Behavioral and Physiological Influences on the Distribution of the Flying Squirrel, *Glaucomys volans*

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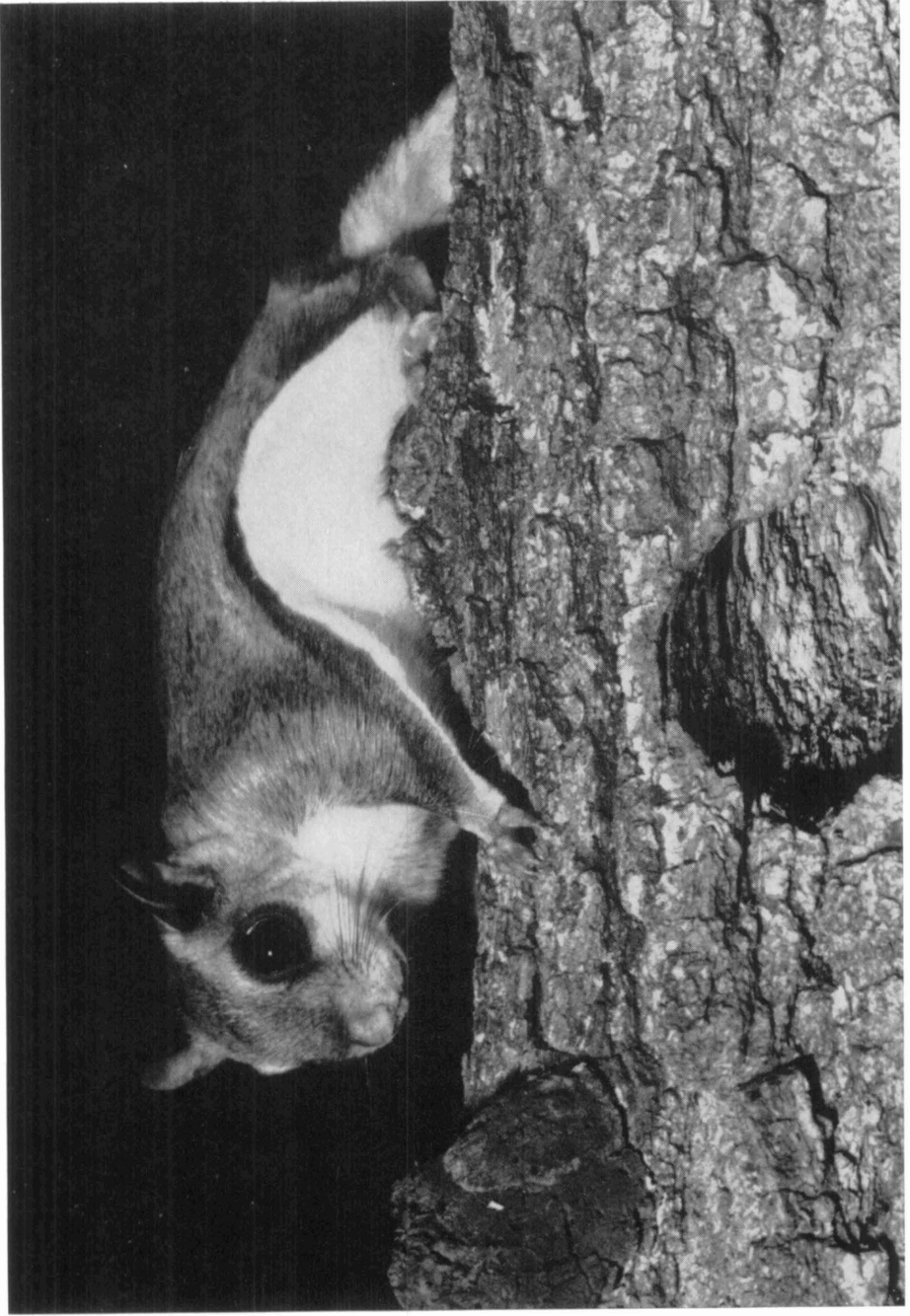
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BEHAVIORAL AND PHYSIOLOGICAL INFLUENCES ON THE DISTRIBUTION OF THE FLYING SQUIRREL, *GLAUCOMYS VOLANS*

THE FACTORS that determine the distributional boundaries of a species are often difficult to define. For non-flying mammals, mountain ranges, large bodies of water, or other discontinuities in the environment are obvious natural barriers, but the boundaries of the geographic range of a species may not follow such physically distinguishable features. Sometimes the distribution of the species can be correlated with the occurrence of certain plant communities. In many cases, the geographic range of a species of mammal includes a variety of habitats with different plant communities and, thus, other factors must be considered. Climate, with its ramifications, certainly influences the behavior of animals and may also affect their distribution. There is ample evidence of shifts in animal distribution associated with climatic changes (Blair, 1958).

Merriam (1892) was one of the first to stress the importance of climatic factors, especially temperature, as determinants in the distribution of North American life forms. He had a large following initially, particularly among mammalogists and ornithologists, but later his "temperature laws" received much criticism (Kendeigh, 1932; Shelford, 1932; Daubenmire, 1938). None of the critics, however, denied the importance of temperature as a limiting factor; they disputed only the degree of its effectiveness, the season during which it might be important, and the manner in which its effects should be quantified.

One way to determine the extent to which environmental factors such as temperature contribute to limiting the distribution of a species is to analyze behavior patterns that adjust energy exchange between the species and its environment. In other words, what is the animal doing about the weather? In northern latitudes temperature regulation can be costly for a non-hibernating homeotherm during the winter, and such a species can exist only in areas where heat loss to the environment can be met by heat production, which in turn depends upon sufficient food intake. Even if sufficient food were available, the animal has other things to do besides ingestion, so the problem of time-budget is introduced.

Heat loss may be reduced through increased insulation, short- or long-term hibernation, and behavioral patterns that tend to provide the animal with a more favorable microclimate. Without such adaptations many species could not survive in as varied environments and in as large geographic

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areas as they in fact occupy. A notable example of this is man, essentially a tropical species that has enlarged its geographic range through the use of technology. Other animals also use technology, albeit rudimentary, to enhance their survival in hostile environments.

The flying squirrel, *Glaucomys volans* L., is especially well suited for a study of relationships between behavior and environment since it lives in various types of habitats over a wide geographic range and is subjected to a correspondingly wide range of climatic conditions. Geographic variation in nesting behavior apparently reflects differences in the environment within the geographic range. In the northern United States several behavior patterns appear to have evolved that tend to place the species in a favorable relationship with its environment.

Food materials are stored during favorable times of the year, and these are consumed later when other food is scarce. Much of the success of the species is also attributable to technology, i.e., nest construction, which provides the animal with an insulated shelter with an improved microclimate. Social behavior leading to aggregation during cold months renders additional thermal and insulative benefits. Also, in those months activity is greatly reduced; the animals may remain within the protective confines of their nests and come out only to feed.

With these behavioral factors considered and with known energy requirements under various temperature conditions, it is possible to construct an energy budget for the species, an essential for understanding the interactions between animal and environment. These interactions and the energy budget will be analyzed in terms of their effect on the distribution of the flying squirrel. The formulation of the energy budget is sufficiently general to make it applicable to any homeotherm, given the necessary behavioral and physiological information.

ECOLOGY OF NESTING BEHAVIOR

METHODS AND MATERIALS.—Field studies of nests were made primarily in the vicinity of Amherst, Massachusetts; Ann Arbor, Michigan; and particularly, on the Edwin S. George Reserve (ESGR) near Pinckney, Michigan. From 1959 through 1963, eighty-nine active nests were studied; these contained a total of 202 adult flying squirrels in addition to young of various ages.

Direct field observations were made during the day by examining hollows in trees, woodpecker holes, and outside nests. Observations were also made at night. Nesting materials from tree cavities were removed for examination. Often animals found in the nest were captured by placing a net or plastic bag over the opening and pounding or shaking the tree or stub; sex, age,

and general condition were determined, then they were ear-marked (Burt, 1940) and released. Some were captured with a hand net as they approached a landing on an adjacent tree. Trapping and releasing techniques were also used.

Secondary nests and retreats were discovered by following an animal that was routed from the primary nest. These secondary nests and retreats were examined for food remains, nesting material, scats, and other foreign objects.

The naturally occurring nest sites were supplemented on the ESGR with 24 nest boxes arranged in a grid, each box about 50 yards from the next; the grid area totaled about seven acres. These nest boxes, with inside dimensions of 6 × 5 × 10 inches, and a 1½-inch opening, were placed on trees at heights of 5 to 8 feet. They were examined at least once a month for inhabitants, nests, and food remains.

Flying squirrels were also studied in captivity in large outdoor cages, one measuring 15 × 12 × 8 feet and the other 18 × 6 × 9 feet; smaller ones in the laboratory measured 2 × 2 × 2 feet. As many as 89 squirrels were maintained at one time. A diet of sunflower seeds, with a few hickory nuts, acorns, and various fruits was sufficient to keep them in good health as long as liquid vitamins were added to the drinking water or vitamin-mineral powder was added to the food.

PRIMARY NESTS.—All but two of the 89 natural-occurring nests studied in Michigan and Massachusetts were in cavities in trees (woodpecker holes, 65; other cavities, 22). The remaining two were outside nests built near the trunk of the tree in the crotch of a branch; leaves and shredded inner bark were used as construction materials—larger fibers on the outside and more finely shredded fibers toward the middle.

Heights from the ground ranged from 5 to more than 40 feet; the mean height was 15 feet, and the mode 20 feet. Nesting sites were found in red maple, *Acer rubrum* (10); oak, *Quercus* (37); aspen, *Populus* (26); birch, *Betula* (3); sassafras, *S. albidum* (3); white pine, *Pinus strobus* (2); eastern hemlock, *Tsuga canadensis* (2); black walnut, *Juglans nigra* (2); butternut, *Juglans cinera* (1); and American elm, *Ulmus americana* (1). Nearly all the nests were a short distance (less than 100 yards) from water (stream, pond, or swamp).

In most instances finely divided inner bark (from aspen or cedar) was used as nesting material; often little or none was used in the summer. Solitary individuals or small aggregations during the winter, and females with litters during the breeding season, used large quantities of nesting material, enough to fill the entire cavity. The nesting material was so arranged that the bark fibers surrounded the inhabitants completely with an insulative layer at least two inches thick,

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Most of the trees (68 per cent) used as nesting sites by flying squirrels were situated far enough from other trees to prevent the other sympatric species of squirrels (fox squirrel, *Sciurus niger;* gray squirrel, *S. carolinensis;* and red squirrel, *Tamiasciurus hudsonicus*) from reaching the trees by strictly arboreal routes. Flying squirrels, on the other hand, can easily glide to and from isolated trees; this may reduce competition between them and other species for nesting sites. Other arboreal squirrels would have to reach such trees by way of the ground, thereby possibly leaving a scent trail that a predator could follow to the nest tree.

Openings to the tree cavities varied in diameter from $1\frac{1}{2}$ to 2 inches, occasionally more. Most of the cavities had entrances sufficiently small to exclude the large tree squirrels. Many of the cavities used as nesting sites were gnawed and enlarged, apparently by flying squirrels—captive animals often enlarged the nest boxes to the point of gnawing completely through the walls.

SECONDARY NESTS AND RETREATS.—In addition to the primary nest—that which a given individual or group occupied more or less continuously—several secondary nests or retreats were always near by (Table 1). These

TABLE 1
TYPES OF SECONDARY NESTS AND RETREATS USED BY FLYING SQUIRRELS
IN MICHIGAN AND MASSACHUSETTS

Type	Number of Nests
Hollow trees	21
Woodpecker holes	20
Subterranean (e.g., under root systems of trees)	21
Knot holes	16
Outside nests	6
Hollow limbs	4
Total	88

were used temporarily as retreats when squirrels were disturbed sufficiently to leave primary nests during the day, or permanently when primary nests were destroyed. The squirrels were often observed to use several different retreats (as many as nine) if continuously pursued. Only a few of the secondary nests or retreats appeared to be suitable for use as primary nesting sites. Their construction usually permitted only temporary use because either the cavities were too small, they were not sufficiently sheltered, or the openings were too large.

Females with young prepare at least one secondary nest with some nesting material; they take the young there when the primary nest is disturbed and

return afterwards to transport the remaining nesting material from the primary nest to the other one.

In Massachusetts and Michigan some retreats contained accumulations of shells of acorns and nuts and thus appeared to be used as sheltered feeding stations. Others were used as defecatoria; in these there were deposits of scats up to 20 centimeters deep. Such defecatoria were most often found in old woodpecker holes or in hollows in trees. In Florida, Moore (1947) found old fox squirrel nests sometimes used as defecatoria by flying squirrels.

Escape routes from primary to secondary nests or to various retreats are specific and well established; a squirrel can be observed to use repeatedly the same ones or standard alternates. The initial glide from the nest tree usually terminates on the trunk of a large tree 50 to 100 feet away. The squirrel then either takes cover in a secondary nest or remains where it landed for 30 minutes or more. Usually it then climbs to the top of the second tree and glides either to a third tree containing a secondary nest or back to the primary nest in the first tree. If the primary nest contains several individuals, all, upon disturbance, usually follow the same glide paths to the same retreats. Direct field observations indicate that much of the active time during the night is spent in the secondary nests and retreats, especially when weather conditions are unfavorable. The routes of travel between these secondary nests and retreats during the night were observed to coincide with those used as escape routes during the day.

