cycle repeats 11 days later, according to Sollberger. The gestation period appears to be 40 days.

While vulva condition seems reliable for judging reproductive condition in females, descent of testes may be a very poor criterion for reproductive condition in males. Work by W. Davis (1963) with Glaucomys sabrinus indicated that the scrotal position of a testis is not necessarily correlated with the presence of motile sperm. Horwich's (1967) study of the social behavior of the gray squirrel (Sciurus carolinensis) suggested that in this species a male can have scrotal testes and not be in breeding condition. Layne (1954) found distinct developmental peaks in the growth cycle of the seminal vesicles and prostate in Tamiasciurus hudsonicus. These developmental peaks corresponded closely with the females' estrus periods, but had no external signs. Layne suggested that the breeding season of males might be more restricted than had been previously assumed. However, he could not demonstrate that the condition of seminal vesicles and prostate actually does indicate preparedness to breed. Hoffman and

Kirkpatrick (1956) clearly showed that the classification of squirrels according to age or breeding condition based upon the length or weight of testes or accessory glands is not reliable. Only histological examination for mature sperm gave conclusive results.

I noticed that testes were less than ½ full-size at time of descent and took 2 or 3 weeks to reach full-size. I have considered males as in reproductive condition only when testes are full-size (about 35 mm or greater).

Even if testis position were a good indicator of testis activity, it would still be desirable to know the cycle of estrus since this is the cycle that seems to be most tightly selected. Understandably, the selective strategy of the males might favor a long period of productive readiness so that no chance for impregnation is missed. Ovulation is a fleeting occurrence and it must be precisely timed so that young are born at an optimal season for rearing. In some years a female might survive to leave more young if she does not breed during both winter and summer seasons. One might expect that ovulation would depend upon more immediate, more short-lived, more variable cues than daylength. Indeed, photoperiod might be the primary, initial triggering mechanism in the breeding cycle of both sexes, as Muul suggests; however, one would expect to find a cue that provides the fine-tuning of the cycle to the vagaries of yearly variations in conditions.

Muul stressed the lack of variability in those experimental animals exposed to natural changes in photoperiod. Yet he noted also that animals in the wild did not exhibit as precise a cycle of testis movement as captive males. My data from animals in the wild indicate variations of a month or more in the onset of testis descent and enlargement between years. Clearly, there are other factors involved in addition to photoperiod.

Admittedly, it is more difficult to determine the breeding status of a population by examination of females. The changes which occur in the vulva are not as obvious or as long-lasting as the changes in male genitalia. Females may show external signs of estrus for only five days at a time (Sollberger, 1943). However, females were routinely examined for swelling of the vulva, and the data are shown, along with data on testis descent, in Table 2. In those seasons when no females were observed in estrus, no young were subsequently caught. It is not safe to conclude, though, that they never were in estrus those seasons. It has been stated that there may be much loss of embryos in this species (Asdell, 1964), at least in some seasons. Uhlig (1956) found a discrepancy between litter sizes <u>in utero</u> and in the nest. So, rather than population regulation by skipping ovulation, embryo resorption may occur. Or, the two mechanisms may both operate depending upon conditions. Embryo resorption may act as a back-up control in case of poor resource supplies during pregnancy.

Asdell's (1964) conclusion that there is much embryo wastage may be very misleading, however. It seems to be based on Uhlig's data from his 1954 observations. Uhlig (1956) stated, "Comparison between embryo counts and litter counts in 1954 also revealed a 10 per cent decrease, 4.00 to 3.60 young." This was based on 19 pregnant females and 10 with litters in the nest. The difference in mean litter size between the two groups may be due merely to sampling error. My analysis of his data by Student's t-test indicates that the difference between the means is not statistically significant, that a difference larger than this might be expected to occur in 50% of all studies of this size where in fact they are the same.

My data on estrus point up an additional interpretative problem. Apparently most females did not become pregnant at the first signs of estrus in late winter. Since spring births occurred in early or mid-April, then impregnation must have occurred (40-day gestation assumed) in mid-February to early March. First signs of estrus were as early as late January. Shook (1976) noted that on several occasions captive females appeared to be in estrus, but they failed to produce litters. It is not clear whether impregnation fails to occur, or embryos are resorbed, or even if embryo storage might occur. There simply is no evidence to determine what is happening. Whatever, it appears that factors other than photoperiod are important in determining when a female will breed. In this regard it is interesting to note that the summer estrus is much more predictable than the winter estrus, which is to be expected if estrus depends on both nutrition and photoperiod. The nutrition of squirrels in summer should be quite constant from one year to another, but not so in late winter.

The evidence suggests that nutrition regulates breeding in the Kalbfleisch population and that acorns are an important component of the food supply. If body weight can be taken as an indication of nutritional state, then the weights of breeding age individuals at various times of the year might give some indication of the importance of nutrition in controlling breeding. Tables 3a, 3b, and 3c give the mean monthly weights of breeding age individuals, while Figures 22-26 present the same data graphically. The most obvious characteristic of these data is that weights appear to fluctuate widely (more than 10% within a year) and rapidly. This could be attributed to poor sample size, which would result in sampling errors that might give these erratic results. However, Figures 27 and 28 give the weight records of individuals for which at least two weights are known. These graphs show that individuals fluctuate in body weight as much as the population means would suggest. These fluctuations are not attributable merely to pregnancies of females; males are shown separately.

Davis (1963), working with Glaucomys sabrinus in Saskatchewan, found similar variations in his animals' weights. He found a decrease in weight after May and an increase as fall came on. My animals showed a similar seasonal pattern in 1973, but other years were different. The average weight for his females, even when not pregnant, was always greater than the average for males (157 g vs. 141 g).

Figure 11 compares the numbers of juveniles captured in various seasons for all years at Kalbfleisch with the mean annual weights of adult males. The data show a rough correspondence between reproductive success and adult weights, both reaching a peak in 1973. 1971 appears to make the correlation a poor one because juvenile captures were low; however, Figure 21 shows that many females were lactating in the summer. There were many births but for some reason young were not trapped. Comparisons are complicated by small weight samples for some months. Since the weight at time of onset of breeding, or perhaps for a month or two previous to the breeding season, might be critical in determining the time of breeding in the winter, these data were extracted for the best data years and shown in Table 4. Winter 1971-1972 and 1972-1973 were times of successful breeding, although apparently not as successful as the summer of 1973 (figure 11). The times of coming into reproductive readiness coincide with high weights in breeding adults. In females, the two months preceding estrus were times of consistently high weights, with small drops during the month preceding first estrus. In males, however, there was a 10.3 gram increase in mean body weight during the month preceding testis enlargement in the 1971-1972 season and an 8.5 gram increase during the two months preceding enlargement in 1973. Mean weights at the time of enlargement were 76.1g and 79.3g, quite high for males in general. It should be noted that the time of greatest weight in the males did not coincide with that in the females. The time of greatest weight in the males was at the time of testis enlargement, which preceded estrus by about six weeks. Table 4 shows the weights of males in brackets next to the weights of females for the same time period. Males actually showed a decline in weight following the peak at testis enlargement. It may be that a consistently high level of nutrition is necessary for breeding in females while a sharp turn for the better is sufficient for males. However, it is not clear why male weights should fluctuate so greatly, whether this is an actual reflection of seasonal nutrition, a hormonal effect, or perhaps the result of incresed activity in seeking estrous females. Males did make up a high proportion of captures at these times (see section on sex ratios, pp. 30-32). It may even be that females are excluding males from areas of best food resources.

Another factor in the reproductive success of a population is the age at onset of breeding. Prior to 1973 I assumed that females did not have young until they were one year or even 1.5 years of age. This appeared to be the situation among females I observed. Also, Sollberger (1943) noted that females born in the spring sometimes had litters the following spring, but did not have litters before one year of age. Jordan's (1948) data indicated that summer-born females did not have young in their first spring.

In 1973 squirrels number 61 and 63 had litters in September, even though they were born in April of that year. Furthermore, four females born in August of 1973 were observed in estrus or pregnant the following February and March. I had expected breeding to be delayed until the following August. For example, females 45 and 62 did show such a delay. The interesting part about this early breeding among the 1973 offspring and the associated rise in juveniles trapped (see Figure 11) is that it coincides with a superabundant acorn crop in the fall of 1973. Only a very subjective measure of crop size can be given for different years, but the fall of 1973 can be said to have been quite remarkable. The acorns remained plentiful on the ground until late spring of 1974. This occurred in no other year of this study. It appears that the large crop which ripened in August-September 1973 may have increased survival of dispersing young so that large numbers were captured in October and November. Many of the juvenile females remained on the study area rather than dispersing, and had litters of their own, earlier than one would have expected from previous years. The appearance of the acorn crop does not adequately explain the early breeding of Nos. 61 and 63, which must have been pregnant in July or early August, at less than 5 months of age and previous to the ripening of acorns.

C.C. Smith (1968) noted a very marked relationship between breeding activity of Tamiasciurus and variations in conifer seed production. This refers only to conifer species preferred by Tamiasciurus; they did have alternative food sources. One year when the preferred cone crop failed, only 6 out of 55 T. douglasii females (collected by shooting) showed signs of having raised spring litters and none of 35 collected later that year showed signs of summer births. The testes of males decreased in size before the usual second annual breeding season. Evidence of litters was not found again in this population until the following year, in late summer, when all females observed were lactating. It was also at this time that the new cone crop was available and it was a fairly heavy crop. Smith's data on relative tooth wear (squirrel molars have determinant growth) as an index of age suggest that heavy recruitment of juveniles occurred two years before the crop failure, reduced recruitment the year before, and none that year. The first of these three years was a good crop year while the second was poor.

Tamiasciurus hudsonicus in Smith's study area had only one litter a year and depended on lodgepole pine production in most years, although this is not the preferred food. While breeding occurred every year in this species, the time of breeding and size of litters were subject to variation. In one year breeding was delayed one month, which made it possible for nursing females to use the new Douglas fir crop. This is a preferred food species that failed the previous year, so squirrels did not have stored reserves of these cones from the previous year. This year was particularly good for Douglas fir and the crop size may have influenced litter size. Litter size was 3-5 with a mean of 3.75 while the previous year it was 2-3, mean 2.88. The difference was statistically significant.

Smith showed that lodgepole pine seeds are difficult to extract from the cones and consequently yield their energy at only $\frac{1}{4}$ the rate of Douglas fir cones. This would account for the preference of Tamiasciurus for Douglas fir cones and the adaptiveness of a delayed breeding season, as well as the feasibility of raising large litters in good Douglas fir years. However, the actual population control mechanism is still unclear. Smith points out that evidence of future crop size is available in the form of buds which appear on the trees at least a year before the cones will be mature. The success of cone pollination is evident before parturition. Also, food caches might serve as indicators. However, the most likely explanation is that when the squirrels eat the superabundant buds their nutritional level serves as a direct triggering mechanism for coordinating breeding with cone crop. Kemp and Keith (1970) explained the synchronization of Tamiasciurus hudsonicus reproduction with spruce cone production in this manner. This seeming "anticipatory response" was probably due to the rich bud supply on the spruces during the previous winter. The squirrels utilized this energy source and perhaps this is what resulted in the high level of squirrel breeding which occurred at the time of good cone production.

Figure 11 shows the numbers of juveniles caught each breeding season at Kalbfleisch with adult male weights. The peak of weights coincides with the peak of juvenile numbers, which was also the peak acorn crop. The preceding years had moderate crops, the following year, fall 1974, the crop failed. Also in agreement are the data on coincidence of breeding in females, Figure 21 and Table 2.

IV. Activity

At Kalbfleisch, a multi-channel portable spring-driven Esterline-Angus event recorder was installed in a watertight shelter (a garbage can) 20 meters north of J13 in BWF1. From April 1972 until October 1973 as many as 8 channels were rigged with sensing devices at different nest boxes, a natural cavity, and a water hole. For each monitored site a light unit was taped to one end of a wooden bar two feet long and the photocell at the other end. The wooden bar was nailed across the front of a nest box or tree, at the lower end of the entrance hole. Since the volume of data obtained in this way was quite large, only some records are shown (Figures 29-34).

The apparatus at Kalbfleisch was similar to a system used for a short period by Muul (1968) in the field in Michigan. However, Muul had difficulty obtaining data on free-living animals because they vacated nests that were rigged with apparatus. The only data presented by Muul are those recorded off nest boxes of 30 captive animals in a single large outdoor enclosure. He stated that the patterns of activity of these animals closely agreed with those of free-living animals. It should be kept in mind that these 30 animals were not breeding and had access to only 10-15 nest boxes, whereas free-living individuals usually have many more shelters available and a larger area for activity.

Both Muul's system and mine have the same limitations and susceptibility to malfunction. The recordings indicate only the comings and goings of squirrels. It is not possible to tell exactly when time is spent inside or outside the nest without direct observation. Both my observations and Muul's show that on any given night there are periods of activity separated by periods of inactivity. My squirrels had definite "nap-times" during the night. Recordings do not always make this clear, especially when several animals occupy the same nest and are following their own individual activity patterns.

Malfunctions were frequent and had many causes. Falling trees pulled down wiring and nest boxes. Raccoons and gray squirrels attempting to enter nest boxes or cavities dislodged the photorelay units so that they were no longer aligned with the light beam. Nest material protruding from an entrance could interrupt the beam and register false activity. Heavy, driving rain could work through the seal of a unit and destroy the filter, upsetting the alignment of the beam. A squirrel peering out of its nest for long periods, as squirrels are wont to do occasionally, gives a misleading picture of activity levels.

For comparison of captives with free-living animals, one two-week sequence of recordings was made in April 1972 in the laboratory. Three adult animals (two females and a male) were sharing a nest box on uneasy terms. They were in a small room exposed to daylight. Neither of the females was breeding. This recording (Figure 29) can be compared with that made from the nest box north of J14 on channel 6 of the recorder at Kalbfleisch, April 1973 (Figure 30). This box was inhabited by a non-breeding female (no. 57), two adult males (nos. 27 and 19) and a fourth unidentified squirrel.

Comparison of the data from captive and free-living squirrels shows that the captive squirrels have higher levels of activity for longer periods of time at the nest entrance than do free-living squirrels. This would suggest that the data presented by Muul (1968) are not precisely comparable with the activity of free-living squirrels, although the generalizations which he makes are probably correct. The wild squirrels show fewer comings and goings which occur during shorter units of time and within a very discrete period of the day (correlated with the onset and end of darkness in the forest).

The free-living squirrels were just as uneasy in their relationships as the captive squirrels. Appearance of the squirrels in the evening was usually preceded by noises from within the box. There were the sounds of kicking against the sides of the box and of vocalizations of the type which are associated with aggressive and defensive behavior. These vocalizations could be characterized as squawking, squealing, and churring, all described in the section on vocalizations.

Recordings supplemented by observations showed that individuals had different activity patterns. Usually, several minutes after the first sounds of activity within the box, a squirrel would peer out of the entrance for a minute or more. Then it might withdraw and soon the same or another squirrel would appear. Shortly, one or two squirrels would leave the nest. Then it might be 30 minutes or more before the next squirrel appeared and exited. This was the case on April 24, 1973, for example (Figure 31), when two squirrels exited at 7:15 p.m., and the other two could be heard vocalizing and thumping inside, but none exited again until after 7:50. Furthermore, different squirrels go in different directions upon leaving. On this night the first squirrel to leave went southwest and was caught several minutes later in a nearby trap. The second went southeast, and the other two were not observed. However, it should also be noted that the same squirrels all exited between 8:30 and 8:40 p.m. on May 7 (Figure 31). Two went to the southeast and two to the southwest, but they did not travel together as pairs. The weather was clear on both nights, so it was not rain that delayed the exit of the two in April. Thus, in addition to variations between individuals, there is variation in the behavior of a single individual. Likewise, Weigl and Osgood (1974) noted in G. sabrinus that individuals sharing a nest have their own individual activity patterns. This was also true of my laboratory squirrels.