Escape routes to the secondary nests and retreats are so stereotyped that a squirrel can be caught easily by choosing the likely landing spot and waiting there while an accomplice drives the animal out of the primary nest. On one occasion a flying squirrel was chased from a nest tree to an isolated rotten stub about eight feet high. The stub was knocked over while the animal was being captured. When a second squirrel was chased from the original nest, it directed its glide to the spot where the stub had stood, but landed on the ground. On another occasion a squirrel glided four times, each time from a different tree, to a spot where a dead tree containing a secondary nest had stood; it finally took refuge in another dead stub.

Secondary nests and retreats, and fixed escape routes within the home range, apparently assure that an animal fleeing from a predator can escape rapidly and take cover quickly. Sheltered feeding stations not only offer some protection from the cold in winter, but may also be of importance in affording protection from predators during the time required by the flying squirrels to penetrate thick nut shells. The use of defecatoria, which are usually 30 yards or more from the nest tree, in addition to keeping the primary nest clean, may divert the attention of predatory animals such as raccoons, *Procyon lotor,* and opossums, *Didelphis marsupialis,* that may follow scent trails, climb trees, and tear open nests.

INTERSPECIFIC COMPETITION FOR NEST SITES

Tamiasciurus hudsonicus: In the summer of 1962 at the ESGR, 12 of the 24 nest boxes (on the 7-acre grid) were inhabited by a total of 14 flying squirrels; none contained red squirrels. By fall most of the openings to the boxes had been enlarged by gnawing, presumably by red squirrels, and none contained flying squirrels during the next year. Eight boxes were occupied by red squirrels from November, 1962, through the summer of 1963, and many more contained empty nests or signs indicating that red squirrels fed in them. One box contained three young red squirrels in the spring of 1963. This total replacement of one species by another in newly available nest sites indicates that the red squirrel may be a major competitor of the flying squirrel for suitable nest sites in areas where their ranges overlap. Flying squirrels may be forced to select isolated trees or cavities with openings too small to admit the larger squirrels.

Glaucomys sabrinus: Nothing is known about competition for nest sites in the wild between the two species of flying squirrels where their ranges overlap, i. e., in Minnesota, Wisconsin, Michigan, Ontario, New York, Massachusetts, Vermont, and New Hampshire, and in the Appalachian region. Only three occupied nests of the larger *G. sabrinus* were found during the current study in Michigan and Massachusetts; all were of the outside type. Farther north (Edmonton, Alberta), *G. sabrinus* often uses tree cavities (Cy Hampson, personal communication).

On several occasions in the laboratory *G. sabrinus* were introduced into cages containing *G. volans.* The latter was always aggressive toward the former, but in reciprocal tests *G. sabrinus* was often tolerant toward the introduced *G. volans.* In one instance a female *G. volans* drove a pair of resident *G. sabrinus* from their nest box.

In three other trials an individual of each species, same sex and about the same age, was placed together in cages unfamiliar to both. One nest box without nesting material was provided per cage and its occupancy was considered to be an indication of relative dominance since both species use nest boxes in captivity. The next day in cages 1 and 2, *G. sabrinus* occupied the nest boxes, in cage 3, *G. volans* was the occupant. Nesting material was then placed on the floor of the cages; by the following day it had been carried into the nest boxes. The nest box occupancy was the same as the previous day. The nesting material was then removed, and the following day each of the three boxes contained both species. During the following two days in cages 1 and 2 both species continued to occupy the same nest box, but in cage 3 *G. volans* occupied the box alone and *G. sabrinus* continued to sleep on the cage floor for the next 3 days.

In the next series of experiments new individuals were tried (3 female

G. volans and 2 male and 1 female *G. sabrinus*). The nest boxes were replaced with new ones. The day after introduction the two species of squirrels occupied the nest boxes together in all 3 cages.

It was observed previously that females of *G. volans* with litters were extremely aggressive toward other adult squirrels of the same species. To test the relative aggressiveness of the two species during breeding, four lactating females (not including any individuals described in the preceding experiments) of each species complete with their litters were matched (one female of each species at a time) as described above with only one nest box available on the floor of a windowless room 4 feet wide and 8 feet long. The nest box was in the middle and the two females with their litters were placed at opposite ends of the room. The room was left undisturbed for 24 hours. In 3 of the 4 matches, *G. volans* was found to occupy the nest box; in the remaining match, *G. sabrinus* "won." No reversal in the nest box occupancy took place during the 3 to 4 days the squirrels were kept in the same room.

Intraspecific Competition for Nest Sites

Some nests appeared to be particularly attractive to the squirrels and were nearly always occupied. One nest on the ESGR contained three adult flying squirrels on 14 April 1962. On 24 June a female with four young was found in the same cavity. On 1 September a different female with five young occupied the nest site (nest sites were never used concurrently by females with litters); she and the young were captured. By 22 September this cavity was occupied again by a female with four young. This litter must have been brought there by the female in the interim following the capture of the previous occupants for the young were too old to have been born there. These squirrels were also captured and by 7 October two adults had moved in. Other nests which were studied in the same manner showed similar results.

Within the species, favorable nesting sites appeared to be in constant demand, with individuals on the alert to move in whenever these sites became available. Not only does the squirrel need a nest site, but other cavities are used as secondary nests, retreats, feeding stations, food storing sites, and defecatoria. There is a continuous turnover of suitable nest sites in any given area. Dead trees decay, and as the wood softens the probability increases of a predator being able to tear open the nest cavity. Rotten trees are also more likely to fall in a windstorm. Some cavities appear to be unsuitable because in rainy weather the wood surrounding them becomes waterlogged and loses some of its effectiveness as an insulator.

Captive squirrels moved to different nest boxes if populations of mites or

fleas became large. If no other nest boxes were available, they slept on the floor in the corner of the cage. In the wild, abandoned nests were often found overridden with fleas.

In view of these considerations, the availability of suitable nest sites would seem to limit population size of flying squirrels. Nearly everything that is important to the survival of the species has some connection with primary nest sites, secondary nests, and retreats, e.g., protection against low temperatures and predators, raising of young, housing of food stores, and other activities discussed above.

AGGREGATIONS

SEASONAL AGGREGATIONS IN THE WILD.—Many naturalist authors have observed the gregarious tendencies of this species. Snyder (1897) found 22 adult flying squirrels in a hollow tree in Wisconsin during the winter of 1890; F. E. Wood (1910) referred to Dr. Schneck, who found 50 in one den in Mt. Carmel, Illinois; and N. A. Wood (1922) discovered "20 or more" in one nest in late December in Michigan. In the present study the largest aggregation found in one nest was 19 squirrels occupying an old flicker nest near Sunderland, Massachusetts. First discovered on 7 November 1959, this aggregation fluctuated from 19 to 9; some of the members that had been marked in February, 1960, were found in early March nesting in a tree about 160 yards distant. By late March, the aggregation had disbanded.

An analysis of 97 observations of nests found in the field in Massachusetts and Michigan over a period of four years (1959–63) showed that 39 "cold weather" nests (November–March) averaged 5.7 individuals per nest, whereas 58 "warm weather" nests (April–October) averaged 1.3 adults per nest (Fig. 1). This tendency among flying squirrels to aggregate during the colder months and disperse during the summer (Burt and Grossenheider, 1964), has been suggested by observers to be a factor in thermoregulation.

AGGREGATION IN CAPTIVITY.—To investigate the effects of various factors that might influence aggregating behavior, 30 adult flying squirrels were kept in a large (15 × 12 × 8 feet) outdoor cage at the ESGR from June, 1962, to July, 1964. This enclosure, at the edge of a woods, was sheltered by several oak trees. The animals had access to at least 10 (sometimes as many as 15) nest boxes. Nesting materials consisting of non-absorbent cotton, shredded bark, and burlap were provided, but they tended to become matted down and wet from urine, and frequent replacement was necessary.

At various times each month records were taken of the numbers of squirrels in each nest box. In spring and summer (breeding season) pregnant females were removed from the cage and replaced by equal numbers of non-
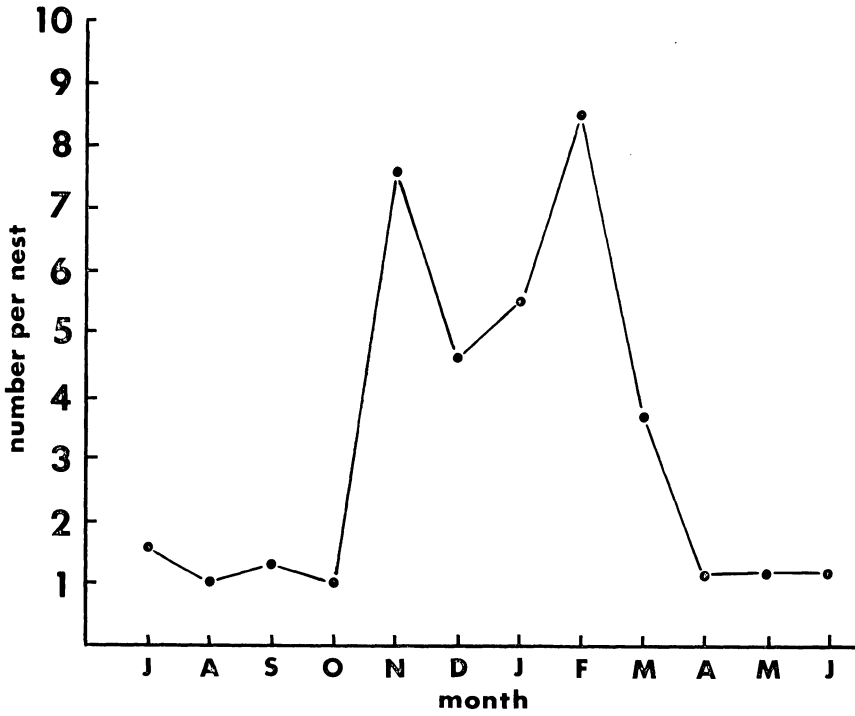
FIG. 1. Annual trend in aggregations in the wild. Monthly averages of adult flying squirrel numbers per nest based on 97 field observations of nests in Michigan and Massachusetts during 1959–63.

breeding females. This procedure insured a constant population size and tended to prevent decreases in aggregation size that might result from territorial behavior among pregnant females.

SOCIAL DYNAMICS OF THE AGGREGATION PROCESS.—In captivity and under natural conditions aggregations were composed of both sexes and various ages (but in extra-familial aggregations, no individuals less than 60 days old). Sexually active males were never observed to be aggressive toward each other.

Although females were gregarious during the cold months, they became strongly territorial just before and after their young were born; under natural conditions females were observed to drive away adults that came to the nest tree containing young. In the laboratory, females tolerated no adults in the same cage (2 × 2 × 2 feet) with the young. In the large outdoor cage, females with litters kept other adults away from the nest boxes con-

taining their litters (spring, 1965). Integration into the family group took place only after the young were over two months old.

Established non-breeding residents attacked any new adults that were placed in the cage with them. Members of an aggregation, when they meet, will give each other a kind of "kiss" similar to that described by King (1955) for prairie dogs (Cynomys ludovicianus).

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; the stance is similar to that taken by other species of rodents, e.g., heteromyids described by Eisenberg (1963). 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 the 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 he is finally accepted into the aggregation.

EFFECT OF POPULATION DENSITY AND CLIMATE.—A clear relationship seems to exist between ambient temperature and size of aggregations, both in captivity and under natural conditions (Figs. 1 and 2). The spring dispersal of animals results from pregnant females leaving the over-winter aggregation and from the other individuals disbanding at a rate proportional to temperature (Fig. 2).

In captivity the average size of aggregations tended to be larger than that found in nature at comparable times of the year. This may have resulted partly because of wetting and matting down of nesting material through the indiscriminate use of nest boxes as defecatoria by the captive squirrels, thereby causing the animals in confinement to spend much of the year without effective nesting material, and partly because there was a high density of animals in relation to number of nest boxes in the cage.

In nature the sizes of aggregations also depend, to a large extent, on population density. Squirrels have to come from greater distances in a low-density situation than in higher densities to form a given size aggregation. The problem is compounded at the northern edge of the geographic range where the temperatures are low and densities might tend to be low because of marginal conditions; aggregations are more difficult to form because the population is spread out, yet more crucial than in areas where temperatures are higher. The effect might discourage "pioneering" by the species and result in a well-defined line of demarcation, especially in winter, between areas in which the squirrels are fairly abundant and those areas where they
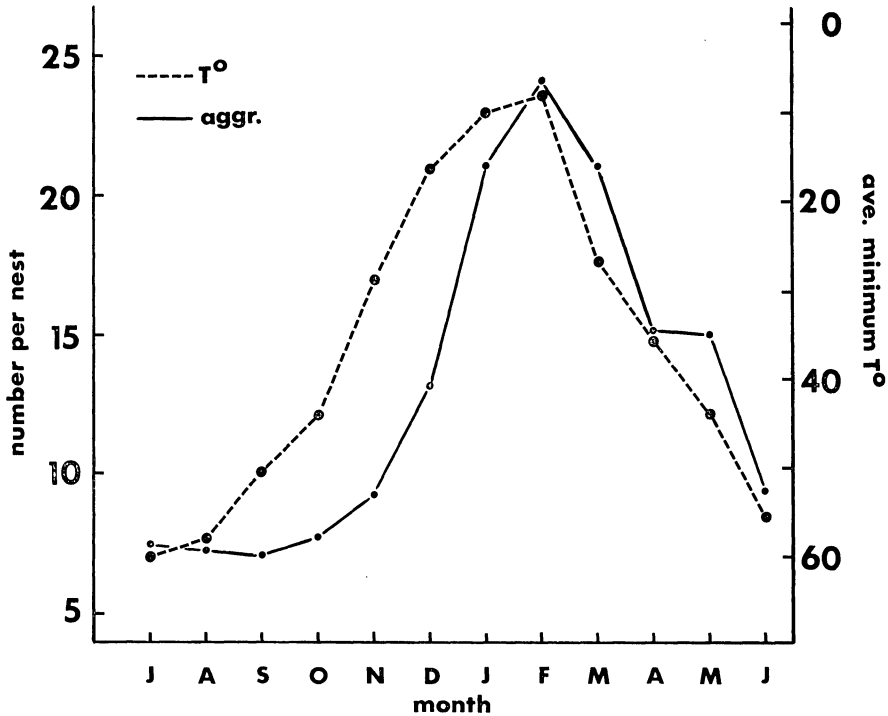
FIG. 2. Annual trend in aggregations in captivity. Monthly averages of the maximum flying squirrel numbers in nest boxes in an outdoor enclosure on the Edwin S. George Reserve, near Pinckney, Michigan. Solid line represents the aggregation tendencies of 30 animals from July 1962 through June 1963. Dashed line represents the inverse of the monthly average minimum temperature (Fahrenheit) as measured during the nights previous to the days the squirrels were censused.

are absent. This effect is noticeable when one traps areas for this species in northern latitudes.

The population densities of flying squirrels reported in the literature vary from one to five per acre. Sollberger (1943) calculated the summer population density of flying squirrels to be five individuals per acre in Aliquippa, Pennsylvania, and 2.2 near Ithaca, New York. Burt (1940) found summer densities of 1.3 and 1.6 per acre on the ESGR. Jordan (1948) estimated one per acre near Ann Arbor, Michigan, in summer, and 1.6 per acre during the winter in Illinois (Jordan, 1956).

On the basis of the number of different animals captured, marked, and released during the winter of 1959–60 there was a population density of 1.5 marked flying squirrels per acre near Mt. Toby, Massachusetts. I believe

that I was able to mark most of the individuals, but I was unable to deter-
mine how many unmarked animals remained in the area. In the summer of
1962, in a woodlot of approximately seven acres on the ESGR, the density
of flying squirrels was at least 2.5 per acre. In the latter instance the density
was determined by marking and counting the individuals that were using
the 24 nest boxes (see above). Fourteen different squirrels were found and
marked in the boxes and four additional unmarked individuals were ob-
served in the area, three in one nest and one in another. At Mud Lake Bog,
roughly ten miles northwest of Ann Arbor, Michigan, the population density
of flying squirrels in September, 1964, was estimated to be at least 2.2 per
acre, based on observations of 13 different adult squirrels routed from their
nests in one day in a woodlot of approximately six acres (all but three were
captured). These variations in density are probably an effect of differences
in the types of habitat and seasons in which the observations were made.

From the above data it would appear that densities in summer are higher
than in winter; this might be expected since recruitment into the population
takes place only in the summer in the northern states. Also, in winter the
population becomes clumped as a result of aggregation, thus one may get
the impression that the density is high or low depending on where trapping
is done.

Burt (1940) estimated the summer home range of flying squirrels to be
about four acres. If each of the squirrels in an aggregation of 20 has a winter
home range of four acres, no matter what the shapes of the home ranges are,
the average population density in the vicinity of the nest must exceed those
reported in the literature. If the animals come from great distances to
sleep together during the day, the winter home ranges must exceed those
of the summer. In most cases, however, the aggregations are small. Often
the female with a litter forms the nucleus of the winter aggregation which
other non-breeding individuals attempt to join. This can be done only
after the young are more than 60 days old, i.e., if the young were born in
September (and many of them are) the aggregation could not begin forming
until November. Before the young are 60 days old the female drives away
all intruders of the same species (Muul, unpublished data). This type of
territorial behavior appears to assure that females with litters can procure
and retain the most favorable nesting sites to raise their young.

The biological significance of the aggregating process may represent a
tendency to balance the advantages gained through solitary life against the
advantages in heat conservation gained through aggregation. This may be
effected by allowing gregarious behavior to predominate only in the event
of temperature stress. In the absence of temperature stress, solitary life
would generally be more advantageous, since more food would be available
to the individual and the attraction of predators into the area would be less

likely. Through behavioral changes brought about by temperature, flying squirrels appear to derive the benefits of territoriality in one season and of aggregation in another. Another effect of the winter aggregations is to bring reproductive individuals together during the breeding season, i.e., February and March.

PHYSIOLOGY OF NESTING BEHAVIOR

METHODS AND MATERIALS.—In order to evaluate the amount of insulation derived by a flying squirrel from the use of a tree cavity and nesting material, and from the presence of other members of the aggregation, a series of measurements was made. Resting metabolic rate was measured at various temperatures to determine the zone of thermal neutrality (see discussion in Scholander, *et al.,* 1950). This was done in an open circuit respirometer in which metabolism was measured as CO_2 production. The animals were placed in a glass chamber through which air passed at a rate between 800 and 1200 cc/min. Prior to flowing into the chamber, the air was routed through a glass cylinder containing "Ascarite" and "Drierite" to remove CO_2 and water vapor, respectively. The air from the animal chamber passed through a "U" tube filled with "Drierite" which was changed regularly before one fourth of it underwent a color change as a result of the collected water vapor. The CO_2 produced by the animal(s) was collected in a second "U" tube containing "Ascarite"; a small amount of "Drierite" was added to this second "U" tube to collect the water produced as a result of the reaction between the CO_2 and "Ascarite." The "Ascarite" was changed before more than a third of the column of this material underwent a color change. This resulted in a routine: the "U" tubes were removed, replaced, and weighed at fixed time intervals, usually 15–20 minutes. The weight difference of the "U" tubes before and after each of the experiments represented the amount of CO_2 produced by the animal(s) during that time interval.

Temperature of the chamber was monitored by using copper constantan thermocouples in conjunction with a Brown Recording Potentiometer. The cover to the animal chamber was sealed with "lubriseal"; the chamber was checked for leaks before each of the experiments. The flow rate of air through the chamber was measured with a flow-meter and adjusted accordingly. All measurements were made during the day and, since feeding activity had ceased 4 to 6 hours previously, it was assumed that the animals were in a post-absorptive state. The temperature range in which the determinations were made was −8° to 26°C, achieved in a Hotpack Environmental Chamber; the animals were exposed to cold for almost two months at temperatures between −13° and 0°C before the measurements were begun.

To measure the insulative value of the wood surrounding a tree cavity in which flying squirrels might nest, segments of tree trunks, cut above and

below woodpecker excavations, were brought into the laboratory to be used in the respiratory chamber. Squirrels were allowed to enter the cavity in a given log and, after they became quiescent, measurements of CO_2 production (with adequate air circulation), as described previously, were made at various temperatures.

Insulative value of nesting material was measured similarly by allowing the squirrel(s) to build a nest of shredded inner bark in the tree cavity (in the northern states this material is commonly used in the wild). Usually the CO_2 production was not measured until the squirrel was inactive in the nest. Measurements of CO_2 production were also taken with 2, 3, 4, 6, and 8 squirrels in the log without nesting material, and with 2, 3, and 4 in a nest in the log.

PELAGE INSULATION.—For comparative purposes all of the CO_2 measurements were converted into calories; 1 cal. = 0.30 mg. CO_2 produced; it was assumed that the animals were in a post-absorptive state (R.Q. = 0.71). The body temperature (rectal) did not fluctuate markedly (36.2°–39.1°C) during the measurements; at ambient temperatures below O°C body temperature remained between 38° and 39°C. Heat lost by the animals as represented by the quantity of CO_2 produced at various temperatures is summarized in Figure 3. The computed basal metabolic rate is about 6.17 cal/(gm. hr.). The lower "critical temperature" is between 19° and 20°C. At temperatures below 19°C, heat production increases at a rate of about 0.29 cal/(gm. hr. °C) down to about 6°C. In plotting this curve the line was drawn through the minimum metabolic rate values at various temperatures. At temperatures below 6°C, a straight line relationship does not seem to hold; but, rising more curvilinearly, heat production down to −6.5°C increases at an average rate of 0.50 cal/(gm. hr. °C). Morrison and Ryser (1951) described for a flying squirrel a curve with a slope of about 0.40 cal/(gm. hr. °C).

In comparing the metabolism/temperature curve of "cold acclimated" flying squirrels with that of desert rodents of equivalent weight, for example the antelope ground squirrel (*Citellus leucurus*), which has a linear slope equivalent to 0.94 cal/ (gm. hr. °C) below the zone of thermal neutrality (Dawson, 1955), one gains an idea of the variability in the insulative properties of mammalian fur. Irving, Krog, and Monson (1955) found that below 20°C the red squirrel in Alaska increased its metabolic rate in a linear fashion equivalent to about 0.15 cal/ (gm. hr. °C).

On the basis of counts of hair follicles, Sealander (1951) concluded that the fur of *Peromyscus* was much thicker during winter than summer. Seasonal changes in the insulative value of fur have also been investigated by Hart (1956). Though no follicle counts were made during the current
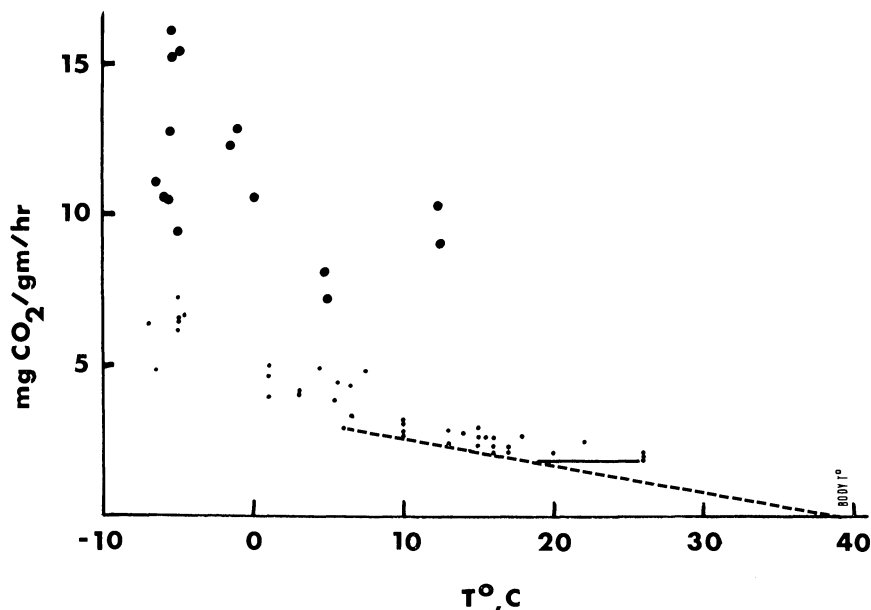
FIG. 3. CO_2 production (measure of metabolic rate) of flying squirrels in post-absorptive state at various environmental temperatures. The dashed line representing heat loss is fitted to the lowest readings and is extrapolated to body temperature. The larger dots represent readings during times the squirrels were active in the metabolic chamber.

study, the fur of flying squirrels appeared to be thicker in the winter. Seasonal changes in the basal metabolic rate were not observed.

INSULATION DERIVED FROM THE NEST AND AGGREGATION.—One can calculate the insulative value of the wood enclosing the nest cavity by comparing the lowest metabolic rates [15 cal/(gm. hr.); N = 44] while the squirrel is in the nest cavity [at −7.5°C] with the lowest readings while the squirrel is exposed [16.2 cal/(gm. hr.)]; both readings are assumed to represent periods of least muscular activity. Since insulation varies inversely with heat loss, the difference in metabolism under these conditions reflects the added insulation derived from the tree. By comparing the above values with basal metabolism [6.17 cal/(gm. hr.)] one can estimate the percentage of energy in excess of basal demands required to maintain homeothermy at this temperature with and without the insulative benefit of the wood. Thus, at −7.5°C. the reduction of metabolism by 1.2 cal/(gm. hr.) amounts to 12 per cent of the energy that is required [10 cal/(gm. hr.)] by an exposed animal in excess of basal expenditures to maintain homeothermy.