Unmarked sections on the recordings show either times spent outside the nest or times spent in the nest and these two possibilities cannot be distinguished without observation. However, observation of wild squirrels did show that they were usually active for an hour or two after darkness, then returned to the nest, apparently for a nap. This nap period was followed by one or more periods of activity outside the nest, usually in the middle of the night and at dawn. My captive squirrels regularly followed this type of pattern and so did Muul's squirrels. Weigl and Osgood (1974) learned from telemetry that G. sabrinus is active in summer for about two hours after darkness begins, then are inactive until a few hours before dawn, when they have a second, shorter activity period. Squirrel no. 105, when released at Kalbfleisch with a transmitter attached, became active (in mid-November) shortly after darkness, remained in the vicinity of his nest tree for about 20 minutes, disappeared from the area, but returned to his nest (which he shared with other male squirrels) by 8:00 p.m. and remained there for at least 2 hours. Afterwards he became active for varying lengths of time.

The onset of activity was quite consistent with photoperiod, as can be seen especially well in Figures 31 and 33. When weather is bad, the squirrels look out of the nest entrance at their accustomed times, but do not leave until conditions improve. This is not clear from the recordings because a squirrel peering out registers on the recorder just as a squirrel leaving the nest would. On May 13, 1973 (Figure 31), for example, it began to rain at sunset. No squirrels were observed leaving box no. 6, and no squirrels were captured that evening before 10:00 p.m. Squirrels did emerge between 10:30 and 11:00 p.m., when the rain had ended. This is not clear from the chart recordings. The same events occurred on April 19, and the recording can be examined in Figure 31.

Muul's data show a fairly good correlation between intensity of activity and the average temperature during the period of activity. My squirrels show the same general depression of activity during very cold weather, but this is best expressed in trapping records rather than chart recordings. Simply because squirrel activity did not occur at a given box does not mean that the residents were inactive; squirrels often changed nests.Squirrels were active even on the coldest nights, but seemed to have shorter periods of activity (Figure 34). Sometimes the morning activity period was omitted entirely, especially during prolonged cold periods when the temperature remained below minus one degree C for several days as from January 6 to January 13, 1973. This was noted when traps were left set until dawn in the winter. There was no evidence of torpidity in my population. It should be noted, though, that winters on Long Island are not as severe as those in Michigan. Monthly winter <u>averages</u> in minimum temperature in Michigan in 1962-1963 ranged from about -1°C to less than -13°C, while at Kalbfleisch in the winter of 1972-1973 the lowest temperature recorded was -12°C.

Muul had difficulty obtaining data on free-living squirrels because they vacated nests that were disturbed. My squirrels did the same, but in at least one case, a female moved her young to another box that was being monitored (Figure 32, June 5, 1973).

In another case, the attachment of apparatus to a box seemed to cause a squirrel to move into it (Figure 33, July 7, 1972). The use of nest boxes the first year they were installed was very light, being confined to use as feeding stations and emergency shelters. In the following year, however, when cross-bars were placed beneath entrance holes for the attachment of electronic equipment, there was increased use of the nest boxes. One breeding female made extensive use of the box located 25 meters south of J13. It seems that the addition of cross-bars made the smooth fronts of the boxes easier to climb on, so the entrance holes became more accessible. The change in the appearance of the boxes was usually investigated the same day the change occurred. The nest box attached to channel 1 had been unused for a long time as evidenced by spider webs and the remains of caterpillar exoskeletons. Figure 33 shows the appearance of a squirrel at the entrance of the box only one hour after the unit was set up. The squirrel established residence here.

Four of the boxes were regularly used as day-time nests and at least three others were used occasionally during the day and as temporary night-time shelters. This is comparable with results of Sonenshine, et al. (1973) in which squirrels were captured in 3 out of 15 boxes in one locality and 21 out of 128 in another locality, in Virginia.

In summary, activity in G. volans has a general pattern which is shared by all, but details differ between and within individuals. This is a point which is not brought out by Muul's data but is suggested by Weigl and Osgood's work on G. sabrinus. Squirrels which share nests, even family groups, do not travel and feed together; at least, not at Kalbfleisch. My observations on peninsular Maryland suggest that this is not the case in all populations of this species, that a closer examination of the behavior of flying squirrels in patchy habitats will probably disclose that foraging squirrels frequently occur in large groups.

Behavioral Repertoire

Before it is possible to analyze the social behavior of a species, it is necessary to have basic information on the behavioral repertoire of individuals. The following is a compilation of my observations on both captive and free-living squirrels, as well as pertinent information in the literature.

Locomotion

Walking, whether on horizontal or vertical surfaces, is accomplished by a crossed extension pattern, as described by Eisenberg (1963), where the contralateral limbs are in synchrony. Walking usually occurs in sporadic spurts, as is the case in the thirteen-lined ground squirrel, Spermophilus tridecemlineatus (Wistrand, 1974). Also similar is their method of movement when disturbed, aptly called a "slink" by Wistrand. The body is held flat on the ground, with the back slightly concave. The animal moves in short, rapid spurts. This slink is often used when the animal is investigating a strange object. The nose is extended toward the object, and the animal may back off frequently and approach several times from slightly different directions.

When foraging in the leaf litter, squirrels frequently use a leaping motion, which seems to be a more efficient method of getting around on the ground. Of course, progression over long distances is best accomplished by gliding. The length of the glide is dependent mainly on the height of the launch point, but squirrels do have considerable control of the rate and direction of descent. Glides as long as 40 m from heights of 14 m were observed in this study and glides up to 50 m are reported in the literature (Jordan, 1948). Gliding squirrels can make surprisingly sharp turns and can drop abruptly in mid-glide to avoid obstacles. Descent can be in a tight spiral when the landing point is directly beneath the launch point. Squirrels frequently use the same launch and landing points over and over again and usually have glide "paths" that are habitually followed.

Preparatory to leaping, the squirrel assumes a hunched posture with all four feet gathered together under its body. The head is thrust forward and downward and is usually bobbed up and down rapidly several times. This bobbing movement may be a means of gaining perspective and so gauging distance (as in owls). A squirrel preparing to leap from an unfamiliar perch or to make a particularly difficult leap will often spend a minute or more bobbing its head. Squirrels released outside their usual area of activity rotated on a high perch and bobbed in several different directions. Only a few quick bobs or none at all are observed before a routine glide.

Eisenberg (1963) described head-bobbing in heteromyids during exploratory behavior, when a sound is heard. The startled animal stands on its hind legs with ears and vibrissae extended, and bobs its head. Eisenberg suggested that this is a way of testing the air. It may not serve quite the same function in Glaucomys, or Eisenberg may be incorrect in his interpretation.

Landing is accomplished by swinging the hind legs forward and bringing the tail abruptly to the vertical position. When landing on a tree trunk, squirrels usually swoop around to the side opposite that of their original approach. Upon landing, they quickly run up the trunk, often in a spiral. Presumably, these are evasive tactics that aid in the avoidance of owls.

When running or gliding, the vibrissae are directed forward, as are the pinnae. The vibrissae, which may be over 55 mm in length, probably aid in landing. The involvement of the pinnae lends some support to the suggestion by Muul and Alley (1963) that ultrasonic vocalizations uttered during glides may serve in echolocation. However, there are no published analyses of these ultrasonic sounds. One of the adult females on my study area had a clouded, milky-white lens and was probably blind in that eye. Yet, she had no difficulty gliding. It was not possible to determine if this particular animal produced ultrasonic sounds during her glides; however, she as well as others, often produced pulsed vocalizations during the glide (see sonagram in Figure 36), and these vocalizations were later found to have ultrasonic components which registered on an ultrasonic detector which I carried in the field. Further details are in the section Vocalizations.

Photographs (Muul and Alley, 1963) show that squirrels usually shut their eyes just before landing. However, I determined with photographs that my squirrels did not close their eyes.

For a description of the patagium musculature, which controls the shape of the patagium and therefore the glide pattern, and a description of the styliform cartilage, which supports the leading edge of the patagium, see Gupta (1966).

Gliding in Young

Gliding is a difficult activity which involves a great deal of skill acquired by learning. Obstacles such as leaves, twigs, and branches must be avoided and landings must be evasive as well as precise. Collisions could be injurious: Flying squirrels weighing in at 75 to 100 grams must develop considerable momentum during a glide.

That the control of gliding is not instinctive was evident from my observations of young nestlings in the wild and the lab. Young Glaucomys just learning to walk can be tossed into the air and they respond by spreading their legs, as will any vertebrate when it falls. However, the young squirrels do not land in a controlled glide, even though the patagium acts as a parachute and softens the landing. The motions involved in spreading the patagium appears to be instinctive in young Glaucomys, but the first jumps occur accidentally or in an attempt to follow the mother and do not result in successful glides.

As the female leaves the nest the young attempt to stay close to her. Usually she bursts ahead and launches into the air, leaving the young behind, on the nest tree. Development is slow in Glaucomys and it is not until the young are about 8 weeks old that they attempt to follow the mother after she leaps. I observed the early glides of the two offspring of Female 26 in July 1972 at Kalbfleisch as well as the first glides of Glaucomys born in captivity.

The young made short leaps in the direction of nearby trees. They landed either on the ground or by catching onto (or perhaps colliding with) a branch in mid-glide. Frequently they slipped and fell to a lower branch. Glides were clumsy, noisy, and often accompanied by vocalizations, especially clicking noises and sharp squeaks. This is in contrast to the glides of adults, which are usually silent and well-controlled. Young squirrels practiced the same glide patterns over and over again until after a week they were almost as proficient as adults. They habitually followed the same glide paths. Behavior and vocalizations were similar both in wild and captive young.

Exploratory Behavior

Flying squirrels show a preference for certain "glide paths", an observation which has been made by many observers. An individual squirrel may glide to the same sequence of trees, even using the same launch and landing points, night after night upon leaving its nest. It may use the same escape route when repeatedly released from the same trap. Squirrels are capable of using secondary routes when the preferred route is blocked by an observer, but these alternatives seem to be used with reluctance. The use of preferred routes may be based upon the reliability of a "kinesthetic memory" as suggested by Lorenz (1952) for water shrews (Neomys fodiens). That is, the rhythm of muscular actions involved in getting from one point to another by a particular route may be memorized and then rigidly, even blindly followed although this is not necessarily the most direct or easiest route between those points. Muul (1968) points out that when the first landing point in a glide path of a squirrel leaving its nest was removed, the squirrel attempted to land at that spot anyway. It tried four times from four different launch points. Of course, this may be more a matter of a panicked animal not looking before it leaped, since it was being forcibly driven from its nest. The important point is that it landed where the site would have been even though it no longer existed, and the squirrel was using memory to direct its motion. This is similar to Mohres' "wiederorientierung," the following of habitual pathways by bats when in familiar surroundings (see Griffin, 1958, for description of Mohres' work).

Whatever the basis, flying squirrels do exhibit a remarkable memory for the 3-dimensional positioning of objects in their environment. The adaptive advantage is obvious, the mechanism is not so clear. Apparently, squirrels spend a large proportion of their time checking out any changes in the physical aspects of their home ranges. This may be the basis for the observation (Seton, 1909) that they are "curious" and therefore easily trapped. New nest boxes, or the addition of perches to already established nest boxes bring on an almost immediate response. One or more resident squirrels soon show up and investigate the changes. This can be seen in activity recorder tracings (Figure 33), or directly observed in the wild or in captivity. Stringing cord across an animal's enclosure, adding or subtracting nest boxes, moving furniture, all bring about an immediate and sharp increase in exploratory behavior.

New objects are approached by "slinking". The animal may approach and retreat repeatedly with rapid, jerky motions. Vibrissae and pinnae are usually directed forward on the approach and backward upon retreat. When contact is finally made with the object, the squirrel sniffs and nibbles at it.

As mentioned above, Seton commented that the species is easily trapped because of its "curiosity". This may be due to the necessity for a squirrel to know its home range well, or it may also relate to territorial patrolling. My trap records show a tendency for squirrels to be caught in a different trap every night, as if the squirrel were patrolling its home range and checking out each different object (Table 5). The squirrels seem to remember which traps they were previously caught in and attempt to avoid these traps, getting caught in a new trap every night. Burt (1940) noticed a similar occurrence: the female which he captured most often was caught 22 times in a summer in 14 different traps. My trap records show that many squirrels (Table 5: squirrel numbers 4, 23, 24, 25) managed to use a different trap every night for the first seven captures. One male squirrel (No. 21) used 13 different traps before he started to repeat.

Trap records from this study also indicate that females either are generally more exploratory than males, or are more active because of the necessities of territorial patrolling, or have a decided preference for the peanut butter and sunflower seed bait used in this study. Individual females are caught more frequently than individual males (mean number of captures for females: 16.4; males: 11.4). Lockie (1966) noted that weasels (Mustela nivalis and M. erminea) were caught more often at the edges of their territories, in traps where there were neighbors close by who might intrude. The demands of patrolling a territory, says Lockie, may create a home range usage pattern that is really a territorial patrol pattern. This patrolling might give the observer the impression of "curiosity" and would result in the observed increased exploratory behavior. However, my analysis of trap records to determine whether or not females are caught more often than one would expect at the edges of their home ranges turned up no significent differences between observed and expected captures at peripheral traps.

Defense

When disturbed in the nest or in a trap, a squirrel may roll onto its back and strike at the intruder with all four feet. Usually the mouth is open and the animal makes squealing and churring (vibratory) noises (sonagrams, Figures 38 and 39). Ordinarily there is no attempt to bite unless the animal is actually grasped. However, some females did actively attack handlers, lunging and biting before they had actually been touched. Males never did this.

Young in the nest show this kicking response as early as eight days of age. At six weeks they may stand on their hind legs and box with their front feet as well as bite. Shook (1976) terms this behavior "sparring." This includes the face-slapping behavior of female Glaucomys attacking other adults, which occurs in the context of territorial defense or the repulsion of sexual advances. It is similar to the slower speed "pawing" observed by Horwich (1967) in Sciurus carolinensis when discouraging rough sexual play.

A captive Glaucomys volans defending her two-month-old young from the investigations of an adult male chased him frequently. When she lowered her head and pointed her nose straight outward and then ran directly at the male, he turned and retreated. When her young attempted to approach him, sniffing, he gave a low vibratory noise, almost a growl, and twitched his tail from side to side while stamping his hind feet. This male showed the same behavior when a strange adult male was introduced. It appears to be a dominance display. Horwich (1967) described foot-stamping behavior in dominant males of Sciurus carolinensis in response to the approach of subordinate males. He noted the similarity of foot-stamping in several species of sciuridm including Glaucomys volans. The tempo of the stamping increases with decreasing body size between species.

Maintenance Behavior

There does not seem to be any particular sequence of grooming movements. As in Wistrand's (1974) Spermophilus tridecemlineatus, flying squirrels seem to groom only those areas that need attention at a particular time. The tongue is used to wash the forefeet which are then drawn across the face or up over the ears from back to front, or along the lower jaw from back to front. After feeding, the lips and sides of the face are wiped on the substrate in the direction of the grain of the fur. The tail is pulled around in front and licked. Scratching of the anterior portion of the body is done with extremely rapid movements of the hind leg. Hindquarters are scratched with the incisors. One animal was observed for several minutes scratching its back against Smilax vines.

Stretching is done on a vertical surface while hanging by the hind toes. The back is arched and concave. The forelegs are stretched outwards, pulling the patagium taut.