The determination of the insulative quality of nesting material and of the other members of the aggregation was arrived at as described above. Comparing the lowest metabolic rate while three squirrels were in a nest in a log with the lowest reading while they were in an empty nest cavity, the insulative value of the nesting material was estimated to be equivalent to a saving of 3.3 cal/(gm. hr.) at $-7.3°C$. This amounts to 33 per cent of the thermoregulatory energy (caloric expenditure in excess of basal demands, i.e., amount of energy devoted to thermoregulation) that is required by an exposed animal at this temperature. When six squirrels are present in a nest cavity, each of the occupants saves an additional 6.6 cal/(gm. hr.) as compared with an animal in a tree cavity alone, or 6.6 per cent of the total thermoregulatory energy at an ambient temperature of $-7.5°C$.

No heat load is engendered under natural conditions of aggregation because of individual positioning and arrangement of the nesting material. As the temperature in the cavity increases, the squirrels lie on their backs and spread their patagia. On warm days much of the time is spent hanging partially out of the nest entrances, or the aggregation may disperse entirely, as was seen in the large outdoor cage (Fig. 2).

Many small mammals escape the full impact of low temperatures by burrowing under the snow or below the frost line in the soil. Although underground retreats are sometimes used, G. volans has not been observed to nest in them. In the winter this arboreal species apparently minimizes the effects of cold through seasonal aggregation (Burt and Grossenheider, 1964) and by nest construction.

Sealander (1952) found that survival of Peromyscus in low temperatures was increased if the animals were allowed to huddle. Pearson (1947) reported lower metabolic rates in small rodents that were in bodily contact with one another than in isolated individuals kept under the same temperature conditions. Prychodko (1958) found that food consumption per gram of body weight in mice kept at 25°, 4°, and $-3°C$ decreased when they were living in pairs; an additional equivalent reduction occurred when mice were kept in groups of five.

In an aggregation, (1) the total heat production elevates the ambient temperature in the nest, creating a more favorable microclimate; (2) as the animals pile up on top of one another, forming a ball-shaped mass inside the nest, they provide one another with insulation; (3) individuals collect some of the radiant heat emitted by others; and (4) the surface area to volume ratio is less than that of the sum of the individual members, thus reducing heat loss per gram of body weight through heat transfer, and less energy is expended to maintain body temperature. The wood enclosing the nest cavity reduces heat transfer from the animal, through radiation and convection, to the atmosphere. The nesting material in the cavity reduces

heat loss through radiation, convection, and conduction (see discussion in A. D. Moore, 1945).

On cold days the squirrels pile up on top of one another and surround themselves with nesting material. Single individuals and small nesting groups use large amounts of nesting material under natural conditions, whereas large aggregations use little or none. During the summer, single individuals sometimes use no nesting material, however, females with very young litters use large quantities of nesting material until the young grow fur. As the young develop, the nesting material becomes progressively matted down and its insulative properties decrease.

Because of the refrigeration limitations of the environmental chamber it was not possible to expose the animals to temperatures below −8°C experimentally, nevertheless an estimate may be made of the lowest temperature at which six squirrels (average aggregation size) of average weight are able to control their microclimate and still maintain homeothermy with only a basal expenditure of energy by taking full advantage of nesting and aggregation behavior. Such a determination may be made by first deriving the potential cumulative insulative value of the wood enclosing the nest cavity, nesting material, and other members of the aggregation, i.e., 1.2, 3.3, 6.6 cal/(gm. hr.), respectively, or a total of 11.1 cal/(gm. hr.). Thus, since the lowest observed rate of metabolism in the lowest temperature range (−8°C) was 16.2 calories/(gm. hr.), or 10 cal /(gm. hr.) in excess of basal demands, and since the squirrel can potentially save about 11 cal/(gm. hr.), lower temperatures could be tolerated. The difference between 11.1 and 10.5 [1.1 cal/(gm. hr.)] represents the additional potential savings in metabolic expenditure with the given amount of insulation if the temperature were even lower. Since the rate of heat loss in this temperature range is 0.50 cal/(gm. hr. °C),

$$\frac{1.1 \text{ cal}/(\text{gm. hr.})}{0.50 \text{ cal}/(\text{gm. hr. °C})} = 2.2°C$$

This means that an additional decrease of 2.2°C can be tolerated without a necessary increase in heat production or that the squirrel can tolerate temperatures down to about −10°C.

One should bear in mind that the above was derived under laboratory conditions and that the animals were never completely quiescent during the metabolic measurements. It is likely that under natural conditions more energy is saved than the experiments indicate. Also, the squirrels have the opportunity to choose their own nest site and have time to construct a more suitable nest than was possible in the metabolic chamber. Nevertheless, members of an average aggregation of six (5.7, Fig. 1) under natural conditions in the northern parts of the geographic range from November

to March (average temperature −8°C) appear to be in a favorable situation from the standpoint of energetics.

The average temperature is based on round-the-clock readings, but the squirrels spend the warmer portion of the 24-hour cycle in the nest. While the squirrels are moderately active their metabolic rate increases roughly four-fold (Fig. 3, large dots). This would probably produce enough heat to compensate for losses resulting from exposure to low nocturnal temperatures, provided activity did not excessively reduce the insulative effectiveness of the fur (Hart and Heroux, 1955). Whenever low temperatures become stressful the animals need only take advantage of the insulation provided by the nest.

FOOD PREFERENCES AND STORING BEHAVIOR

Nuts, acorns, seeds, buds, bark, and fruits of various kinds were observed to be readily consumed by flying squirrels, as were insects and in some instances birds' eggs, birds, and small mammals. In the outdoor cage the squirrels often hung by their hind legs, under the light situated on top, and used their forefeet in capturing flying insects attracted to the light. They actively pursued insects such as *Phyllophaga* that landed on the ground. Mice *(Mus)* placed in the cage with them were often pursued, captured, killed, and sometimes consumed. On several occasions inverted skins of *Blarina* and *Peromyscus,* that had entered, apparently through the ½-inch wire mesh, were found in the nest boxes in the outdoor cage.

In southeastern Michigan a large portion of the diet of flying squirrels appears to consist of hickory nuts and acorns. These are accumulated during a period of intensive storing from September through December, or even as late as January, and are consumed throughout the year, including the summer, until the next crop ripens.

In the fall of 1962 there was a large hickory nut crop on the ESGR. Acorns also were abundant. Food utilization by flying squirrels was determined during the subsequent year by monthly examination of food remains in the 24 nest boxes used as feeding stations by these animals. Other rodents also used the boxes, but the food remains of *Glaucomys* could be distinguished from those of others (Sollberger, 1940). In the 1962–63 season, hickory nuts comprised 93.8 per cent of the empty shells found in the feeding stations while the remainder consisted primarily of acorn shells (Fig. 4). It thus appears that flying squirrels preferred hickory nuts over acorns for storage when both were available.

In the 1963–64 season, the hickory nut crop largely failed on the ESGR as well as in surrounding areas. During this season 83 per cent of the items found in the nest boxes consisted of acorn shells; hickory nut shells made
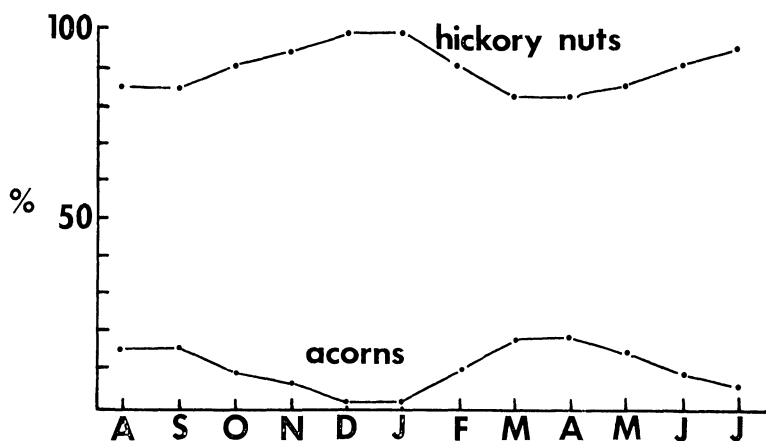
Fig. 4. Proportions of acorns and hickory nuts utilized by flying squirrels during a year of hickory nut abundance, 1962–63, based on monthly examination of food remains in 24 nest boxes used as feeding stations by flying squirrels on the Edwin S. George Reserve.

up the bulk of the remainder (Fig. 5). This lability in feeding behavior probably contributes to the success of the species in areas where a food item may vary in abundance from one year to the next. It may also be of importance in permitting the species to exploit a wide range of habitats in which one or another food item is abundant.

It is common knowledge that squirrels store food, apparently for later use in winter. In the laboratory, flying squirrels continued to store some food throughout the year. However, during the fall months storing behavior was greatly intensified coincident with the ripening of the nut and acorn crops. In captivity more than 300 nuts may be stored by a single individual in one night. In the wild at this time, exploratory behavior, which leads to the discovery of nuts and acorns, is also intensified. The squirrels seem to locate these items among the leaf litter on the ground by olfaction. Nuts placed in a cloth bag were readily found by captive squirrels.

Many nuts and acorns are also cut from the trees. Layne (1958) observed flying squirrels gathering nuts in the trees during October. However, when the crop fell to the ground in November, the squirrels spent most of their time gathering nuts among the leaves.

Nut handling by flying squirrels is similar to that described for *Sciurus vulgaris* (Eibl-Eibesfeldt, 1963). The nut is lifted with the teeth and forefeet, then manipulated, mouthed, and notched in the shell on each side of the peduncle. The animal's teeth fit into these notches when the nut is carried. If the husk is still present the squirrel usually removes it before transporting
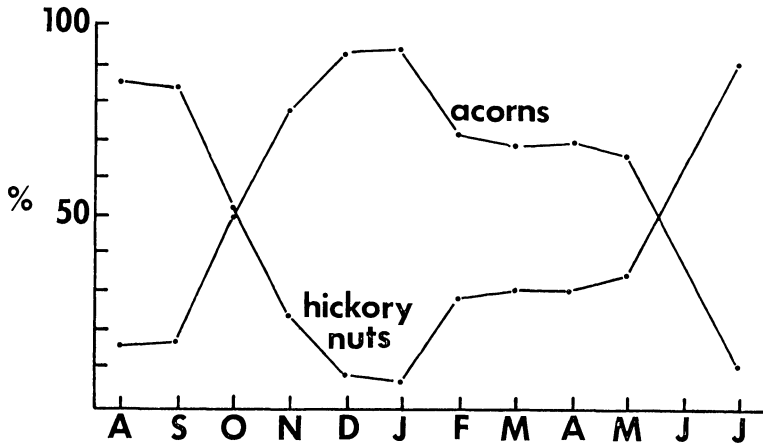
FIG. 5. Proportions of acorns and hickory nuts utilized by flying squirrels during a year of hickory nut scarcity 1963–64, based on monthly examination of food remains in 24 nest boxes used as feeding stations by flying squirrels on the Edwin S. George Reserve.

the nut. Empty or spoiled nuts are discarded during the manipulation process.

Food is stored in a variety of places. Sollberger (1938) assumed that flying squirrels stored food primarily in trees since he believed that these rodents were not strong enough to dig nuts out of the frozen ground. In the present study, nuts and other food material were found to be stored in various places; e.g., in the leaf litter on the ground, wedged in cracks and other cavities in trees, in rough bark, or between branches. Flying squirrels do not dig extensively in the ground—the animal merely parts the leaf litter and pushes the nut under it, between its legs. The tail is raised vertically in the process and the nut is pushed firmly into place with bared incisors. The nut is then concealed in leaf litter, but not buried in the soil. Nuts stored in forks of branches, in cracks, and between rough bark are wedged there by the squirrel pounding with its bared incisors.

The consumption of stored nuts is a two-stage process. Initially, a small round hole is gnawed into the shell and a part of the meat is dug out with the lower incisors. Later the squirrel returns to these accumulations of partially eaten nuts in the "feeding stations," enlarges the opening in the shell and digs out the remaining meat.

In winter, as do the fox squirrels, *Sciurus niger* (Cahalane, 1947), flying squirrels locate previously stored food apparently by olfactory cues. They sometimes tunneled under the snow when it was deep; this was also noted in the large outdoor cage.

EFFECT OF PHOTOPERIOD AND TEMPERATURE ON FOOD-STORING BEHAVIOR

In reference to food storing by a pet flying squirrel, F. H. King (1883) stated:

> Have we in this instance . . . evidence that an act, executed repeatedly during particular seasonal conditions, and under certain sense impressions, as sight and smell, may impart so definite a set to the organization as that it shall be transmitted to an offspring? Is this set a molecular one and located in the nervous tissue? Is it so sensitive that if, when a body is experiencing those seasonal changes due to the change of seasons in the earth during which the original set had its origin, a combination of vibrations . . . (such as) . . . the sight and smell of an acorn . . . like those which were instrumental in producing the set are again imposed upon the nervous tissue, similar feelings will be awakened which tend to culminate in a desire like the ones which had prompted former generations to act in question?

In more modern terms, a part of King's question appears to be: what cues are involved in the initiation of physiological and behavioral processes leading to the intensive food-storing characteristic of the fall season? In this study availability of food, photoperiod, and temperature were tested as cues.