Feeding, Food Storage, and Drinking

Food is held in the fore-paws and may be eaten while the animal is hanging vertically by its hind toes or while sitting on its haunches with the tail curled over the back. Nuts in the shell that are not to be eaten immediately are rotated between the jaws and then notched with the incisors so that they can be easily gripped. Food to be stored is carried to the ground, tucked under the leaf litter and hammered into place with the incisors. According to Muul and Alley (1965), food is also stored in crevices in the bark of trees and sometimes in tree crotches and holes, although I have never observed the latter in the wild. Avenoso (1968) noted that Muul and Alley (1963) are the only authors who report this, all others describing storage under leaf litter. I frequently released animals after daybreak so that they could be more easily followed. Released animals travelled directly to a water hole and drank for a long time and then went to food cached under the leaf litter. They were seen to lift a leaf and pull out a sunflower seed, acorn, or hickory nut.

Frequently, when foraging for feed or when storing an item, flying squirrels produce a series of faint squeaky snorts. The sound is made with the mouth closed. This is most often done when the squirrel is investigating a possible place to store an item of food, or while actually hammering the nut into position. The sound is like that of air being rapidly and explosively inhaled and exhaled through the nose. This may be a way of doing a quick olfactory check of the site so that it can be easily located again.

Avenoso (1968) reported that the odors from food-storage sites remained on the stored food and were highly inhibiting to restoring of that food. It appears from his work that the odor from these sites may be the most important clue to squirrels as to the "processing history" of a food item. With a marking system, squirrels do not waste energy in the repetitious storing of the same items. Food storage sites do seem to be remembered. I have seen squirrels proceed directly to stored food from distances of 3 m or more, when it seemed unlikely that the odor of the food alone could have led them to the site.

Detailed study of food-storing behavior in this species has been done by Avenoso (1968) and Muul (1968), and their results are briefly described below. Unfortunately, the adaptive significance of food-storing behavior is still not understood. Smith and Follmer (1972) suggested that storing of nuts in the "scatter-hoarding" method used by many sciurid species is adaptive for individual squirrels because the food is (1) spread out and therefore less accessible to deer and other squirrels, and (2) out of sight and so inaccessible to jays or other birds. I would also suggest that nuts stored under the leaf litter retain their moisture longer and so remain plump and suitable as food all through the winter. The same observation was made by Lastinger (pers. comm.). I propose that a very important function of storage is to improve upon the keeping qualities of the nuts. In support of this, Fox (1974) reported that gray squirrels often cut out the embryo of white oak acorns without husking the nut. White oak acorns, unlike those of black oaks (meaning the entire subgenus), germinate in the fall rather than lying dormant over the winter. Food reserves in the taproots of seedling white oaks are no longer available to squirrels. It appears that (p. 2) "embryo excision is a coevolved tactic against white oak's autumn germination". Up to 60% of stored white oak acorns may have their embryos excised by gray squirrels, but none of the more plentiful black oak acorns are treated in this manner. According to Fox, it takes more time, per unit of energy consumed, to cut out and eat embryos alone than to eat entire acorns. This tactic on the part of gray squirrels suggests that storing behavior may be just as adaptive as a means of preserving food as it is for making it inaccessible to other animals.

Smith (1968) observed a great deal of storage activity by _Tamiasciurus hudsonicus_ and _T. douglasii_ in British Columbia. He noted that the larger species of fungi were cut and placed on logs and trees in exposed locations where they dried. This made them available as food all through the winter, while uncut fungi froze and disintegrated. Whole cones were cut down from the trees before the seeds were shed. They were stored in damp places, which resulted in the retention rather than release of seeds. The cones became large packets of reserve food, rather than scattering their seeds. The tiny scattered seeds would have been difficult to gather and defend.

Avenoso (1968) noted that Florida flying squirrels (G. volans querceti) store nuts although the absence of subzero winters or snow cover in Florida would seem to render these activities unnecessary. He assumed that storage means simply stockpiling food against times of hardship. Here again, it seems to me that the main adaptive advantage of storage would be to preserve the food in usable condition, rather than simply accumulate it. He did observe that squirrels stored partially opened nuts, but says nothing regarding embryo excision.

This is not to imply that squirrels are aware of what they are doing. Simply, a population which develops storage habits that preserve the food will be more successful than one which merely accumulates food.

Muul (1965) and Avenoso (1968) both reported that photoperiod influences the level of storage activity when temperature and humidity are held constant. Muul found that decreasing day-length increased storage activity while increasing day-length was accompanied by a sharp drop in storage activity. Avenoso, however, did experiments which showed that activity was strongly correlated with the availability of large numbers of ripe nuts and that storage ceased when unstored nuts became scarce and storage sites became filled. Thus, I would conclude that the initial triggering mechanism for food storage is decreasing day-length, but that storage behavior is also modified by the availability of items suitable for storage. The scent of storage sites which clings to previously stored nuts inhibits the unnecessary and wasteful re-storage of food as the unstored crop dwindles.

Vocalizations

Glaucomys produces a variety of vocalizations, some of which have been described in the literature (Wood, 1910). There are no published sonagraphic analyses, however, and verbal descriptions are not accurate enough to characterize these calls.

1) Alarm call

This is a sequence of high-pitched squeaks which begins at ultrasonic frequencies. The animal can be observed repeatedly opening its mouth and heaving its sides as if expelling air and vocalizing, but no sound is heard. This activity is continued for a minute or more until the utterance becomes just barely audible to the observer. The sounds which are made gradually descend in frequency with each utterance until they soon register on a Uher 4000 Report-L recorder with AKG D200E microphone (respond to frequencies up to approximately 16 kHz). The call may be repeated at intervals of 0.2 to 0.6 seconds in continuously descending frequencies until the sound is rather like the "clear whistling note" described by Wood, and, at lower frequencies, having a rasping quality. The main output can be in the 9 to 12 kHz range with components down to 3kHz, as in Figure 35a or much higher pitched as in 35b. These and other calls were analyzed on a Kay spectrographic analyzer (Kay Electric Co., Pine Brook, N. J.). Audible calls in mid-range have ultrasonic components that register on a McCue - Bertolini ultrasonic detector with a 15 to 200 kHz filter.

When first startled, animals often give a sharp, high-pitched squeak and then ascend a vertical surface, moving with quick, jerky motions. When 2 m or more above ground, the animals usually freeze, with head pointing upward but stiffly drawn back into the neck and shoulders, hanging by fore- and hind-claws, tail parallel with substrate and ears either laid back against the skull or held stiffly vertical. They usually remain silent for several seconds and then begin the alarm call pattern described above. Alternatively, an animal may move to a horizontal perch, assume a sitting position with back hunched and tail slightly curled, and give the alarm call. The repetition of the call at regular intervals for several minutes suggests to me that this may be a "mobbing" call, such as are used by many bird species to advertise the location of a predator. Seton (1909) thought this was an alarm call and described it as a "prolonged squeak not unlike the complaint of a red-eyed vireo whose nest is threatened."

Blair (1935) noted that G. volans in Florida can be located by their squeaking in response to an imitation of the scream and hoot of a great horned owl; however, just about any loud noise elicits the same response. That great horned owls are predators of flying squirrels has been verified. Moore (1945) reported that flying squirrels made up 5-10% of the remains in great horned owl pellets in Putnam Co., Florida. Pearson and Pearson (1947), however, found no Glaucomys in the pellets of barn, short-eared, or long-eared owls in Delaware Co., Pennsylvania, although Glaucomys were fairly common in that area. Seton (1909) noted that a barred owl in Manitoba contained a G. sabrinus in its stomach.

I observed a screech owl which roosted about 25 m from a flying squirrel feeding station. This observation was made on an October evening in an oak-hickory-maple-beech forest near Clarksburg, West Virginia. The owl began to call and soon the flying squirrels near the feeder started their alarm calls. However, they did not approach or retreat, so it is not clear that they were definitely responding to the owl's vocalizations and not to some other stimulus. The owl flew away and the squirrels gradually ceased to call.

At Worthington State Park on the New Jersey side of the Delaware Water Gap on August 14, 1975, I heard many flying squirrels vocalizing in the early evening in the large trees over the campsites along the river bank. At about 2 a.m. that same night a screech owl called for several minutes. While the owl called, I heard a flying squirrel give two short, sharp squeaks, but not the prolonged, repetitive squeaks described above.

Likewise, a screech owl once roosted 5 m from my lab window at Kalbfleisch. Squirrels were feeding on the window sill, but there was no observable interaction between the two species. There is nothing in the literature to indicate that screech owls prey on _G. volans_. The only period during which a known avian predator of flying squirrels occurred on my study area was in mid-November, 1975. A great horned owl was frequently observed roosting and flying near the lab, but no squirrels were vocalizing.

Sollberger (1940) observed that if a stone is thrown at flying squirrels which are giving the alarm call (he termed it "tseeping"), they will call more loudly. I have observed that in both captive and wild animals the loud notes of one squirrel will cause others nearby to run upwards and freeze for several minutes. Often, other squirrels will join in giving the alarm call. This vocalization was most frequently heard in the wild from late April to November, when leaves were on the trees, and squirrels were most active. It appears that squirrels give the alarm call only when they are in a position safe from predators. Captured animals just released from a trap will give the call at almost any time of the year, but only from an elevated position, and not in daylight. The main periods of vocal activity seem to be in May, early June, and September, which are times when young are leaving the nest. Those breeding seasons when young were not captured, especially spring 1975, were notably quiet.

As mentioned, the high frequency portion of the alarm sequence grades downward into a series of rasping squeaks. It appears that frequency is related to intensity of stimulus. When first disturbed, squirrels give the higher pitched end of the sequence, sometimes preceeding it with short, sharp squeaks or a short burst of "chittering". As the observer remains quiet, the pitch of the continuous squeaking descends into a rasping hiccoughing. If the stimulus is renewed, the higher frequency calls are evoked. Other squirrels in the vicinity (25 m or more distant) may be heard giving the high-pitched call, but they usually cease after a few minutes. The closest squirrel may keep up the calling for 10-15 minutes, until the observer has been silent and unmoving for about 10 minutes, or has moved away completely. Thus the response to disturbance seems to be graded, with frequency relating to intensity of disturbance. Contrary to my observations on adults, Shook (1976) noted an inverse correlation between distress call frequency of nestling G. volans and degree of distress. Greater stress elicited audible components, higher frequencies were more common under "mildly stressful conditions."

2) Pulsed sequence

Another vocal pattern, mentioned in the section on locomotion, is that represented by the sonagrams in Figure 36. The sequence in 46a was recorded while an animal was gliding at Kalbfleisch. The sound is similar to that made when the coarse teeth of a plastic comb are rubbed. The three pulses illustrated are spaced at intervals of about 0.1 second, each pulse lasting about .04 second and having a frequency range between 8 and 10 kHz. Two of the pulses also show lower frequency components at 5 to 7 and 2.5 to 3.5 kHz. The introductory note has an ascending and a descending component both between 10 and 12 kHz. A similar sequence given by a captive squirrel is shown in Figures 35b and 35c. The pulsed set of calls was infrequently heard in any season. It may be given when an animal is gliding or quickly running up a tree trunk. Several times it was heard while I was observing young squirrels just learning to glide. They repeatedly slipped and crashed down to lower branches, uttering this vocal pattern during the descent and while running up the trunk. This audible sequence does have an ultrasonic component, but it has not been recorded.

It is difficult to assign a function to this pulsed pattern of calls. It may simply be part of the alarm pattern. On the other hand, it may be an orientation signal. It is unnecessary to hypothesize an ultrasonic orientation system, as suggested by Muul and Alley (1963). Flying squirrels could use low frequency orientation cries, as do several species of birds. Four species of swiftlets in the genus

Collocalia use orientation vocalizations which have their highest energy output at frequencies below 10 kHz, and, in *C. hirundinacea*, having an average repetition rate of 10.6/second (range 4.0-17.1) when the bird is flying out of an unobstructed mine shaft (Fenton, 1975). The repetition rates in the short sequences of *Glaucomys* calls shown in Figure 36 are 6 to 9/second, within the range of swiftlet signal repetition.

Theoretically, the wavelength of an optimal echolocation signal should be shorter than the diameter of the object to be detected. If flying squirrels are using signals merely to locate suitable landing sites on tree trunks several inches in diameter, then their observed audible vocalizations ought to be more than adequate. The signals used by *Collocalia hirundinacea* are suitable for detection of objects as small as 1.5 mm in diameter, as experimentally determined by Fenton (1975). Flying squirrel signals of the same wavelength might be suitable for avoidance of even small twigs, which could be damaging if collided with at gliding velocity. Muul's data (1968) suggest that bright moonlight inhibits squirrel activity in outdoor cages, probably as an adaptation to reduce predation. Radvanyi (1959) noted a similar occurrence in *G. sabrinus*, but apparently neither worker noted a reduction of activity on very dark moonless nights, when visually directed glides would be especially hazardous.

Weigl and Osgood (1974) noted that *G. sabrinus* glide less frequently in bad weather, when visibility is poor. This could be related to the reluctance of animals to leave the vicinity of shelter in wet weather. I have observed that *G. volans* will curtail activities and seek shelter at the onset of rain. That they glide less when visibility is poor does not necessarily indicate that they do not echolocate, but may simply mean that they prefer not to get wet.

If flying squirrels do echolocate, it is possible that they use ultrasonic as well as audible signals for different types of information about their surroundings. This has been suggested for shrews, which produce audible twitterings of which the function is unclear, as well as ultrasonics which appear to be used for orientation (Gould, Negus, and Novick, 1964). Use of a bat detector (filter 15-200 kHz) determined that the pulsed series in Glaucomys has ultrasonic components; however, until these sounds are recorded and analyzed nothing more specific can be said about the qualities of these ultrasonics.

As more and more experiments have been performed to test for echolocation behavior in various species of mammals, it has been found that many species in different orders possess this ability. The insectivores Sorex cinereus, S. vagrans, S. palustris, and Blarina brevicauda can echolocate (Gould, et al., 1964). Echolocation has been demonstrated in all species of Microchiroptera which have been studied and some species of the Megachiroptera (eg.: Griffin, 1958). Likewise, many cetaceans make extensive use of echoes (eg: Norris, Prescott, and Perkins, 1961). So far, however, none of the gliding mammals has been shown to echolocate. Although Tate (1947) described the sounds of Cynocephalus (Dermoptera), a very large glider from Malaya and the Philippines, as resembling those made by sharply drawing a pencil point across the teeth of a comb, these vocalizations have not been recorded and analyzed. Gould, et al. (1964) suggested that the use of echolocation has evolved more than once among mammals (as it appears to have in birds), but it seems more likely that this ability is a primitive characteristic for placentals and will be demonstrated to have an even wider occurrence than is presently known.

At this point it cannot be conclusively stated that flying squirrels do or do not echolocate. That they do occasionally bump into objects does not rule out echolocation since bats, too, will use vision or memories of habitual flyways and disregard information from echoes (Masterson and Ellins, 1974; Griffin, 1958). Only carefully controlled experiments will resolve the question.

3) Faint, squeaky snorts

Given in rapid series, these sounds are described in the section on feeding and food storage. No recording was obtained because this is a very low intensity sound.

4) Louder, single snort

A single sound with a very nasal quality. The main energy production is between 8 and 12 kHz, with additional faint components between 16 and 15 and below 6 kHz. It has a duration of .08 second. (Figure 37) It has been given by a resident captive female and male. This call may be limited to dominant animals. The male snorted at a newly-caught male that was introduced for the first time. The snorting was accompanied by foot-stamping and tail-jerking, both apparently signs of threat in a dominant animal.

5) Churring

A very explosive, vibratory noise which is repeated over and over again. It is often interspersed with high-pitched squeals and low-pitched squawks. The main output is between one and two kHz. Usually the animal is on its back with all four feet poised to kick at a provocateur. The incisors are bared and the ears are laid back. Churring noise may be produced when an animal turns its side toward an aggressor. From either position the defensive squirrel may kick at an aggressor, but does not usually bite. Sonagrams were obtained (Figure 38).

6) Squeals

The main energy output is between 13 and 15 kHz with lower frequency components, usually at 10-12 kHz, and a duration of .07 second (Figure 39). These sounds are produced at the height of an agonistic encounter and are usually interspersed with squawks.

7) Squawks

The energy output is fairly evenly distributed from 3 kHz downward (Figure 40). These sounds are emitted by defensive animals during physical contact with an aggressor.

8) Faint squeak

A call given by mothers to their young when attempting to lead straying nestlings back to safety. No recordings obtained; this is a very low intensity sound.

The Possible Role of Scent in Behavior

Whenever scent glands in mammals have been studied they have been found to play an important role in social behavior, especially territoriality and dominance (Thiessen, et al, 1974; Muller-Schwarze, et al., 1974; Ralls, 1971). This aspect of behavior is very difficult to study and was not among the main objectives of my work; however, I do have some observations to record.

I noticed that the ventral cream-colored fur of many Glaucomys was often spotted with cinnamon brown in the throat and pectoral region. Adult females had especially large, deeply colored spots in the mid-ventral pectoral and throat area and additional spotting on the belly. It appears that this coloration may be caused by a skin secretion. Occasionally the "staining" of the fur appears to spread outward from the spots resulting in an overall orange-buffy coloration of the ventral fur. Under ultraviolet light the stained fur glows a deep rose-pink, unlike the violet tinge of the fur of animals without cinnamon spotting. Squirrels in some seasons did not have the spotting. Spots were usually noticed shortly before and during breeding seasons. In 1975, when no breeding occurred in the spring, all animals had unspotted cream-colored ventral fur until mid-May, when animals of both sexes had small spots scattered on the chest and belly. By the time the females were in estrus the first week in July, the females had dark cinnamon throat patches and the males had small spots on the belly and sometimes on the jaw below the corners of the mouth. In the previous year, when breeding did occur in the late winter, deep brown spots were apparent by early April, and perhaps occurred even earlier but were not recorded. The spotting was found on all animals but was most prominent on breeding females and young in the nest. The spots were apparent through September and disappeared during October. In 1975 there was a marked decrease in the degree of spotting on all animals during October and November until by early December none of the females had spotting and only two of the males had spotting just anterior to the penis. These males had scrotal testes that were not full-size in early December, but were nearly full-size by mid-December.

To my knowledge, these markings have not been previously reported in the literature. Hamilton (1963) gave a thorough description of coloration in this species, with variations among the subspecies. He described the underparts as pure white, occasionally creamy white. For _Glaucomys volans saturatus_ Hamilton stated that underparts are creamy white or white, sometimes tinged with pinkish buff. However, this subspecies occurs from coastal South Carolina through the Smokies to Georgia, Florida, Alabama, Mississippi, and eastern Louisiana. It is not clear if this coloration is merely a subspecific color variant or the same seasonal change that I am describing. Shook (pers. comm.) did not find any such spotting on his breeding _G. volans_ trapped in the area of Ithaca, New York, so it appears that this characteristic does vary between populations.

This spotting, if it is indeed the product of a skin gland, may contain pheromones which might function in marking female territories, marking young in a litter for recognition by the mother, providing the olfactory stimulus for the "following reaction" of the young (Hailman, 1960) with respect to the mother, marking aggregations of squirrels for group recognition of inhabitants of the same nest, or providing information on breeding condition. Unfortunately, it would take extensive histologic, chromatographic, and experimental studies to determine the nature of these suspected pheromones and their precise role in the behavior of this species. While it seems probable that scent would be used by females to mark their territories, no behavior has been observed which can be confidently described as marking behavior. I have frequently observed animals wiping their chins, throats, and faces against branches, but this may be merely a grooming activity. The attempts of young Glaucomys to follow their mothers suggest olfactory stimuli. Young just barely old enough to crawl attempt to follow the mother when she leaves the nest. As Hailman (1960) suggested, following behavior probably helps the young to develop agility and to learn what items are edible and how to find them. The urge to follow seems to be especially important in inducing young flying squirrels to attempt their first glides, as discussed in the section Gliding in Young.

It may be that the brownish substance has nothing to do with these behavior patterns. Perhaps urine acts as a scent mark: the urine glows yellow under ultraviolet light and can be found spread all over the nest boxes and pathways used by captives. Furthermore, there is a sticky substance on the soles of their feet which may be a sebaceous gland secretion or simply urine (as in bushbabies, Galago, and some other primates). The primary function of this substance is probably to maximize traction, but it might also serve as an olfactory marker of territory. Clean smooth surfaces exposed in a forest or an enclosure where these squirrels live soon show sticky footprints of

Glaucomys.

Avenoso (1968) and Muul (1968) were able to make some statements about the scent-marking of stored food, but even after considerable work, they did not attempt to pinpoint the actual gland, nor were they able to determine the adaptive advantage of marked stored food. The marking secretion is not water soluble, but does lose its effectiveness when the food is washed in fat solvents. It is probably a product of the sebaceous and sudoriferous glands on the lips and jaw (as determined experimentally by Muul, 1968; glands described by Quay, 1963). Quay reported atrophic tubules on the lips and angle of Glaucomys (which species not specified), more developed than in some sciurids, but not as developed as in Spermophilus.

Captive squirrels tend to ignore those nuts previously marked, even though they may be lying in conspicuous places. Avenoso found that free-living squirrels preferred fresh, unmarked pecans over those which had been rubbed on the mouths of squirrels, yet paid little attention to olfactory marks when the pecans had also been physically marked with notchings and scrapings. Avenoso concluded that, since oral olfactory markings are not normally applied without physical markings, it seems likely that olfactory clues do not normally prevent the re-storage of nuts in the wild. However, other experiments by Avenoso (1968) did show that scent from storage sites was strongly inhibiting to re-storing in free-living squirrels. The scent mixture used was from feces and wood chips in tree cavities.

That olfaction may play a role in the winter, non-breeding behavior of Glaucomys is suggested by some of Muul's (1968) observations of winter aggregations. Although captive females with young litters would not tolerate the presence of other adults in the same cage (60 cm on a side), females with young over two months of age allowed other adults to join the group. Even non-breeding residents in large outdoor cages attacked any newly introduced adults. The following description is from Muul (1968, p. 10): "When a non-resident flying squirrel approaches the vicinity of a strange nest, initially the resident makes some sort of contact with him (usually sniffing around the mouth or genitalia); then the two stand side by side with the heads pointing in opposite directions.... Each attempts to sniff the genital region of the other, but is discouraged from doing so by repeated blows in the face by the outwardly turned sole of the other squirrel. During this ritual there is a great deal of stamping of feet, dancing around, and lateral flicking of the tail, while both individuals remain in bodily contact. If the stranger wavers during the process he is immediately driven away; if he persists through the ritual with each of the members (of the aggregation) he is finally accepted into the aggregation."

Furthermore, Muul describes how members of an aggregation will "kiss" when they meet, in a manner similar to that described by King (1955) for prairie dogs (Cynomys ludovicianus). I have observed this oral contact between mother and young but have never seen it among members of wild aggregations. Although it does appear that individual recognition is accomplished by scent, Muul's conclusions must be qualified somewhat because my observations in the wild indicatethat "ritual" confrontations such as those described by Muul frequently occur between members of aggregations and littermates, with apparently antagonistic intent.

Molt

Howell (1918) recorded that the fall molt starts on the sides and spreads over the back, then the head and shoulders. Sheldon (1971), however, noted that during the fall molt of captive animals, the loss of old hair began near the head and proceeded posteriorly down the back and sides. Howell further noted that *G. volans volans* has white hind toes in winter, but brown in summer. This to Howell suggested a partial spring molt; however, such a color change might result from the wearing of the tips of multi-colored hairs. Howell also noted that the soles are hairy in winter and naked in summer.

My observations indicate that adult *Glaucomys* on Long Island have a partial spring molt and a complete molt later in the year. This is unlike *Tamiasciurus hudsonicus* in Ithaca, New York, (Layne, 1954) which has two complete molts every year. Also unlike *Tamiasciurus*, the two sexes may differ in the time of onset of molt into winter pelage.

The spring molt occurred from mid-April to mid-May in both sexes. It was apparent only on the head and neck. The brown guard hairs were either worn or lost from the top of the head so that the area had the dark gray coloration of the underfur. The line of demarcation between the area of exposed underfur and the unmolted area was well-delineated as a collar around the neck. New guard hairs were apparent in mid-May. This head molt was not reported by Howell. I did not notice any changes in the color of the toes or the hairiness of the soles.

The change to winter pelage in adult males commences in late July and is usually completed in early November. In late July most of the males had large patches of fur on the rump where guard hairs were sparse, and the dark gray underfur was visible. In mid-August new guard hairs were visible on the flanks, tail, and a narrow strip on the mid-dorsum. Replacement began anteriorly on the mid-dorsum and spread from the shoulder region backwards and down the sides. A V-shaped molt line was usually apparent across the shoulders, pointing posteriorly. The head, neck, and tail were the last places where replacement occurred. Fur on the head and neck was replaced from the nose backward. Molt lines were often visible when new brown guard hairs were growing in across the top of the head adjacent to areas of worn fur, which is devoid of guard hairs and so shows the dark gray underfur.

The sequence of molt in adult females was the same as in males; however, the timing was different. Females with August litters began molting in early September, while adult females without litters molted when the males did. Females which had recently bred reached their peak molt in October and finished molting in December.

These observations suggest that molting to winter pelage requires large amounts of energy and is best undertaken when breeding requirements are nearly fulfilled. Molt in males occurred when testes had regressed, molt in breeding females reached its peak when young were capable of feeding on their own.

CONCLUDING REMARKS

This study indicates that the social variability of Glaucomys volans contributes to the ability of this species to succeed in a variety of forest types, including the relatively dry oak-hickory and oak-maple forests of northern latitudes, the wet maple-gum, cedar, cypress, and Florida hammock forests, and even the high altitude, cloud-beshrouded pine-oak forests of middle America. It would be interesting to know whether this lability is based on genetic difference between populations or controlled by a genetic system which allows for a variety of responses according to changes in environmental stimuli, both social and non-social. Knowledge of the factors controlling this variability would give insights into the roles of intrinsic and extrinsic factors in population regulation. Since even mortality rates and causation are unknown in this species, it is quite impossible to say which of many factors is most important in the actual regulation of population, which can also be affected by changes in breeding success, age at onset of breeding, dispersal, and dispersion.

Answers to these questions would require very intensive work in several localities and the application of more costly technology. It appears that the current work has reached limits imposed by techniques and the work capacity of an individual. Trapping requires many hours in the field for relatively few bits of data: each capture in this study required at least 2 hours of work (time spent waiting for traps to fill is not included) and each new individual animal captured was the result of about 20 hours work. However, with telemetry it was possible to acquire a home range estimate in about 3 nights that was comparable in size to that obtained by 3 to 4 months of trapping. Nevertheless, following one telemetered individual at a time is not very illuminating, and, in most cases, is not even feasible with only one receiver. The high-speed activity of free-living flying squirrels makes it extremely difficult to triangulate for exact positions without two workers who are both equipped with receivers, compasses, walkie-talkies, and maps, in an area which is divided by grid markers. Ideally, an institution that specializes in radio-tracking would be best capable of carrying out the amount of monitoring necessary to answer these questions. All residents in an area should be followed and all young tagged in the nest before they disperse or are preyed on. Accurate, abundant, computerized location data will not answer all questions, though, since energetic problems require knowledge of time budgets and food sources and observations of social interactions. For this, a light amplifier is probably the best solution, and a rather costly one.

Future work using technology now available and involving a team of workers would determine what is the full spectrum of social variation in this species, the degree of social plasticity within populations, and the relationships between social organization, population regulation, and habitat characteristics.

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Table 1: Squirrel occurrence and tree species distribution. Trap data and tree survey for 34 quadrats at Kalbfleisch from 1970-1974. Each quadrat is centered around a trap location and is identified by grid position. For each quadrat is listed the number of captures of males (cp), the number of different individuals (id), the same for females, and the total number of nights that location was trapped (t-n). Trees over three inches in dbh are listed by species: Quercus velutina (Qv), Quercus alba (Qa), Acer rubrum (Ar), Castanea dentata (Cd), Cornus florida (Cf), Betula lenta (Bl), Sasafras albidens (Sa), Quercus prinus (Qp), and Carya sp. (Cs).

Quad.	♂♂		♀♀			Tree Species								
	cp	id	cp	id	t-n	Qv	Qa	Ar	Cd	Cf	Bl	Sa	Qp	Cs
SWL15	2	2	12	4	186	13	4				1			
SK15	6	4	16	5	182	16	22			2				
SWK15	8	7	10	8	197	13	1	6					1	
SJ15	3	3	4	4	190	11	3	7						1
SWJ15	1	1	7	4	185	15	1	2		1				
SH15	1	1	0	0	156	18	3	1		1		2		
SWH15	1	1	4	2	156	10	7	2						
WL14	3	2	2	1	200	20	6	2						
K14	8	6	1	1	195	20	9	5					2	
WK14	13	7	12	7	209	9	5	7						
J14	14	9	3	2	193	12	8	11						
WJ14	2	2	3	3	194	10	1	5						
H14	2	2	5	2	193	10	3	3						
WH14	2	2	9	3	172	17	3	2	1					
G14	3	3	8	3	172	8	4	1						
SWL14	17	7	7	5	207	12	5	6	1					
SK14	7	5	3	3	207	15	2	5		1				
SWK14	5	5	7	7	207	12		8						
SJ14	10	6	5	4	211	8	5	19		5				
SWJ14	21	11	15	13	212	13	2	9						
SH14	7	6	5	2	207	14	3	9						
SWH14	2	2	1	1	187	16	1	1					1	
SG14	11	7	15	8	187	13	6	3		1		1		
SWG14	0	0	3	1	185	16	6	1						
WL13	29	9	9	6	201	19	5	3						
K13	9	6	4	3	201	17	10	5						
WK13	20	10	5	5	201	11	3	9	1	1				
J13	8	8	9	5	209	9		26		1				
WJ13	1	1	6	2	202	9	6	24						
SWL13	7	4	7	3	142	18	4	2						
SK13	10	8	9	4	142	20	6	7						
SWK13	7	5	10	4	142	16	2	8	1	1				
SJ13	11	8	4	4	142	18	1	18						
SWJ13	8	3	2	1	142	12		8						

TABLE 2- Reproductive cycle at Kalbfleisch, 1971-1976. Note that testicular descent actually occurred a few weeks prior to the dates given, but was not considered a sign of reproductive readiness until the testes were full-size.

YEAR	TESTIS DESCENT	REGRESS	ESTRUS	PARTURITION	ESTRUS	PARTURITION
1971	March	late July	____	____	late June	early August
1972	mid-Dec.	early Aug.	early Feb.	early April	late June	early August
1973	early Jan.	mid-Aug.	late Feb.	late April	late June	early August
1974	early Jan.	mid-Aug.	late Jan.	early April	____	____
1975	early Mar.	early Aug.	____	____	early July	mid-Aug.
1976	mid-Dec.		late Feb.	mid-April		

Table 3a: Mean Monthly Body Weights, in Grams, 1970 and 1971.