METHODS AND MATERIALS, 1962–63.—From August 1962 through March 1963, 40 squirrels, divided into four experimental groups of ten animals each, were maintained at various temperatures and photoperiods. In each group the animals were kept in bisexual pairs, one pair in each $2 \times 2 \times 2$-foot wire cage. A nest box and a five-compartment storage box were placed in each cage (Fig. 6). Food (mainly sunflower seeds) and water were offered *ad libitum*, and liquid vitamins were added to the drinking water.

Fifty or more hickory nuts were placed on the cage floor at various intervals, and those stored were counted the next day. An effort was made to keep the nut supply in excess of the number stored. The squirrels stored the nuts in the storage box, nest box, and in the corners and edges of the cage.

Initially the nuts that had been stored in a given test were removed from the storage sites and replaced in a pile on the cage floor; the performances were then recorded for the second night. It became apparent however, that the storing behavior in response to these nuts differed from that recorded previously (see below), and after 15 November only "new" nuts were given except in specific cases.

The nuts, collected from various trees, were initially presented as gathered, some husked and some with the husks intact. Until used, the nuts were stored in burlap bags (they turned moldy in metal containers).

The experimental groups were maintained 4–6 weeks prior to the first tests on food storing under the following conditions:

FIG. 6. Type of cage used in the food-storing experiments, with the nest box and the five compartment storing box (with two openings on one side, one on the other, and one on each end); the bottom of the storing box was on hinges and could be opened to allow the nuts to fall to the cage floor for counting. The bottom of each cage was covered with wood shavings.

Group A was kept outdoors, exposed to seasonal temperatures and photoperiods.

Group B was kept in an unheated room, open to the outside, and thus followed a seasonal temperature pattern (usually a few degrees higher than outside). The photoperiod was kept constant with a timer operating the lights (15 hours light, 9 hours dark) until 3 March when the group was exposed to seasonal day lengths (about 12 hours).

Group C was exposed to the same photoperiod as **B** except that the day length was decreased by one hour ($\frac{1}{2}$ hour in the A.M., $\frac{1}{2}$ hour in the P.M.) on 13 December and again by the same amount on 14 December. The temperature was maintained at $20°C \pm 4°C$.

Group D was exposed to seasonal photoperiods by operating the room lights through an astronomical timer, but the temperature was maintained at $20°C \pm 2°C$.

METHODS AND MATERIALS, 1963–64.—To continue the tests of the effect of photoperiod and other factors on food storing, three experimental groups were set up in the same kind of cages as used in 1962–63. Of two groups (12 animals each) exposed to seasonal temperatures and photoperiods, one consisted of adult animals, the other of individuals born in the spring of 1963. Early in the experiments it became evident that no significant difference in the storing performance existed between these groups; subsequently only adults were used.

The remaining group of 12 animals was exposed to predetermined photoperiods of varying lengths, starting on 20 September with 12 hours light and 12 hours dark. Under this photoperiod regime the animals were initially exposed to a seasonal light-dark cycle, but the photoperiod was subsequently reduced to lengths shorter than normal for that time of year.

RESULTS, 1962–63.—The food-storing experiments with **groups A, B, C,** and **D** in 1962–63 indicated that photoperiod, independent of temperature cues, was sufficient to induce an increase in storing behavior. In Figures 7–10 the data on daily storing by all of the pairs in each group were lumped
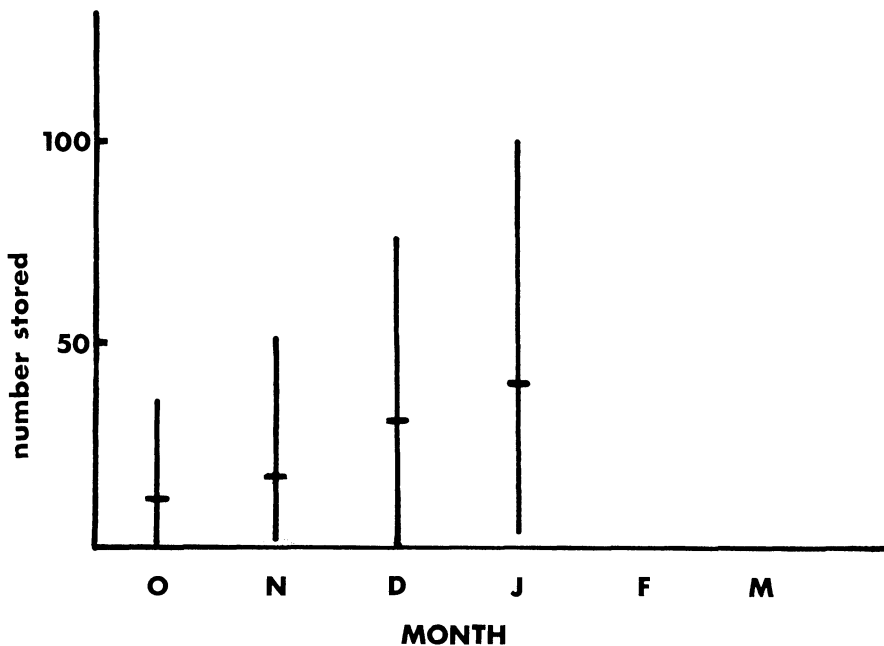

FIG. 7. Food-storing performance of group A, 1962–63; kept outdoors and thus exposed to seasonal temperature and photoperiod changes as well as precipitation and wind. Vertical line indicates monthly range of numbers of nuts stored by the pairs of squirrels in this group; small horizontal line indicates the monthly mean,
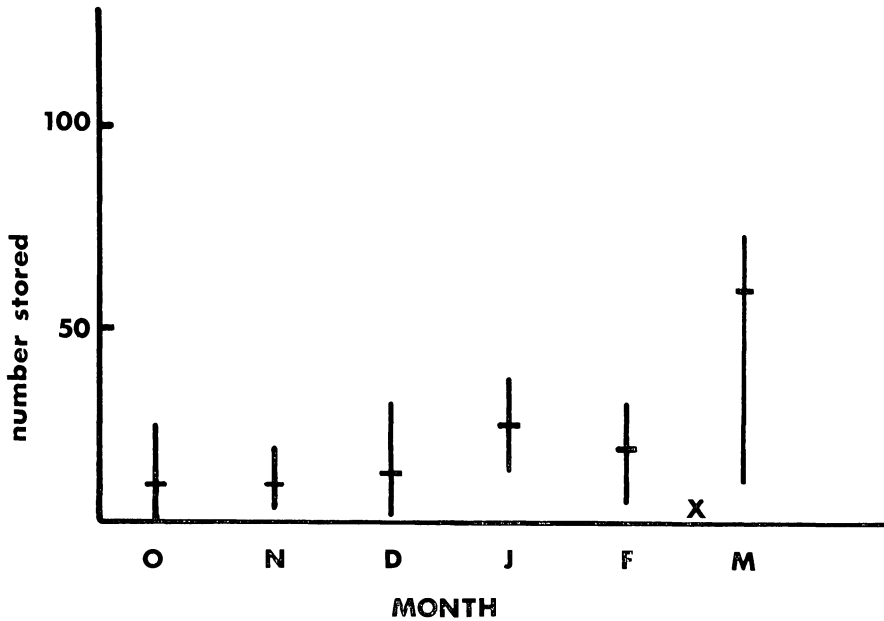
FIG. 8. Food-storing performance of group B, 1962–63; kept in a room in the barn laboratory (ESGR) that was open to the outside and thus followed a seasonal temperature pattern; the photoperiod was held constant (15 hours light, 9 hours dark) until 3 March when the group was exposed to the seasonal photoperiod (little less than 12 hours at that time); X indicates the time of change in photoperiod. Range and mean as in Fig. 7.

for each month. The range is often quite large, but much of this is the result of some individuals storing only a few nuts throughout the tests. For this reason more emphasis is placed on the maximum performance of the best performing pair each month than on the mean when comparing groups. When the animals were selected it was impossible to anticipate what proportion of them would not store under laboratory conditions.

Group A (seasonal photoperiod and temperature) showed a general increase in the intensity of storing from early October to the beginning of January (Fig. 7), as did **group D** (Fig. 10). In comparing equivalent days by the Mann-Whitney "U" test, I found that these groups, although not significantly different from each other, were different from **group B** (constant photoperiod, seasonal temperature) (p < .01, one tailed) (Fig. 8). **Group B** stored at a basal level characteristic of summer until the photoperiod regime was changed on 3 March. (By this time the performance of the other groups was decreasing.) This decrease in the photoperiod in the spring after the animals had been kept under a 15-hour photoperiod through the winter,
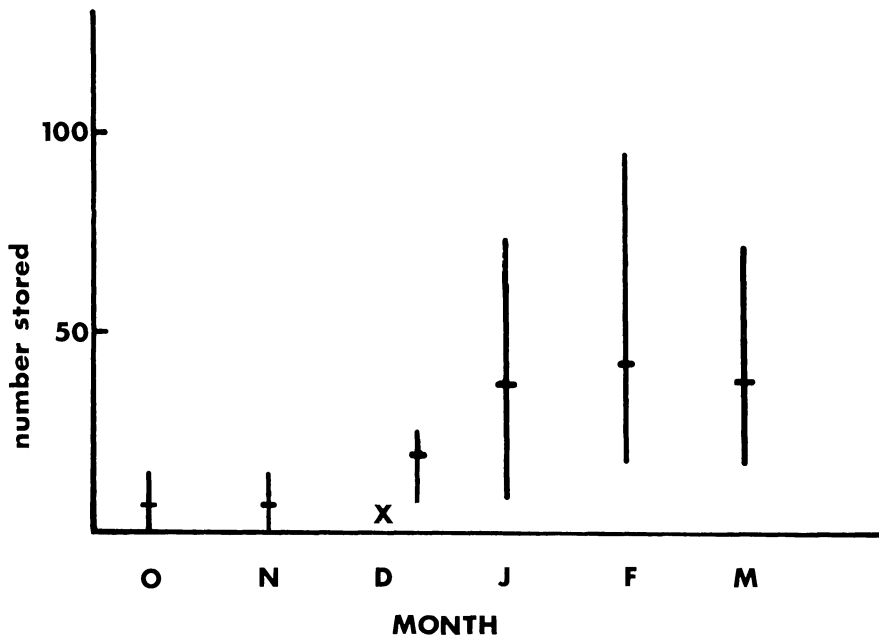
Fig. 9. Food-storing performance of group C, 1962–63, at a constant temperature (20°C ± 4°C) and a 15-hour photoperiod until 13 December when the photoperiod was reduced by ½ hour in the morning and ½ hour in the evening and by an equal amount on 14 December. X indicates the time of the changes in photoperiod. Range and mean as in Fig. 7.

resulted in an increase in the storing response to a level characteristic of mid-October in the group exposed to normal photoperiods.

Group C (constant photoperiod and temperature) (Fig. 9) stored at a rate that was significantly lower than that seen in **groups A** and **D** until the photoperiod regime was changed on 13 and 14 December (Mann-Whitney "U," one tailed p < .001). After this time the storing performance increased and shortly approximated that of **groups A** and **D**.

RESULTS, 1963–64.—The level of storing shown by the group subjected to controlled photoperiods approximated that seen in the group which was concurrently subjected to normal photoperiod, as long as the former was exposed to a photoperiod regime nearly the same as outdoors, i.e., 12 hours light, 12 hours dark (Figs. 11 and 12). The first experimental reduction of the photoperiod, however, brought this group out of phase with the normal photoperiod for that time of year and subsequent reductions increased this difference. The squirrels were, in effect, encountering photoperiods charac-
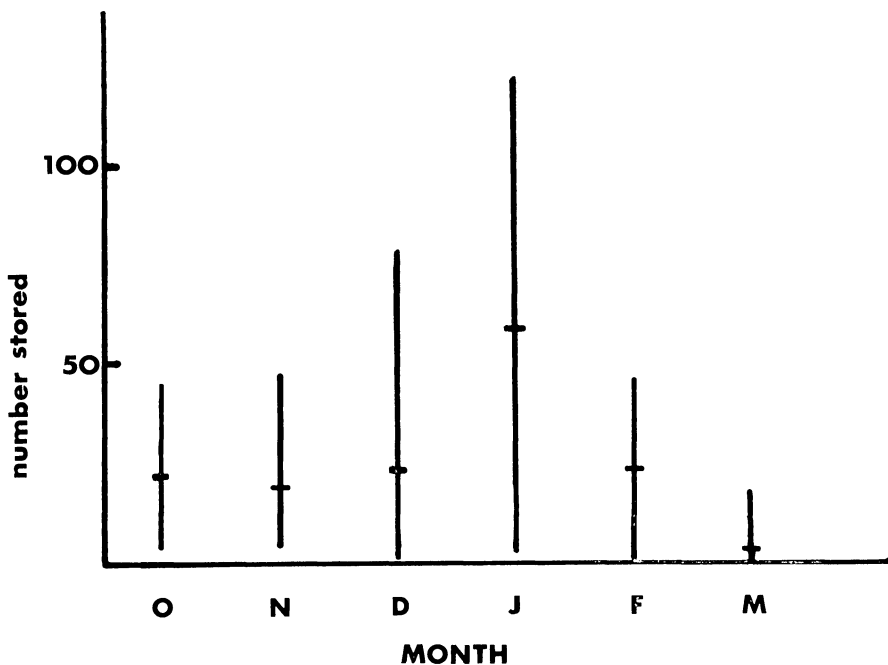
FIG. 10. Food-storing performance of group D, 1962–63, exposed to natural photo-periods (room lights operated through an astronomical timer) and constant temperatures (20°C ± 2°C). Range and mean as in Fig. 7.

teristic of later in the year; the level of storing increased so that these squirrels were storing at an accelerated level compared with the group on normal photoperiod.

By 5 November the storing activity of the group subjected to the controlled constant photoperiod reached a maximum of 340 nuts per pair in a night, which is roughly one-third more than the number stored by any pair in the normal photoperiod group at the same time of year. During this time, the controlled photoperiod to which this group had been exposed had been adjusted to a 9-hour photoperiod for 10 days, i.e., approximately two hours shorter than the normal photoperiod at this time of year. Unfortunately, because of their high performance, some of the pairs never had a surplus of nuts. However, the performance of pairs representing the low end of the range increased as well. Perhaps these pairs at least were not limited by supply.

On 6 November the photoperiod was changed to 15 hours. Within five days of the reversion the maximum performance of the group on this constant photoperiod dropped from 340 to 290 nuts per night; the low end of
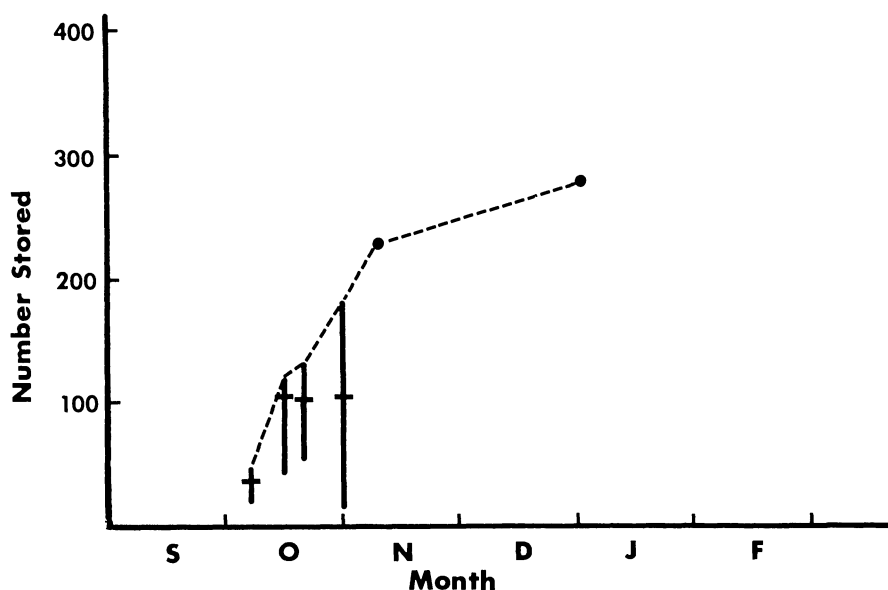
FIG. 11. Food-storing performance of the normal photoperiod group in 1963–64. Range and means (as in Fig. 7) are given for each experiment except for the two closed circles which represent the performance of the only pairs tested in the last experiment.

the range dropped from 210 (30 October) to six by 12 November. By 13 November the maximum performance of this group (still on a constant, 15-hour photoperiod) had dropped to 190. The level of storing remained at approximately this level until the tests were terminated in early December. In the meantime, the performance of the group subjected to normal, seasonal photoperiods continued to increase.

DISCUSSION.—Since insects, fungi, tree buds, and fruits are available during the warm months of the year, food supply is probably not a short-term limiting factor at that time. The food habits of flying squirrels appear sufficiently variable to allow exploitation of many potential sources. In winter when low temperatures prevail, a relative scarcity of many food items could be severely felt among the non-hibernating homeotherms.

Food-storing behavior appears to have evolved in many groups of vertebrates and invertebrates as a kind of buffer against this stress. Storing may be in the form of fat accumulations in the body (bears, ground squirrels, woodchucks, and various insects) or in the form of food items gathered during favorable weather, stored, and consumed later during the winter season. Many kinds of animals store foods. Some examples are: honey bees, chipmunks, tree squirrels of various kinds, and some species of woodpeckers.
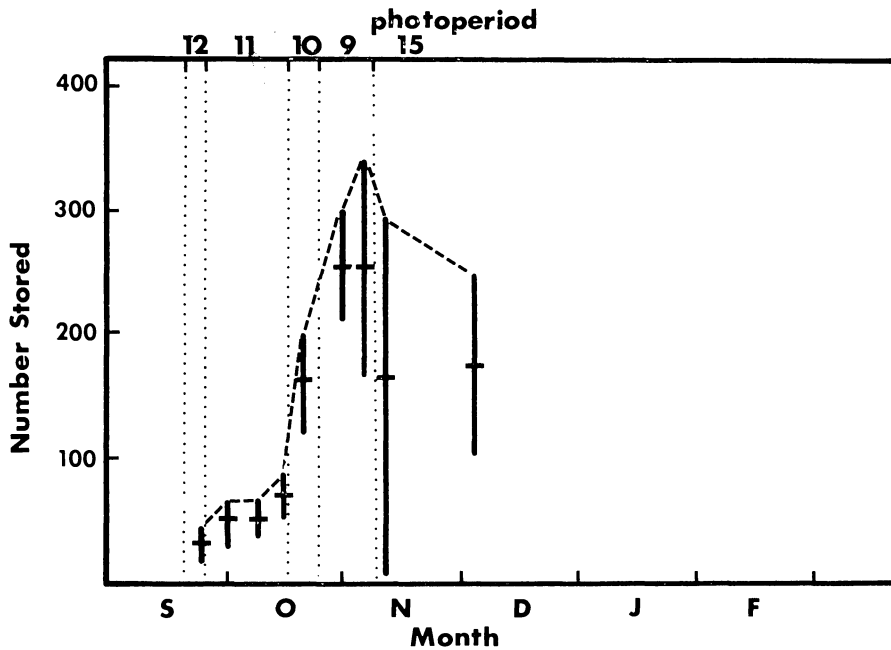
Fig. 12. Food-storing performance of the controlled photoperiod group in 1963–64. The photoperiod was reduced (as indicated on top of the graph) from 12 hours by ½ hour in the morning and ½ hour in the evening beginning on 25 September and again on 17 and 20 October; on 7 November the 9-hour photoperiod was increased to 15 hours. Range and mean as in Fig. 7.

Among some of these food storers, behavior has evolved that tends to assure the accumulation of sufficient food material to meet the metabolic needs during the period of cold stress. In flying squirrels this behavior is activated by photoperiod, a precise environmental cue, on which the animals can depend from one year to the next.

When **group C** (1962–63) (initially exposed to a 15-hour photoperiod) was placed under a 13-hour photoperiod on 14 December, the increase in the storing performance approximated that seen in **groups A** and **D** during the middle of October and early November. In October and November 1963, the group subjected to photoperiods that were shorter than normal exhibited a higher level of storing than did the group on the normal photoperiod during the same time. Thus, there was a direct relationship between the level of storing and the length of the light-dark cycle. The storing process appeared to be dependent on photoperiod, whether this cue was provided later or earlier than it occurred naturally.

The triggering of the storing response by photoperiod does not occur in

the same manner that sign-stimuli evoke fixed action patterns. Rather, the processes leading to food storing remain dependent on photoperiod. This was demonstrated when the accelerated storing during the fall of 1963 was greatly reduced as the unseasonably short day was reverted to a long (15-hour) day.

The increase in the level of storing can be thought of in terms of a staircase: each step up can be evoked by an increased differential between the amount of light and dark, in favor of the dark. Although high levels of storing were obtained unseasonably early by the group subjected to advanced controlled photoperiods, the curves for maximum storing vs. length of the dark period are the same as that of the group on normal photoperiod. (Fig. 13).

With decreasing photoperiod, more storing time is available for this nocturnal species. But the animals do not spend the entire night in storing activity, and the levels of storing seen in the experimental groups could be achieved in a much shorter time. Time tests during the fall of 1964 indicated that 400 nuts could be stored by a pair of captive squirrels in less than two hours. It thus appears that changes in photoperiod alone, rather than the time available, are responsible for evoking the increase.

Apparently, many physiological processes are triggered by photoperiodic-
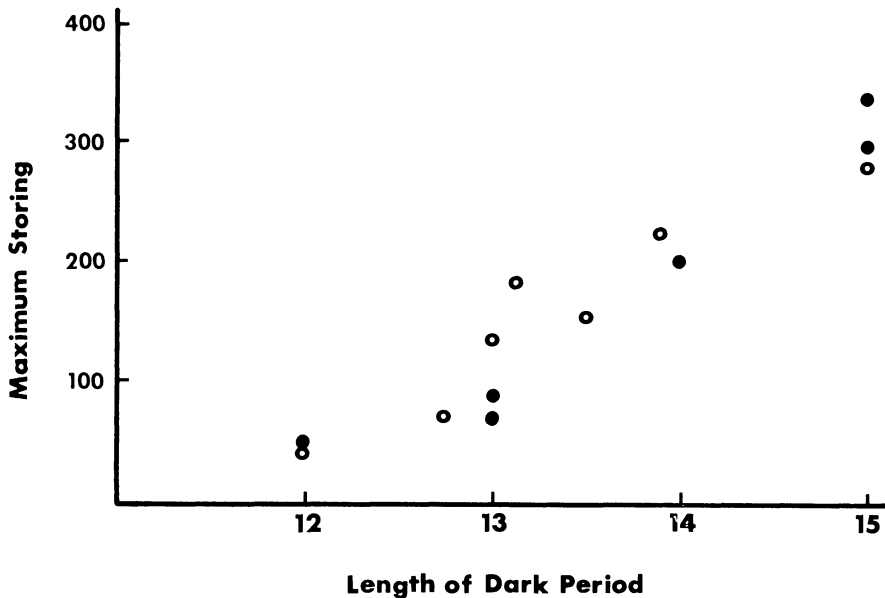

FIG. 13. Maximum storing performance of the groups on normal (open circles) and accelerated (closed circles) photoperiods in 1963–64 plotted against the length of the dark period during the nights in which the storing experiments were conducted.

ity. Notable among these is the control of reproductive cycles in birds (for review see Farner, 1964). Many animals depend on it for phase adjustment of their circadian rhythms of activity (Aschoff, 1960; Rawson, 1959; Roberts, 1962), as has been demonstrated for flying squirrels by DeCoursey (1960). This basic sensitivity to changes in photoperiod may have become more highly developed during the evolution of the species with the result that physiological processes which have annual cycles such as those leading to food storing, and perhaps others, now respond to annual changes in photo-period.

With the search for food and its subsequent storing a predominant activity only during a specific time of year, a time that may be physiolog-ically anticipated and is synchronized with the ripening of most crops, the animal is free from such activities during the remainder of the year. It would be energetically wasteful for the squirrel to devote its efforts to special forms of exploratory behavior at times when little food suitable for storing is available. Further, it might interfere with other activities necessary for the survival of the species, e.g., nest building and reproduction, and needlessly expose the animal to predation. By delaying the intensive food storing activity until a specific time, premature harvesting of the mast crop would also be prevented.

Five days after the photoperiod was changed from 9 to 15 hours in 1963 in the group exposed previously to accelerated photoperiods, the average storing performance dropped roughly by half; in six days the maximum had dropped about 50 per cent, while the minimum performance dropped to less than 5 per cent of the performance level before the increase in photo-period (Fig. 11). This indicates that the reduction of storing activity seems also to be dependent on photoperiod; as the photoperiod increases the storing decreases. Such a response to increasing photoperiod would not only prevent the animals from wasting energy in search for scarce food items during winter, but the squirrels would probably tend to conserve more energy through the tendency to remain inactive in the nest during cold weather than they would gain by discovering a few more food items that might have been missed earlier.

RESPONSES OF FLYING SQUIRRELS TO PREVIOUSLY STORED NUTS

Early in the experiments on food storing it became evident that the squirrels were reacting differently to nuts that had been previously stored than to those with which the squirrels had no previous contact. In an at-tempt to determine the factors involved in this apparent discriminatory behavior, a series of experiments were conducted both in the 1962–63 and 1963–64 seasons.

METHODS AND MATERIALS.—On 24 January and 1, 6, 14, and 28 February 1963, groups **C** and **D** were given twice the usual number of nuts, half of which had been stored previously and half with which the squirrels had no previous encounter. Both kinds of nuts were marked with ink or pencil, so that later they could be identified, and placed in separate piles on the cage floor. Also, at various times during the 1963–64 experiments, previously stored nuts along with fresh ones were presented to the squirrels to test the apparent discriminatory ability. Nuts that had been stored during the current year as well as those stored during the previous year were used.

On 12 and 13 November 1964, pairs of squirrels were given 150 unhusked and 150 husked hickory nuts (marked); the same was given to another pair on 13 November.

On 9 November eight of the adults that had been exposed to normal photoperiods were presented with 150 each of previously stored and unstored nuts. Both types of nuts were washed with detergent ("Tide") and hot water, rinsed, and dried before given to the squirrels.