	MALES				FEMALES			
MONTH	MEAN	N	SE	95% CI	MEAN	N	SE	95% CI
1970								
June	65.1	6	2.16	69.3-60.9	65.0	6	3.07	71.0-58.9
July	63.6	2	9.6	82.4-44.6	65.8	6	2.9	71.5-60.1
Aug	66.6	1			64.1	2	2.6	69.2-59.0
Sept	63.3	1			----			
Oct	63.9	1			----			
Nov.	63.0	1			70.3	2	.63	74.2-66.4
Dec	63.2	2	1.4	65.9-60.5	----			
1971								
Feb	67.3	2	1.8	70.9-63.7	----			
Apr	67.3	2	2.45	72.1-62.5	----			
May	72.9	4	4.2	81.1-64.6	69.6	2	1.26	72.0-67.1
June	68.3	6	3.0	74.2-62.4	74.3	5	3.2	80.6-68.0
July	66.2	9	2.2	70.5-61.9	83.8	4	5.17	94.0-73.6
Aug	66.9	7	2.2	71.2-62.5	76.0	6	.58	77.1-74.9
Sept	62.3	1			----			
Oct	65.1	7	2.2	69.4-60.8	72.0	2	3.0	77.9-66.1
Nov	66.9	5	2.7	69.6-64.2	76.3	2	2.75	81.7-70.9
Dec	75.2	3	7.5	89.8-60.6	78.5	3	2.13	82.7-74.3

Table 3b: Mean Monthly Body Weights, in Grams, 1972 and 1973.

	MALES				FEMALES			
MONTH	MEAN	N	SE	95% CI	MEAN	N	SE	95% CI
1972								
Jan	71.1	3	2.06	75.2-67.0	74.2	2	.8	75.8-72.6
Feb	71.6	3	4.76	80.9-62.3	79.5	5	2.4	84.0-74.8
Mar	69.0	6	2.4	73.8-64.2	76.4	3	2.25	80.8-72.0
Apr	68.0	6	2.5	73.0-63.0	82.3	5	1.6	85.4-79.2
May	73.3	7	1.8	76.8-69.8	78.8	6	.87	80.5-77.1
June	66.5	2	1.3	69.1-63.9	79.5	4	2.08	83.6-75.4
July	67.9	6	2.4	72.6-63.2	78.3	5	4.0	86.2-70.4
Aug	72.6	5	3.6	79.6-65.6	78.7	5	1.5	81.7-75.7
Sept	----				80.0	2	1.0	82.0-78.0
Oct	65.4	5	1.93	69.2-61.6	----			
Nov	70.9	8	2.2	75.2-66.6	79.8	4	3.24	86.2-73.4
Dec	75.4	5	3.9	83.1-67.7	76.9	1		
1973								
Jan	79.3	1			83.2	2	5.2	93.2-73.2
Feb	75.2	2	4.2	83.5-66.9	77.5	1		
Mar	69.6	6	2.7	75.0-64.2	72.4	4	5.7	83.6-61.2
Apr	71.4	6	2.2	75.8-67.0	73.6	3	6.3	85.9-61.3
May	79.9	3	5.0	89.8-70.0	83.8	2	2.3	88.3-79.3
Jun	71.5	5	3.5	78.3-64.7	82.9	4	1.9	86.6-79.2
Aug	66.9	2	.8	68.5-65.3	81.8	2	.5	82.8-80.8
Oct	64.2	2	12.3	88.2-40.2	75.3	5	1.3	77.9-72.7
Nov	61.3	1			----			
Dec	78.0	1			----			

TABLE 3c: Mean Monthly Body Weights of Adults, 1974-1975.

	MALES				FEMALES			
1974	MEAN	N	SE	95% CI	MEAN	N	SE	95% CI
Feb.	65.0	1						
Mar.	71.5	9	1.7	74.8-68.2	61.5	1		
April	67.9	6	1.2	70.3-65.5	77.5	10	2.5	82.3-72.7
July	76.0	1			77.3	2	3.8	84.8-69.8
Nov.	68.4	6	2.4	73.1-63.7	63.2	3	3.4	69.9-56.5
1975								
Jan.	71.4	1						
May	68.3	5	3.2	74.5-62.1	65.0	6	2.1	69.1-60.9
Aug.	79.8	1			72.7	1		
Oct.	71.5	1			58.9	1		
Nov.	70.1	12	1.5	73.0-67.2	71.1	5	2.5	76.0-66.2
Dec.	66.6	3	2.0	70.6-62.6	70.8	2	4.6	79.8-61.8

TABLE 4- Mean weights of breeding adults for winters of 1971-1972 and 1972-1973. Female weights are given for the time of estrus, one month preceeding estrus, and two months preceeding estrus. Male weights at the same times are in brackets; sample size for females in parentheses. Male weights are also given for the times of testis enlargement, one month previous, and two months previous.

MEAN FEMALE WEIGHTS IN GRAMS

	2 months preceeding	one month preceeding	estrus
1971-1972	78.4 (3) [75.1]	74.2 (2) [71.1]	79.5 (5) [71.6]
1972-1973	82.6 (2) [79.1]	78.1 (2) [74.8]	83.4 (2) [69.9]

MEAN MALE WEIGHTS IN GRAMS

	2 months preceeding	one month preceeding	testis enlarge.
1971-1972	65.8 (8)	65.8 (5)	76.1 (4)
1972-1973	70.9 (8)	75.4 (5)	79.3 (3)

TABLE 5- Squirrels' avoidance of traps where previously caught. Data are given for six squirrels. Trap locations are numbered in order of captures, not according to location.

SQUIRRELS	ORDER OF TRAP USE
4-male	1, 2, 3, 4, 5, 6, 7,2, 8, 9, 8, 10, 11, 12, 13, 13, 14, 15, 12, 16, 8, 17, 6, 12, 14, 11, 8, 18, 19, 20, 6, 14, 15, 9, 15, 14, 18, 6, 12, 17, 9, (June 29, 1970-July 6, 1973)
19-male	1, 2, 2, 3, 4, 5, 6, 7, 8, 9, 1, 10, 1, 9, 8, 4, 2, 7, 11, 12, 7, 12, 2, 4, 1, 4, 12, 13, 10, 14, 15, 16, 14, 10, 17, 17, 18, 4, 19, 7, 20, 20 (Sept. 13, 1970-July 31, 1974)
21-male	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 9, 14, 12, 9, 15, 16, 16, 17, 16, 18, 19, 20, 19, 9, 21, 13, 13, 22, 17, 9, 23, 24, 16, 9, (Oct. 11, 1970- July 6, 1972)
23-female	1, 2, 3, 4, 5, 6, 7, 2, 8, 4, 9, 1, 1, 10, 11, 12, 3, 8, 13, 11, 2, 9, 4, 14, 15, 11, 16, 17, 16, 16, 4, 18, 2, 9, 17, 19, 20, 21, (May 29, 1971- Aug. 31, 1972)
24-male	1, 2, 3, 4, 5, 6, 7 (June 1, 1971- May 18, 1972)
25-female	1, 2, 3, 4, 5, 6, 7, 4, 1, 4, 8, 10, 11, 12, 13, 14, 15, 16, 17, 6, 6, 13, 4, 17, 14, 4, 18, 16, 14, 10, 14, 14, 4, 18, 19, 14, 14, 21, 22, 23,24, 25, 21, 25, 26, 27, 19, 17, 28, 4, 10, 28, 4, 23, 8, 28, 8, 4, 19, 11, 29, 3, 30, 28, 17, 31, 3, 30, 32, 33, 23, 11, 34, 17, 30, 8, 20, 8, 35, 21, 36, 37, 20, 20, 38 (June 19, 1971-July 31, 1974)

Figure 1- Distribution maps, adapted from Hall and Kelson (1959) with modifications from Anderson (1972), Goodwin (1961, 1969), and Wrigley (1969).

A. Glaucomys volans

B. Glaucomys sabrinus

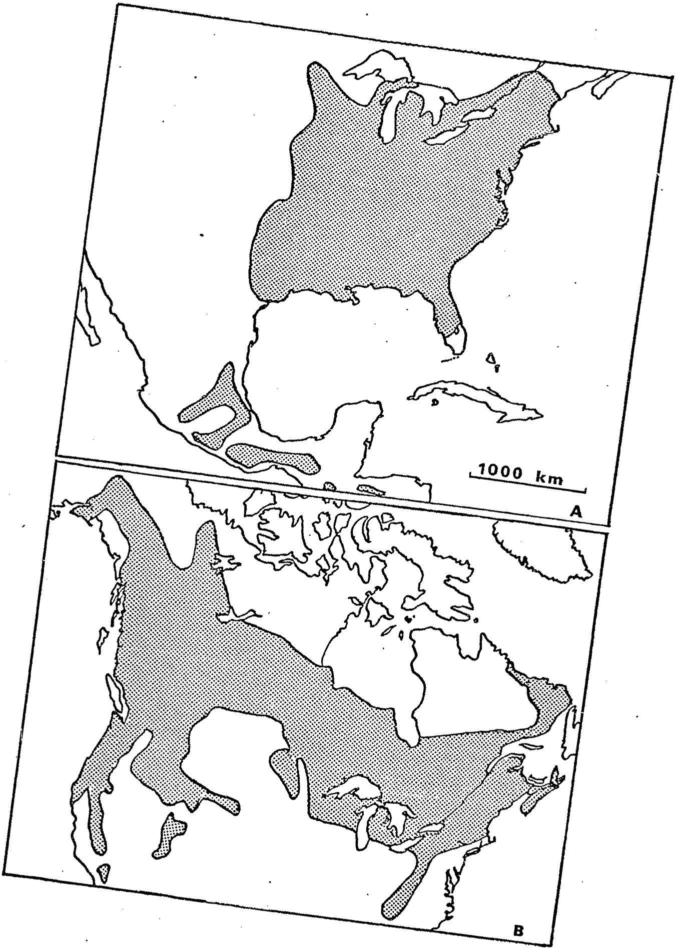

1000 km
A
B

Figure 2- Study area at Kalbfleisch Field Research Station, Dix Hills, Long Island, New York. Dots represent trap locations in BWF1. A and B are feeding stations, C is the laboratory. The Station grid system has 50-m intervals, the trapping grid spacing is 25 m.

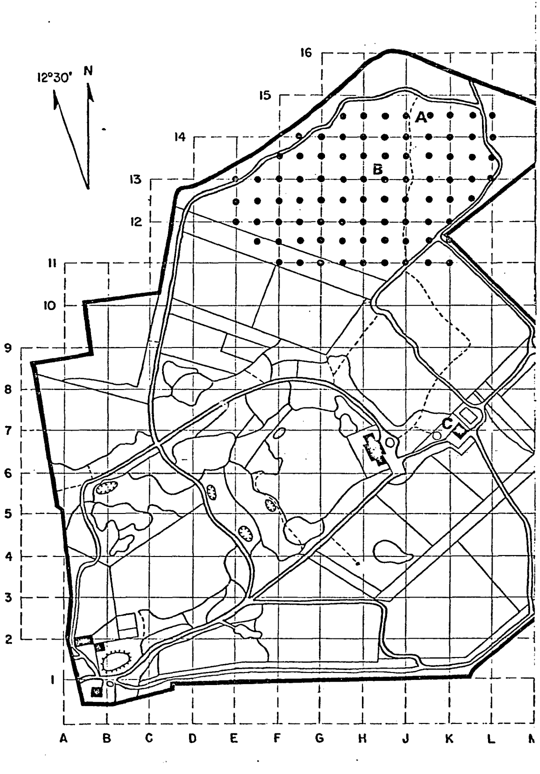
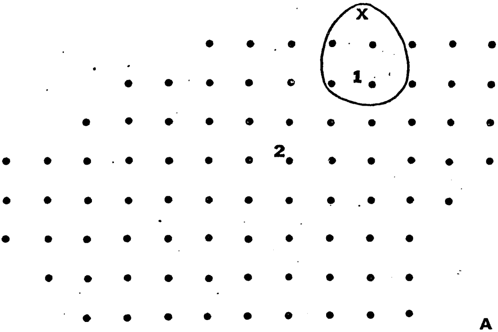

12°30'
N
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
A
B
C
D
E
F
G
H
J
K
L
A
B
C

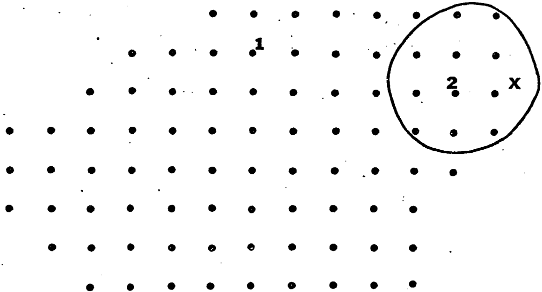
Figure 3- Activity areas of telemetered *Glaucomys volans*. Dots represent trap locations in BWF1. Circular areas are activity areas as determined by telemetry. Numbers are sites of trap captures, x's are nests.

a. immature female, June 1970.

b. adult male, November- December, 1975.



A



B

Figure 4- Map of Connetquot River State Park, Oakdale, Suffolk County, Long Island, showing study area in a section of red maple-black gum swamp. Shading represents swamp.

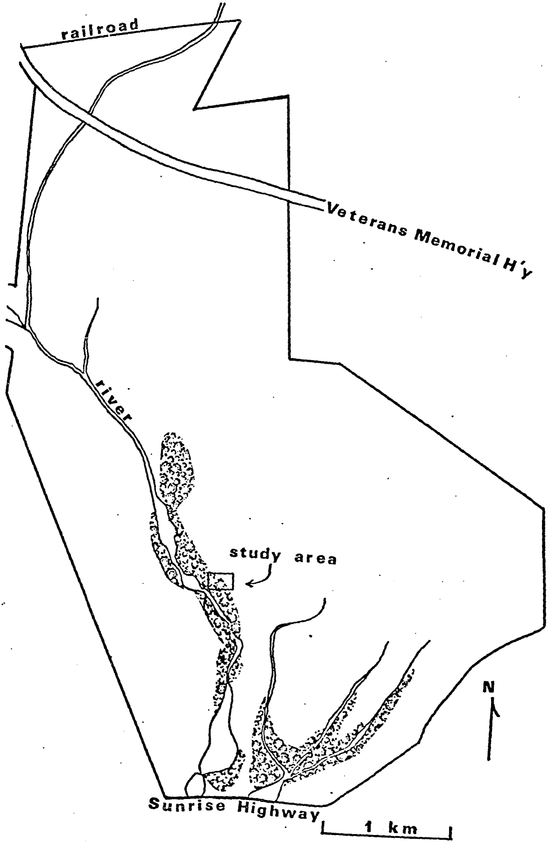
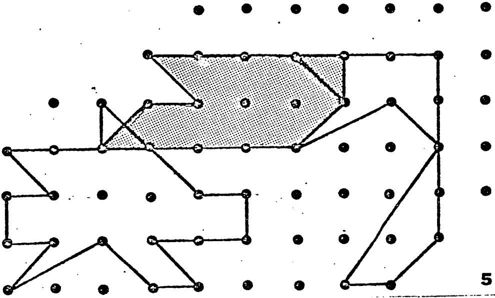
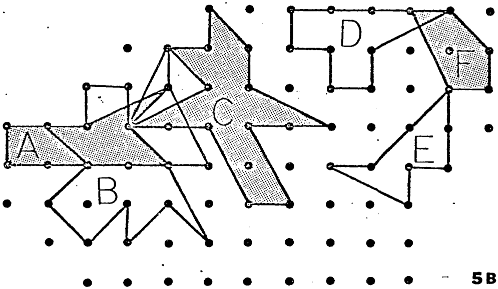

railroad
Veterans Memorial H'y
river
study area
N
Sunrise Highway
1 km

Figure 5- Home ranges of adult females in BWF1 in (a) 1971 and (b) 1972. Dots represent trap locations spaced at 25-m intervals. Shading is used to differentiate confusing boundaries.