On 1, 3, 4, and 5 January 1964, pairs of squirrels were given equal quantities of stored and unstored nuts, both of which had been washed in CCl_4 and rinsed with water.

On 7 January a pair of squirrels was given 40 fresh nuts and 40 nuts that had been handled by other squirrels by the forefeet only through two layers of wire situated on top of the cage so that the nuts did not come in contact with the mouth. The squirrels attempted to pull the nuts into the cage, thereby making about as much contact with their feet as during the manipulation stage during food storage. These "handled" nuts and fresh nuts were marked and placed on the cage floor on a tray. The proportion of each type taken was determined after the squirrels had removed half of the nuts from the tray.

RESULTS AND DISCUSSION.—Given a choice between "new" nuts and those that had been stored during the previous year, the squirrels took the "new" ones more frequently (Fig. 14). If "new" nuts and nuts stored during the current season were presented, the squirrels took "new" nuts at a ratio of approximately 4:1 (Fig. 14).

Since the preference ratio for new nuts to previously stored nuts was less than 2:1 when the latter had been stored during the previous year, as compared with a ratio of 4:1 when the nuts had been stored during the current year (Fig. 14), an odor marker was thought to be involved; something apparently was wearing away during a year's time. This hypothesis was further substantiated when stored and unstored nuts were washed with hot water and a detergent. Although the response to these nuts was generally lower than to unwashed nuts, the acceptance ratio of unstored nuts to those stored during the current year became 2:1 (Fig. 14).
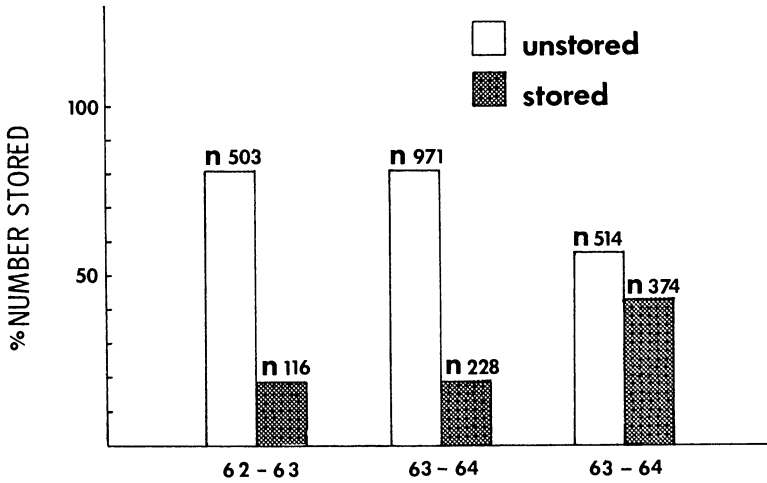
FIG. 14. Observed preference by flying squirrels for unstored over previously stored nuts. Groups C and D were tested in this regard in 1962–63 (left pair of columns) on 24 January and 1, 6, 14, and 28 February. In 1963–64 (center pair of columns) the controlled photoperiod group was tested on 30 October and 13 November. The right hand pair of columns represents experiments using nuts stored during the previous year. During the tests both stored and unstored nuts were marked and placed in separate piles on the cage floor ("n" represents the numbers of nuts stored by the groups of squirrels under the various conditions).

After nuts were washed in CCl_4 and rinsed with water, the squirrels did not seem to find them as attractive as fresh nuts, but no discriminatory behavior was observed when the treated nuts (stored and unstored) were offered (Fig. 15). Since oils are soluble in CCl_4 it seemed likely the odor marker was an oil secretion from either the mouth or the feet.

According to Quay (1963, 1965), *G. volans* has enlarged sebaceous-like and sudoriferous glands in the labii and the inflexi pelliti of the labii superioris. Since, during the manipulation process, both the mouth and forefeet come in contact with the nut, the marker could come from either or both sources. The choice was finally narrowed down to the mouth when the squirrels did not discriminate against nuts handled by the forefeet alone.

The inflexi pelliti and labial glands described by Quay were not assigned a specific function, and it is still not clear whether they actually are the source of the marker. They are certainly a possibility since they are numerous and roughly three times the size of normal sebaceous glands.

When presented with a choice of unhusked and husked nuts, the squirrels showed about a 5:2 preference for the unhusked ones (Fig. 15). Usually when surplus nuts were available, the squirrels husked most of them even
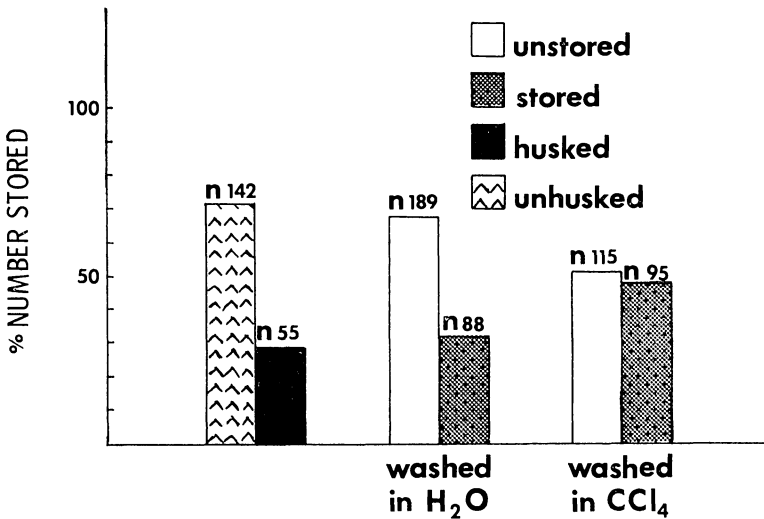
Fɪɢ. 15. Observed preference by flying squirrels for unhusked nuts over husked nuts (left hand pair of columns), and the reduction of the preference for unstored over stored nuts as a result of washing with detergent and water (middle pair of columns) and in CCl_4 (right hand pair of columns) ("n" represents the numbers of nuts stored by the groups of squirrels).

though they did not store all of them. Husking therefore appears to be a prefatory stage to later discriminatory processes. The second stage in discrimination appears to result from the squirrels' handling the nuts, which not only is the effect of the structural difference in the nut as a result of husking, but also depends on the odor marker deposited during the mouthing and manipulation process.

Cahalane (1942, 1947) demonstrated that fox squirrels do not "remember" where they store their nuts, but rather locate the cache by using olfactory clues. Flying squirrels store food materials to a large extent in trees as well as on the ground. The routes of travel are fairly restricted (see section on nesting behavior), and it is along these routes that the food material is cached, with the result that the squirrels frequently encounter their own food stores and those of other members of nesting aggregations. If the squirrels were not able to recognize previously stored food and react to it differently from unstored food, the consequence would be repeated re-storing of the food materials, since being already in the trees the previously stored food would be more readily available. Thus, there would be wasted energy and interference with rapid accumulation of food necessary for winter.

ESTIMATE OF NUMBERS OF NUTS STORED

Since the storing sites are so scattered, it is very difficult to estimate how much food is stored by flying squirrels in nature. Under natural conditions in Michigan the intensive storing activity begins in mid-September, reaches its peak in late November, and ends in January. The largest number of nuts stored in one night by any single individual in confinement was 277. Using this value as the peak of a curve having the same shape as one constructed to seasonal changes in photoperiod (since storing is proportional to photoperiod, Fig. 13), and using the length of the intensive storing period (as indicated by food remains in the nest boxes on the ESGR) in 1962 as a base, I have made a quantitative estimate of the maximum potential storing performance by an individual squirrel. The left leg of the curve, or the increase in storing activity, should be proportionally dependent on decreasing photoperiod and the ripening of the nut crop; the right leg, or the decrease in storing, should be dependent on the exhaustion of the nut crop and increasing photoperiod.

This model yields an estimate of the maximum potential storing performance of over 15,000 nuts by one flying squirrel. This estimate represents only the maximum behavioral capacity for storing and assumes that some nuts are available throughout the season. Also, the assumption is made that ideal weather conditions prevail, whereas under natural conditions inclement weather may alter the storing performance.

ACTIVITY

Glaucomys volans and *G. sabrinus* are the only strictly nocturnal tree squirrels in the New World. It has been noted by many investigators that the most intensive periods of activity of *G. volans* are immediately after sunset and again just before dawn (F. H. King, 1883; Sollberger, 1940; Layne, 1958; Hazard, 1960; DeCoursey, 1960).

DeCoursey (1959) showed that in *G. volans* there is an inherent cycle of activity averaging about 24 hours even in complete darkness, and that the onset of activity can be manipulated by changes in photoperiod.

Sollberger (1940) and Hazard (1960) claimed that activity of this squirrel was reduced during rainy and windy nights. DeCoursey (1960) found that caged animals kept outdoors during cold weather tended to show less running time than those kept indoors. Kiel (1927) assumed that flying squirrels hibernate, since a group he had under observation for several years did not come to his feeding tray during the winter. On the basis of unsuccessful trapping in the cold months, Sollberger (1940) concluded that flying squirrels are inactive during cold weather in areas that he studied. On the other

hand, Jordan (1956) captured flying squirrels in Illinois throughout the winter.

In the current study, active individuals were observed under natural conditions in every month of the year, although torpid or semi-torpid individuals were also found.

ANALYSIS OF DAILY AND SEASONAL ACTIVITY

METHODS AND MATERIALS.—Thirty *G. volans* were kept in a large cage, at the edge of a woods on the ESGR, from April 1963 through July 1965 to evaluate the effect of various environmental factors such as photoperiod, temperature, precipitation, wind, and cloud cover on their activity. The cage was sheltered by a group of oak trees on a site similar to that which a flying squirrel might choose for nesting; wild individuals were seen occasionally on the cage top. These squirrels had access to 10 to 15 nest boxes. Food was available on a central feeding platform and water was supplied.

The squirrels' activity was observed intermittently throughout the years. In addition, from April 1963 through the end of the study, a continuous record was kept of the activity by means of activity-gates that were fitted at the entrances to the ten nest boxes most frequently used by the squirrels (Fig. 16). The gates completed a circuit to an Esterline-Angus Event Recorder that was kept in an instrument shed near the cage.

Initially, two-way mercury switches were used in conjunction with an overhead wire gate that the squirrels deflected in entering or leaving the nest box (Fig. 16). The mercury switches were wired so that each of the two poles completed a circuit to separate electromagnets in the recorder. In this way events of egress and entry could be differentiated. The swinging arc of the overhead gate was damped by an elastic band.

Although these gates worked satisfactorily in the beginning, they gave trouble later. With each swing of the gate the mercury switch moved also, consequently the wires leading from the switch became weakened; this, coupled with corrosion resulting from humidity, led eventually to one or both of the poles becoming inoperative. Also, because the operation of the switch depends on deflection, the two-way switch had to be exactly balanced. Activity sometimes jarred the switch and the mercury flowed to one end and remained there, thus keeping the circuit closed.

Because of these difficulties the mercury switches were later replaced by magnetic "reed switches." In addition, a new type of overhead gate, constructed from "plexiglass," was fitted with a magnet on one side and hung across the opening to the nest box so that it was deflected in one direction during entrance and the other during egress. Two "reed" switches were placed between the dobule wall of a metal entrance box containing the gate.
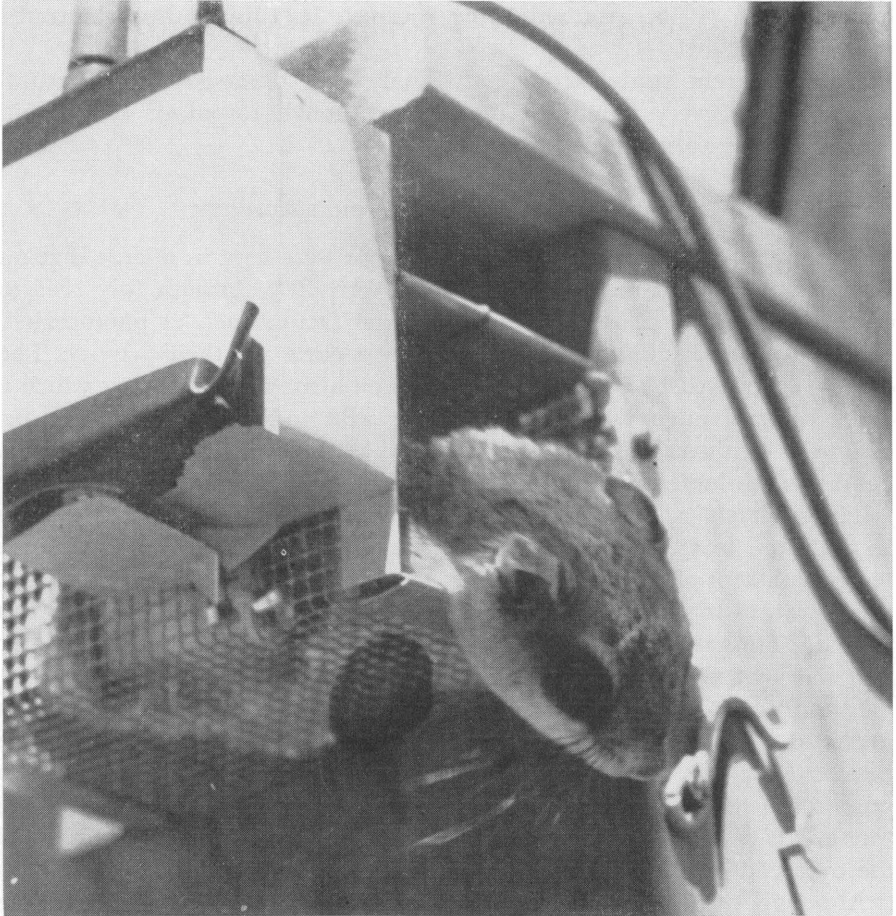
FIG. 16. Flying squirrel leaving the nest box through the activity gate.