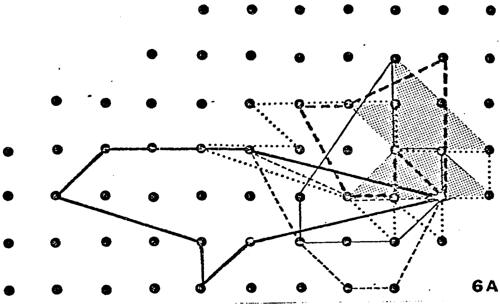


5A

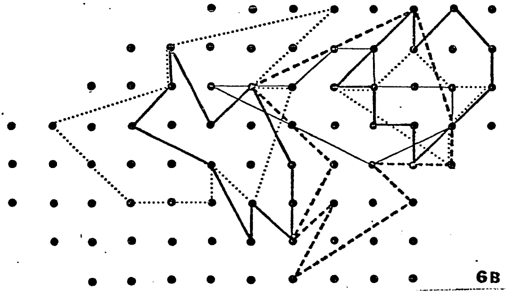


5B

Figure 6- Home ranges of adult males in BWF1 in (a) 1971 and (b) 1972. Symbols as in Figure 5.

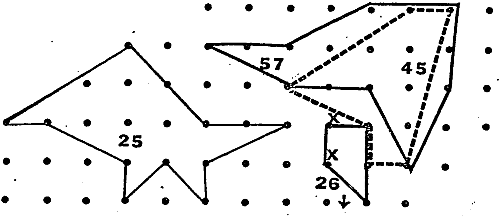


6A

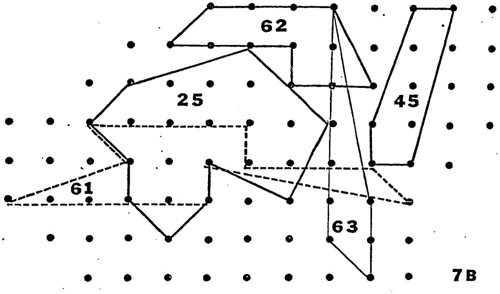


6B

Figure 7- Home ranges of breeding age females in 1973, (a) January to June, (b) June to December. Dots represent trap locations spaced at 25-m intervals, numbers identify females, x's mark brood nests of no. 26.



7A



7B

Figure 8- Home ranges of adult males in 1973. Symbols as in previous maps.

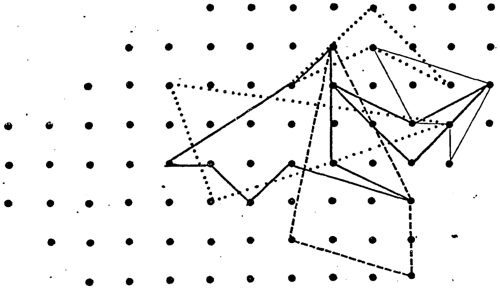
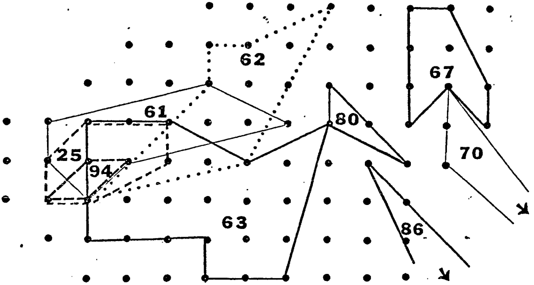


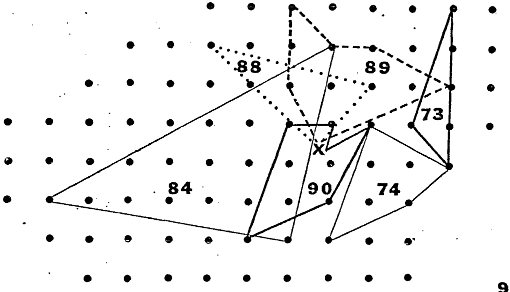
Figure 9- Home ranges of adults in 1974.

(a) females

(b) males



9A

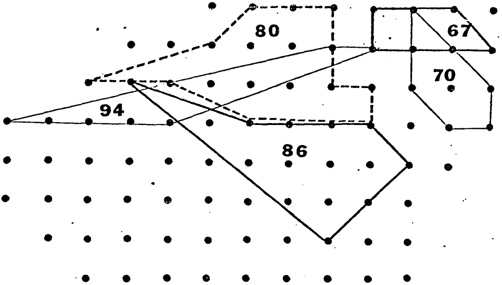


9B

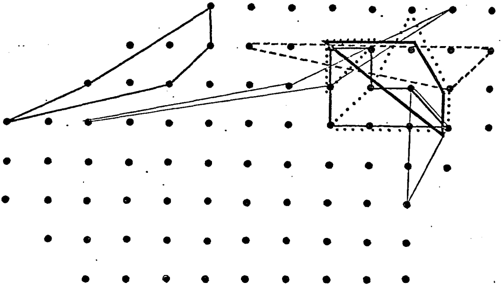
FIgure 10- Home ranges of adults in 1975.

(a) females

(b) males



10 A



10 B

Figure 11- Numbers of juveniles caught, 1970-1975, and mean weights of adult males (dots connected by lines). The fall of 1973 was a very good season for acorns.

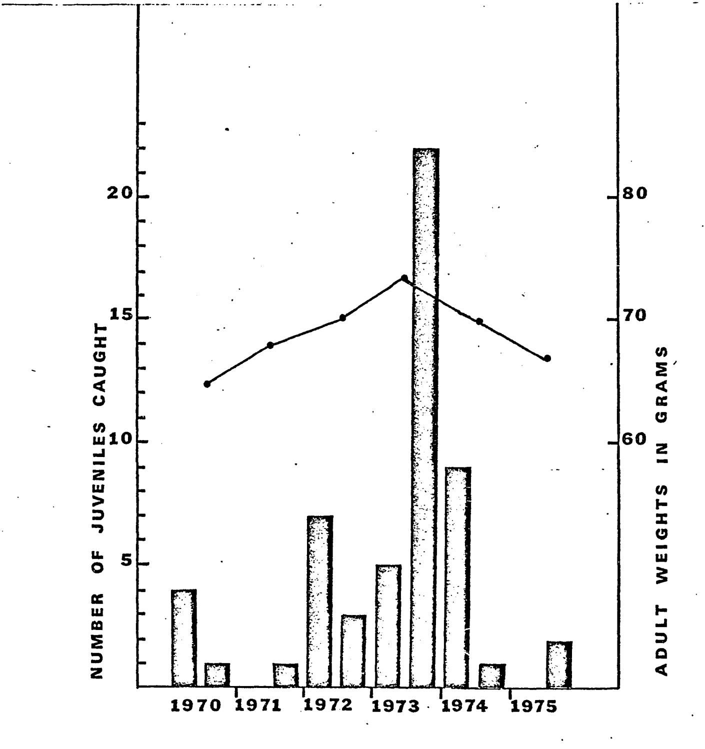

NUMBER OF JUVENILES CAUGHT
5
10
15
20
ADULT WEIGHTS IN GRAMS
60
70
80
1970
1971
1972
1973
1974
1975
YEAR

Figure 12- Map of study area at Connetquot River State Park, Suffolk County, New York, showing floristic areas and trap locations.

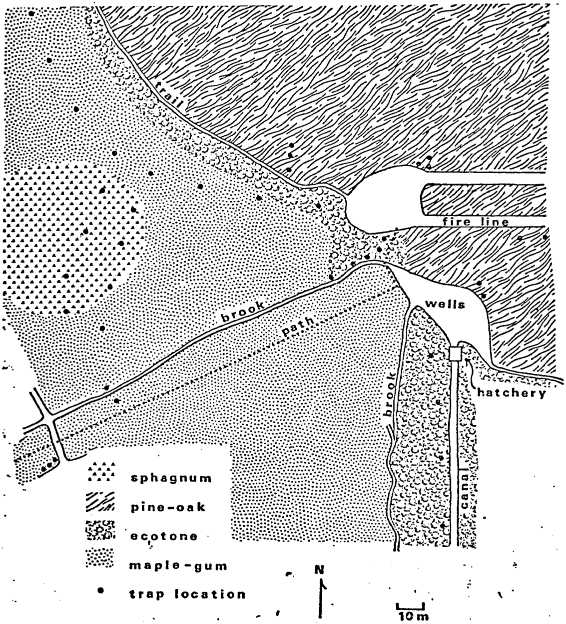

trail
fire line
wells
brook
path
brook
hatchery
canal
sphagnum
pine-oak
ecotone
maple-gum
trap location
N
10 m

Figure 13- Home ranges of four females at Connetquot. Dots represent trap locations, scale is same as in Fig. 12.

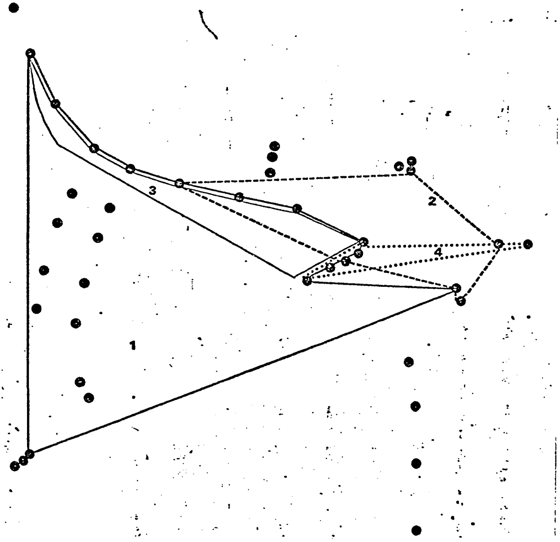

3
2
4
1

Figure 14- Percentages of males caught monthly in 1970. Solid line is the percentage of captures which were male. Dotted line is the percentage of males among the individuals captured.

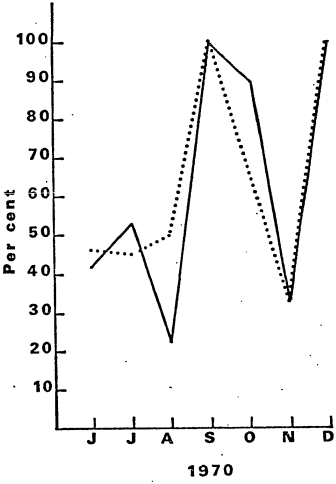

Per cent
100
90
80
70
60
50
40
30
20
10
J
J
A
S
O
N
D
1970

Figure 15- Percentages of males caught monthly in 1971. Designations same as in Fig. 14.

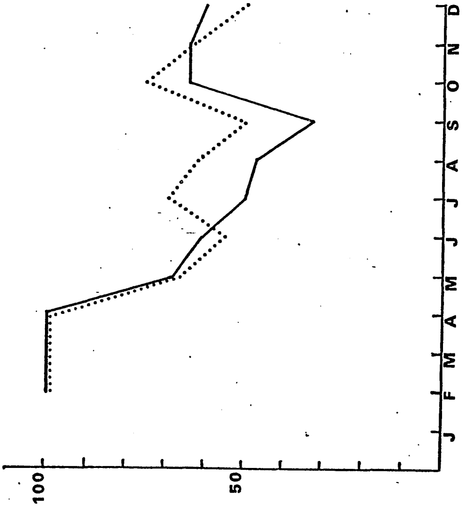

100
50
J
F
M
A
M
J
J
A
S
O
N
D
1971

Figure 16- Percentages of males caught in 1972. Designations same as in Fig. 14.

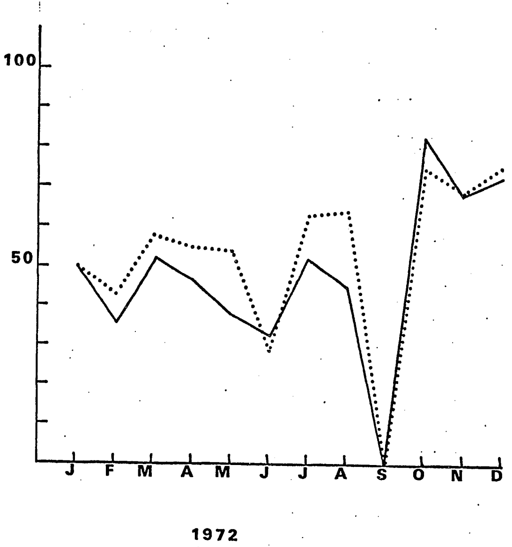
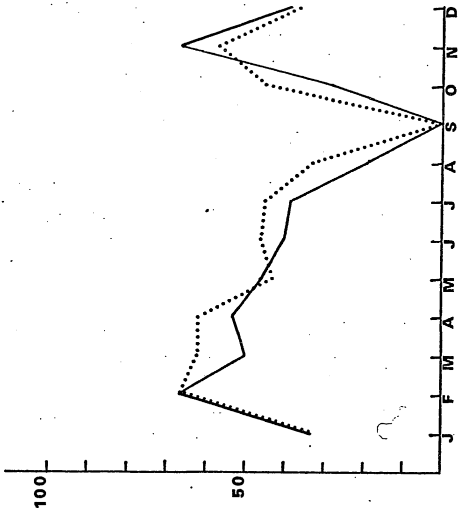

100
50
J
F
M
A
M
J
J
A
S
O
N
D
1972

Figure 17- Percentages of males caught in 1973. Designations same as in Fig. 14.



1973

Figure 18- Percentages of males caught in 1974. Designations same as in fig. 14.

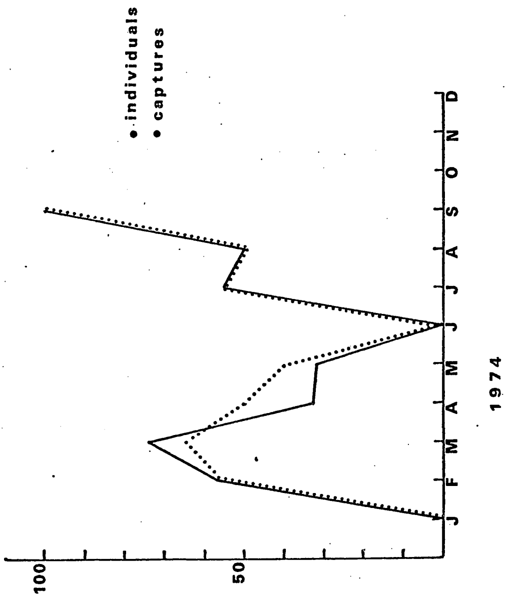

● individuals
● captures
100
50
J
F
M
A
M
J
J
A
S
O
N
D
1974

Figure 19- Percentages of males caught monthly in 1975. Designations same as in Fig. 14.

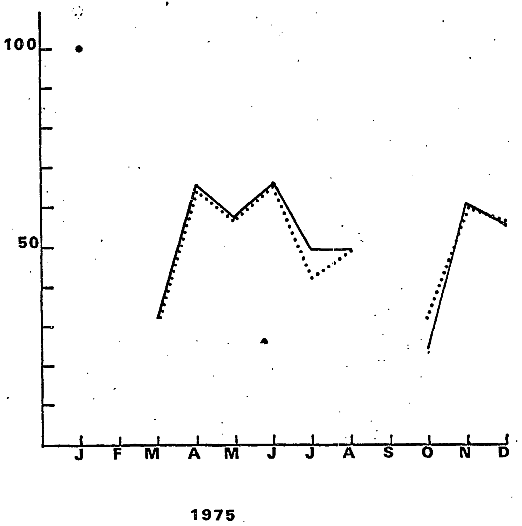

100
50
J
F
M
A
M
J
J
A
S
O
N
D
1975

Figure 20- Time of occurrence of individual flying squirrels at Kalbfleisch. Dashed lines are males, solid are females. Slash indicates first capture, B is time of birth, D is time of death (known in only one case). When age is unknown, the time-line has been carried back to the most recent breeding season prior to first capture.

(a) squirrels identified by numbers 4-62

(b) squirrels 63-107

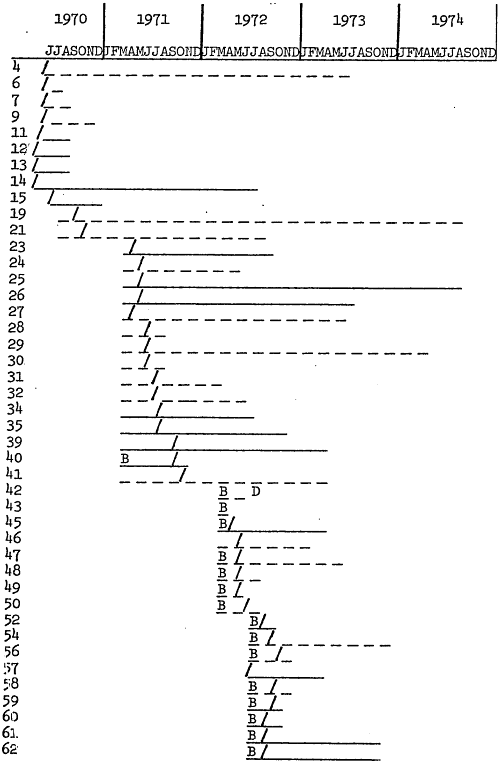

1970
1971
1972
1973
1974
JJASOND
JFMAMJJASOND
JFMAMJJASOND
JFMAMJJASOND
JFMAMJJASOND
4
6
7
9
11
12
13
14
15
19
21
23
24
25
26
27
28
29
30
31
32
34
35
39
40
41
42
43
45
46
47
48
49
50
52
54
56
57
58
59
60
61
62
B
D

Figure 20(b)- Time-lines of squirrels 63-107. Symbols as in Fig.20(a).

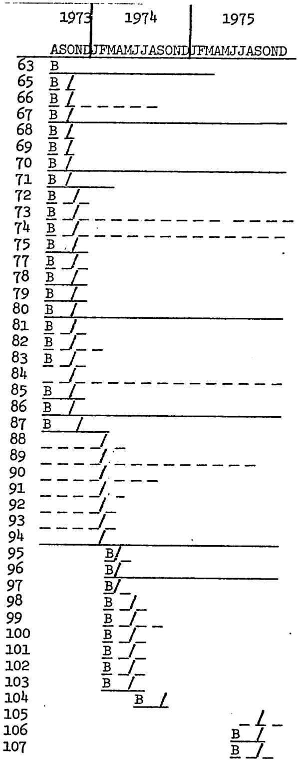

1973
1974
1975
ASONDJFMAMJJASONDJFMAMJJASOND
63
65
66
67
68
69
70
71
72
73
74
75
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
B

Figure 21- Breeding histories of females at Kalbfleisch, 1970-1975. Numbers in lefthand column are identification numbers of individuals, asterisks represent parturitions, crosses represent each time female was observed in estrous condition, B indicates known birthdate, and question marks indicate that the female was not observed during the appropriate period to determine if parturition occurred.

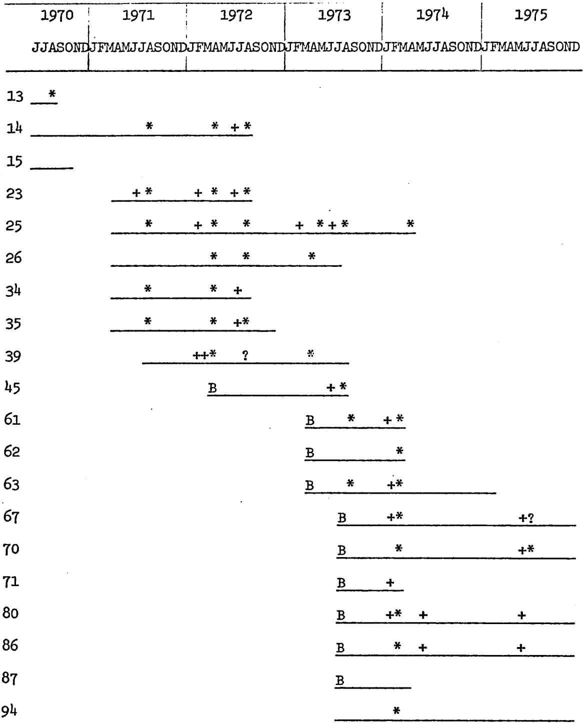
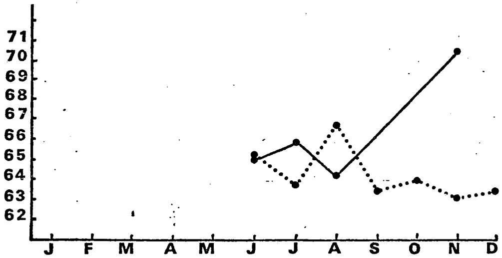
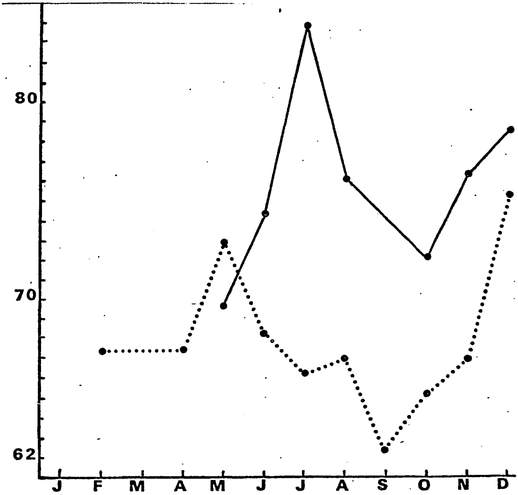

1970
1971
1972
1973
1974
1975
JJASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJASOND
13
14
15
23
25
26
34
35
39
45
61
62
63
67
70
71
80
86
87
94
B
?
+?

Figure 22- Mean monthly adult weights at Kalbfleisch in 1970. Solid line is females, dotted line is males. Weights are in grams.



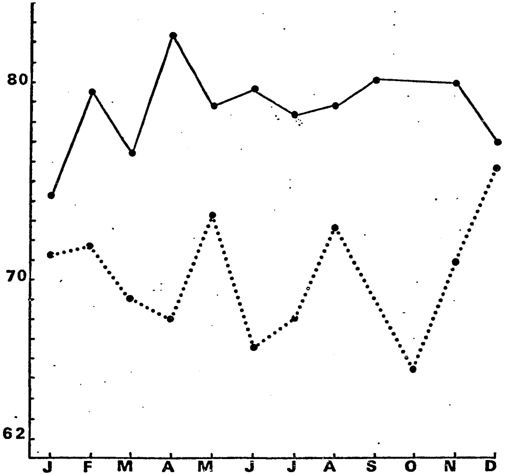
1970

Figure 23- Mean monthly weights of adults at Kalbfleisch in 1971. Solid line is females, dotted is males. Weights in grams.



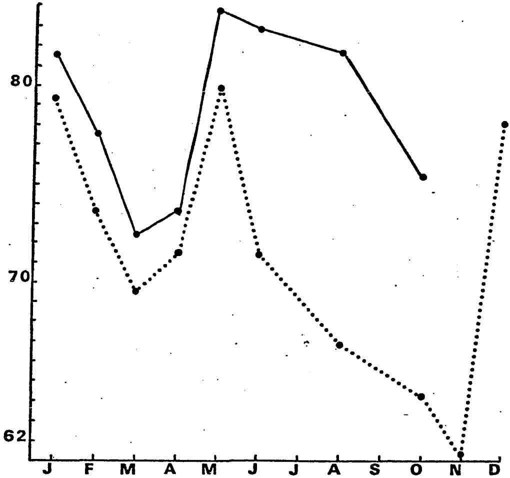
1971

Figure 24- Mean monthly weights of adults at Kalbfleisch, 1972. Solid line-females, dotted-males, weights in grams.



1972

Figure 25- Mean monthly weights of adults at Kalbfleisch in 1973. Solid line-females, dotted-males, weights in grams.



1973

Figure 26- Mean monthly weights of adults at Kalbfleisch, 1974, in grams. Solid line is females, dotted is males.

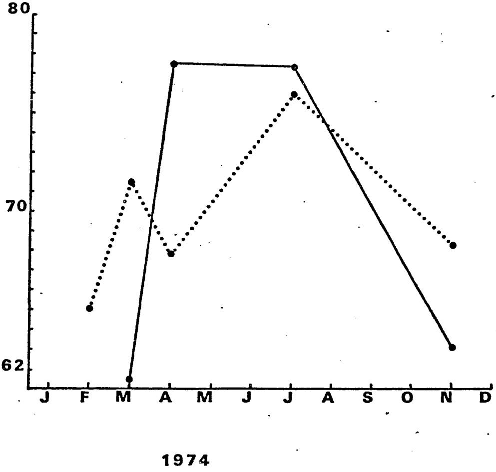

80
70
62
J
F
M
A
M
J
J
A
S
O
N
D
1974

Figure 27- Weights in grams of all individuals at Kalbfleisch, 1970-1973, for which at least two weights are known. Solid lines are females, dotted lines are males.

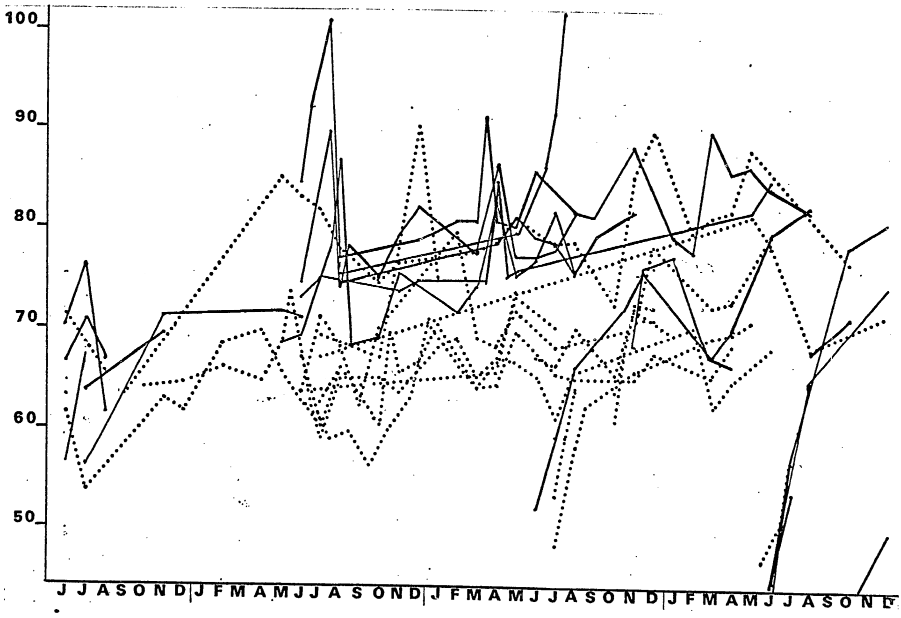

100
90
80
70
60
50
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D

Figure 28- Weights of all individuals at Kalbfleisch, 1974-1975, for which at least two weights are known. Solid line is females, dotted is males.

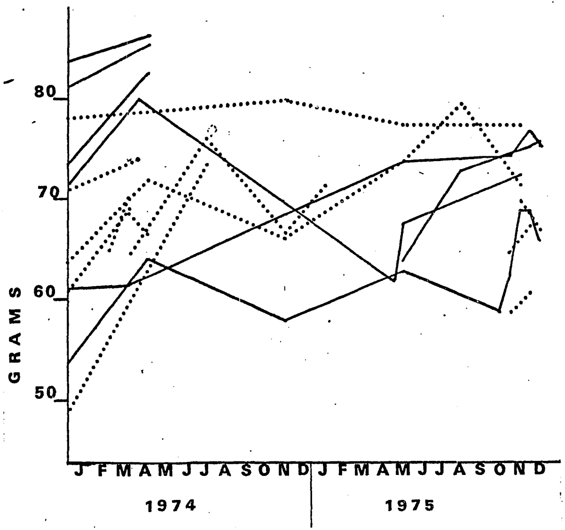

80
70
60
50
GRAMS
J F M A M J J A S O N D J F M A M J J A S O N D
1974
1975

Figure 29- Activity levels of three adult _Glaucomys_ in the lab. The photoelectric unit was placed across the entrance of the nest box which they shared.

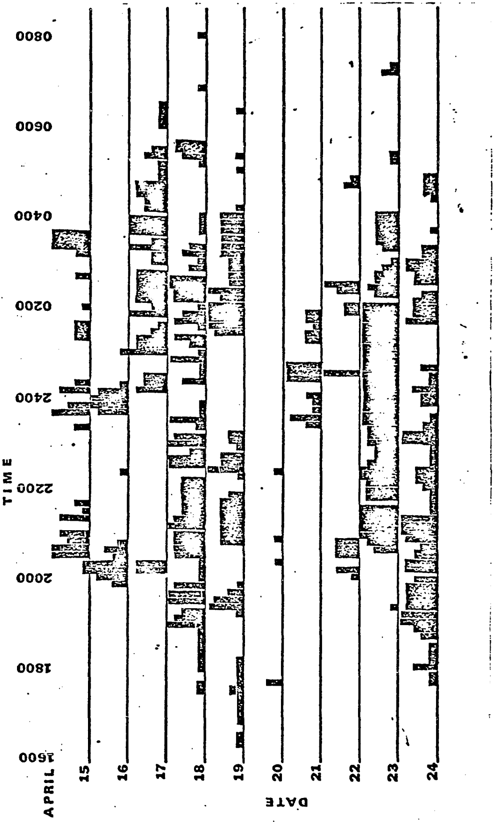

TIME
1600
1800
2000
2200
2400
0200
0400
0600
0800
APRIL
DATE
15
16
17
18
19
20
21
22
23
24

Figure 30- Activity at nest box north of J14, Kalbfleisch, April, 1973. Inhabited by one non-breeding female, 2 adult males, and one unidentified squirrel. Symbol M indicates short period of malfunction.

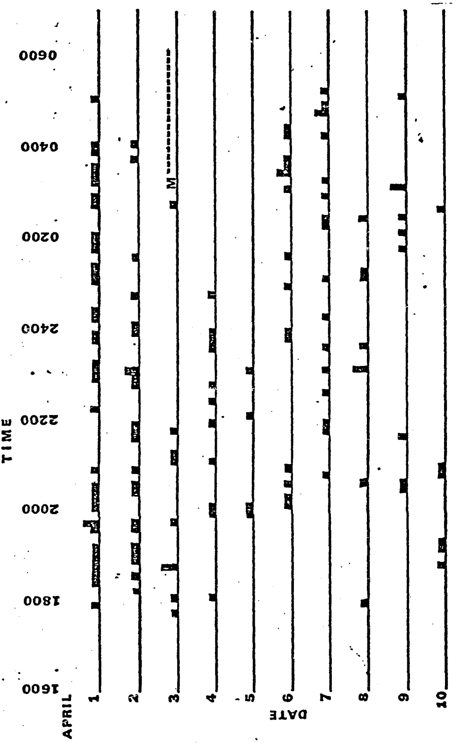

TIME
1600
1800
2000
2200
2400
0200
0400
0600
APRIL
1
2
3
4
5
6
7
8
9
10
DATE
M

Figure 31- Activity at nest box north of J14, April-May 1973. Times of rain are indicated for April 19 and May 13: squirrel activity registered on the recorder although squirrels were observed to merely look out and did not actually exit until the rain ended.

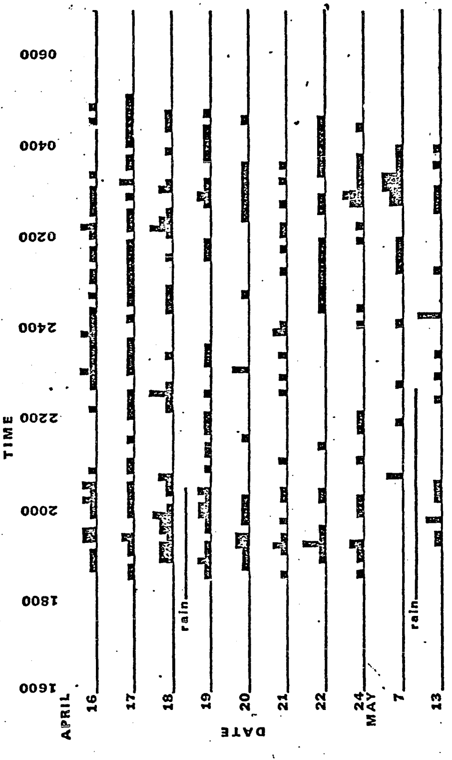

TIME
1600
1800
2000
2200
2400
0200
0400
0600
DATE
APRIL
16
17
18
19
20
21
22
24
MAY
7
13
rain
rain

Figure 32- Activity at nest box 25 m N of J13, June 1973. Female 26 moved her young into this box (time indicated by N) when she was disturbed at another monitored box.

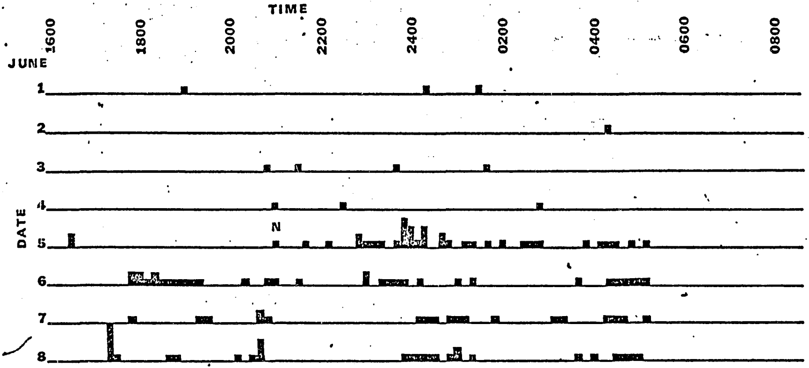

TIME
1600
1800
2000
2200
2400
0200
0400
0600
0800
JUNE
DATE
1
2
3
4
5
6
7
8
N

Figure 33- Activity at nest box which was vacant until a photoelectric unit was attached (designated by "start"). The entrance hole had been shrouded in spider webs and the interior contained only the remains of insects.

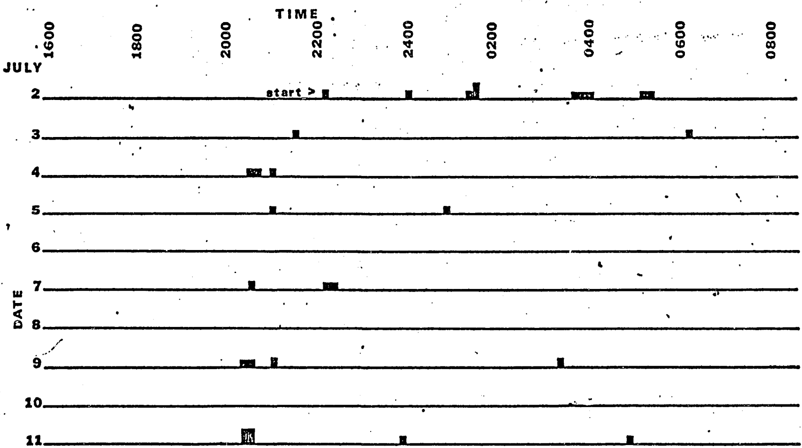

TIME
1600
1800
2000
2200
2400
0200
0400
0600
0800
JULY
DATE
2
3
4
5
6
7
8
9
10
11
start >

Figure 34- Activity at nest box in January, 1973. Ambient temperatures in degrees Centigrade are indicated at 1800, 2400, and 0600 hours.

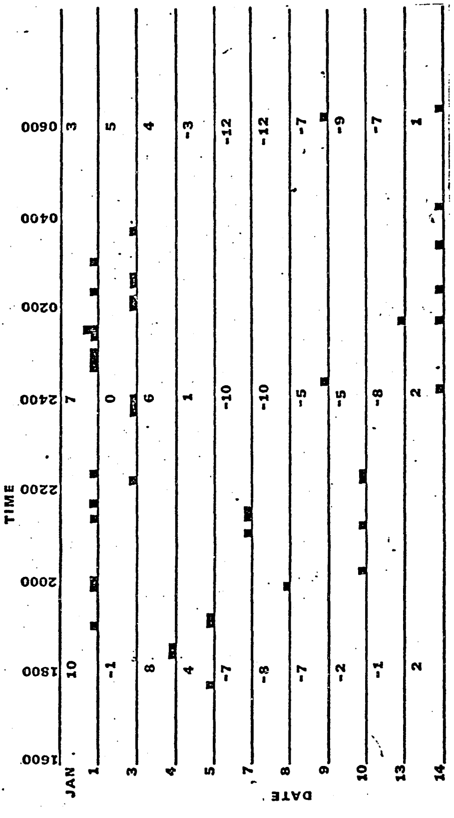
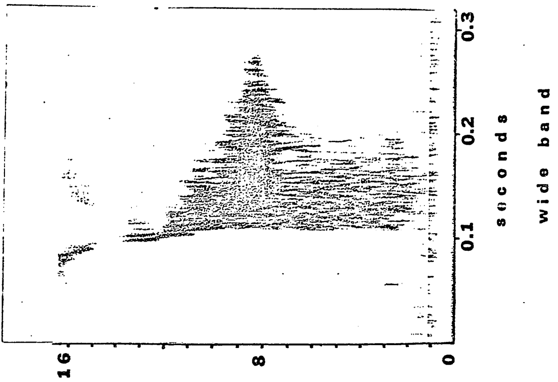
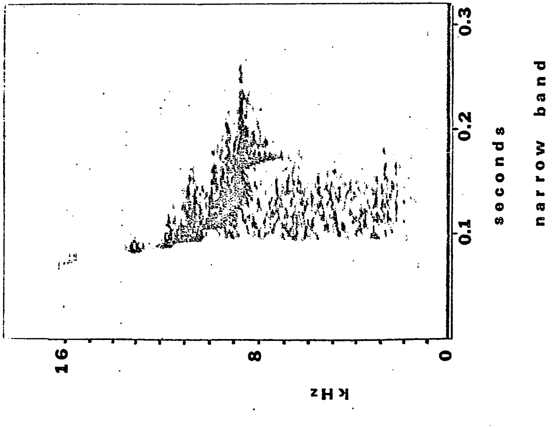

TIME
1600
1800
2000
2200
2400
0200
0400
0600
DATE
JAN
1
3
4
5
7
8
9
10
13
14
10
7
3
-1
0
5
8
6
4
4
1
-3
-7
-10
-12
-8
-10
-12
-7
-5
-7
-2
-5
-9
-1
-8
-7
2
2
1

Figure 35(a)- Sonagrms of rasping squeak portion of alarm sequence. Narrow band pass filter (left) for accurate frequency representation and wide band pass filter for accurate time representation. All recordings were made at 7.5 inches per second (13cm/s) and analyzed at half-speed on a Kay Spectrographic Analyzer.



wide band



narrow band

Figure 35(b)- Sonagrams of higher frequency portion of alarm sequence.

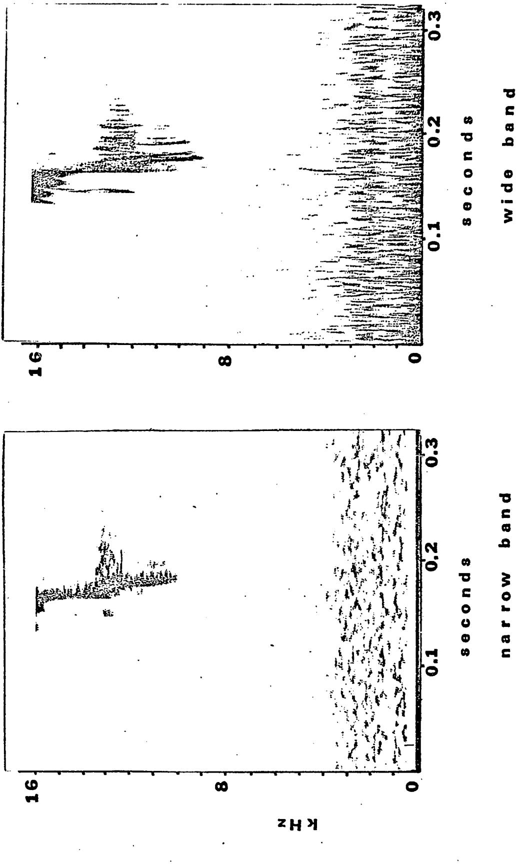

16
8
0
k Hz
0.1
0.2
0.3
seconds
narrow band
16
8
0
0.1
0.2
0.3
seconds
wide band

Figure 36(a)- Wide band sonagram of pulsed sequence recorded in the field at Kalbfleisch.

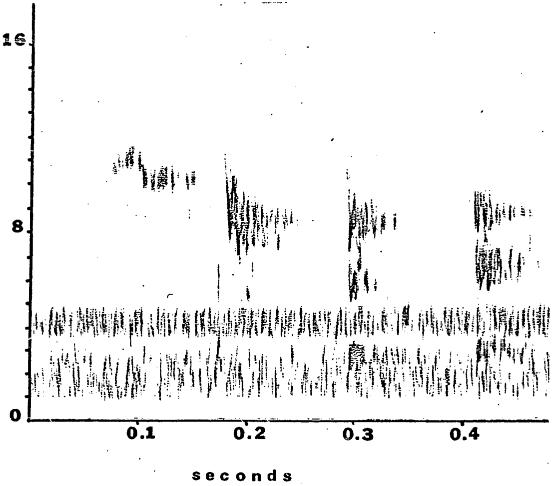

16
8
0
0.1
0.2
0.3
0.4
seconds

Figure 36(b) and (c)- Narrow and wide band sonagrams of pulsed sequence recorded in captivity.

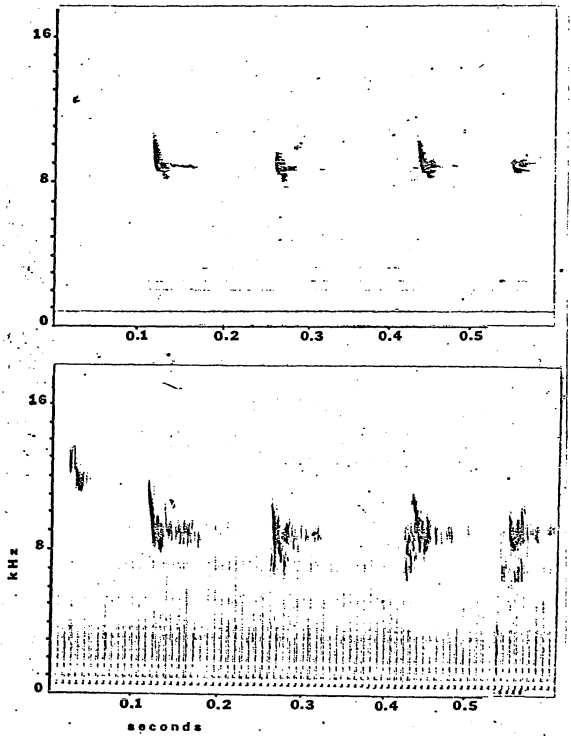

16
8
0
0.1
0.2
0.3
0.4
0.5
16
8
0
kHz
0.1
0.2
0.3
0.4
0.5
seconds

Figure 37- Sonagram of loud, single snort.

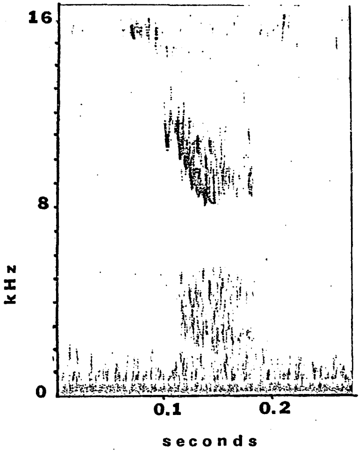

16
8
0
kHz
0.1
0.2
seconds

Figure 38- Sonagram of churring.

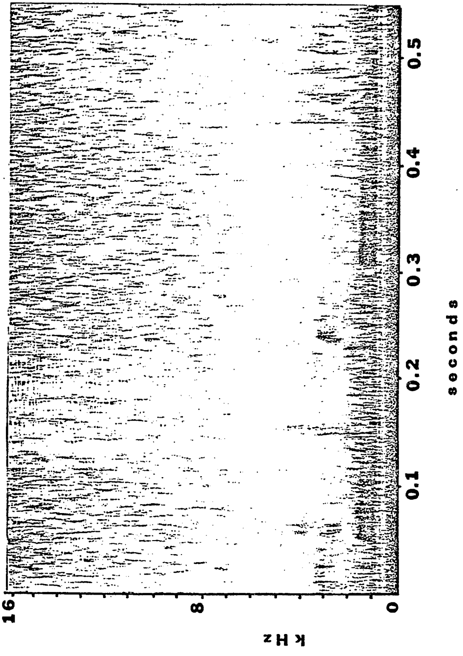

16
8
0
k Hz
0.1
0.2
0.3
0.4
0.5
seconds

Figure 39- Sonagram of squealing.

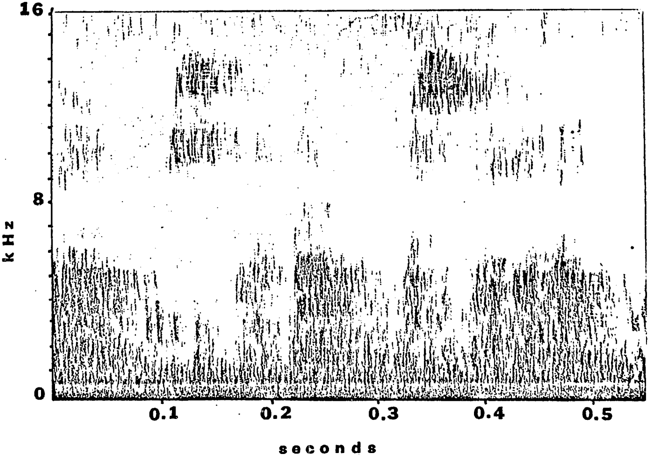
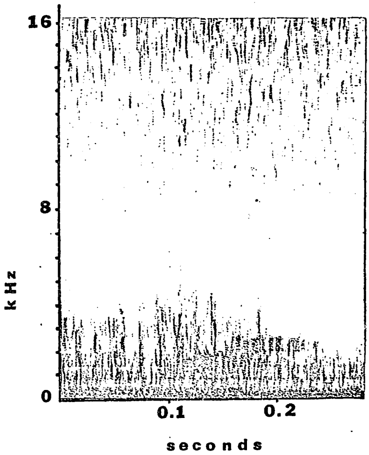

16
8
0
kHz
0.1
0.2
0.3
0.4
0.5
seconds

Figure 40- Sonagram of squawk.


16
8
0
kHz
0.1
0.2
seconds