When the squirrel passed through in either direction the magnet on the gate became aligned with one or the other switch and thereby completed a circuit to a separate electromagnet in the recorder. The swinging arc of the gate was damped by another magnet situated in the double wall of the metal entrance box.

An attempt was also made to record activity in free-living squirrels. A motorized camera triggered by a relay operating in conjunction with a transistorized photocell circuit similar to that described by Abbott and Coombs (1964) was mounted opposite active nests. A red-filtered light beam crossed the nest entrance, and when the animal crossed the beam upon en-

tering or leaving the nest, the camera was tripped. Various support towers were built to bring the camera to a level with the entrance to the nest; some were 15 to 20 feet high and were also used for observation.

Only a small amount of information was gathered in this way since the squirrels vacated the nest cavity immediately or soon after the apparatus was set up. I had some success using a recorder (modified Taylor temperature recorder) in conjunction with a photocell circuit and plexiglass gates similar to the ones used in the outdoor cages. The Taylor temperature recorder was modified by adding an extra pen arm that indicated on a kymograph when the squirrels crossed the light beam or deflected the plexiglass gates. The extra pen arm was activated by an electromagnet that was in the same circuit as the triggering device used at the entrance to the nest.

Year-round weather records were maintained in a small weather station on the ESGR. Temperature was continuously recorded by a Bristol Thermo-Humidograph. Other meteorological data, such as rainfall, wind, and cloud cover, were collected and recorded daily and are on file at the University of Michigan Museum of Zoology.

RESULTS AND DISCUSSION.—The following is a summary of the recorded activity of thirty animals subjected to natural environmental conditions in the outdoor enclosure from July, 1963, through June, 1964. Examples of monthly records from each of the four seasons appear in Figures 17–22. The records for the remaining months are available at The University of Michigan.

July, August, and September: Because of the mild weather, these months can be considered as a period in which the animals were operating under minimal cold stress. The onset, duration, and end of activity appeared to follow changes in photoperiod. There seemed to be very little daily variation (Fig. 17).

No differences in activity levels could be seen between cloudy and clear nights, although the onset and end of activity was somewhat affected (11, 12, 18, 19, 26, 29 September). Rain and heavy wind sometimes (13, 21, 22, 28 July) reduced activity. Rain (19 July, A.M. only; 7, A.M. only, 11, 12, and 21, A.M. only, September) or wind alone (1, 6, 12, 18, 27 July) did not seem to affect the level of activity. On extremely warm days (over 31°C), e.g., 17 July, some activity occurred during daylight hours resulting from gate deflection while the squirrels hung out of the entrances to the nest boxes.

A partial solar eclipse in the afternoon of 19 July had no apparent effect on the onset or level of activity during the subsequent night. There was little or no indication of a bimodal pattern of activity during these months.

October and November: The level of activity during overcast nights appeared no greater than on clear nights. Little precipitation occurred during
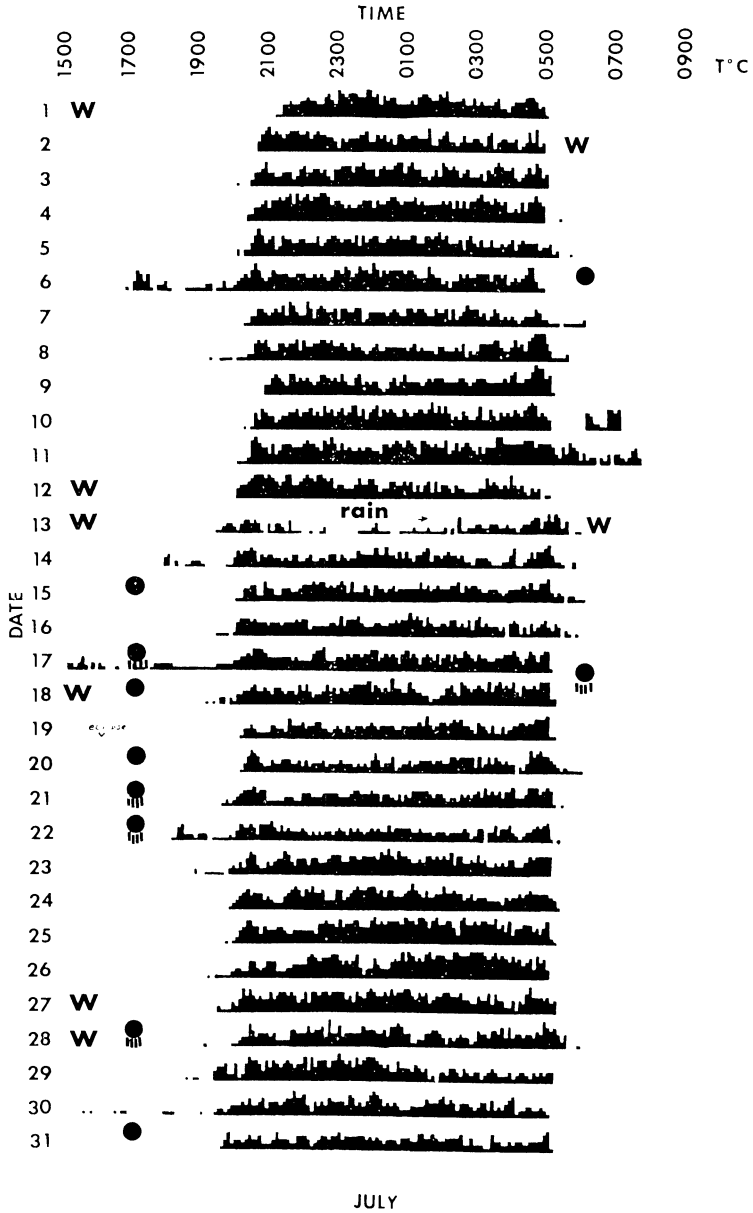
FIG. 17. Pattern of activity of flying squirrels in July 1963, on the Edwin S. George Reserve. The time appears at the top of the page, the days in the left hand column. Each horizontal series of lines represents the extent of activity during each night. The smallest squares represent deflections of a single gate during a six-minute interval; ten such squares filled in on the vertical axis would indicate that all ten gates were deflected during the six-minute interval. W represents moderate wind during the afternoon if to the left, or morning if to the right of the active period; WW represents heavy wind. Closed circles represent overcast afternoons or mornings; closed circles with four short vertical lines under them represent rain; precipitation during the active period is written in. "B" represents breakdown. For some months the average temperature during the active time appears in the right hand column.
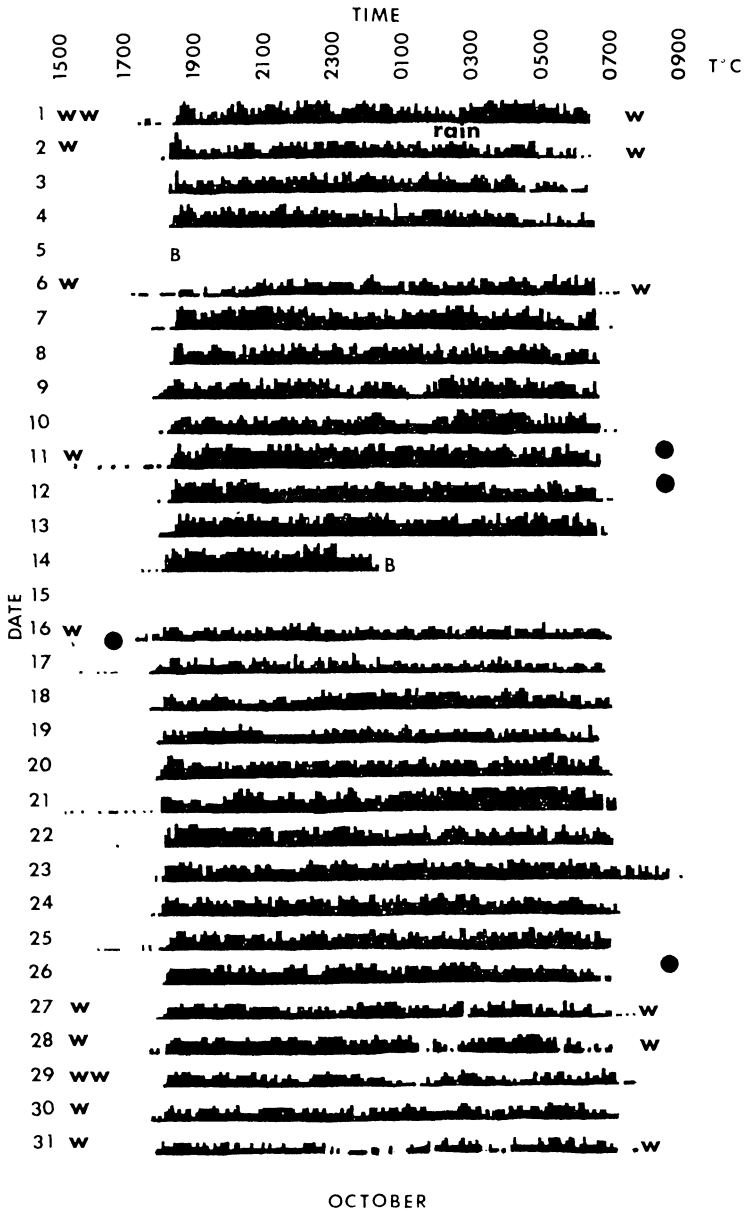
Fig. 18. Pattern of activity of flying squirrels in October 1963 on the Edwin S. George Reserve. Legend as in Fig. 17.
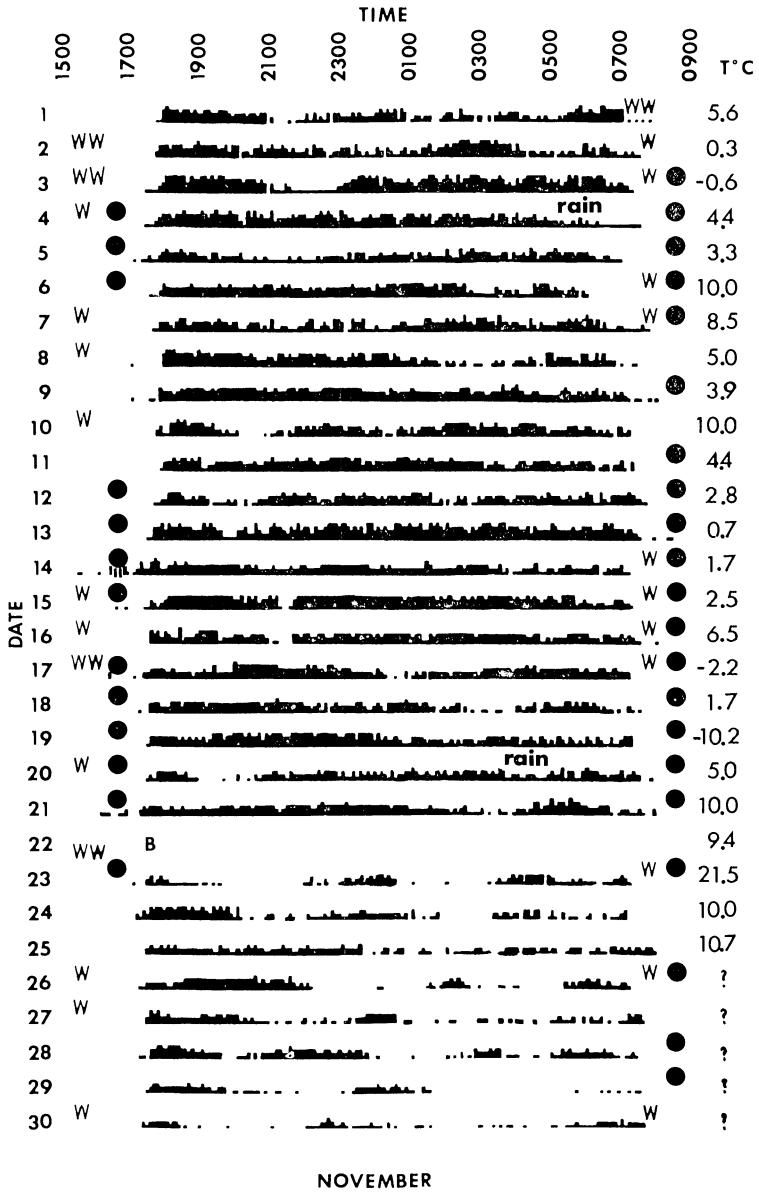
Fig. 19. Pattern of activity of flying squirrels in November 1963 on the Edwin S. George Reserve. Legend as in Fig. 17.
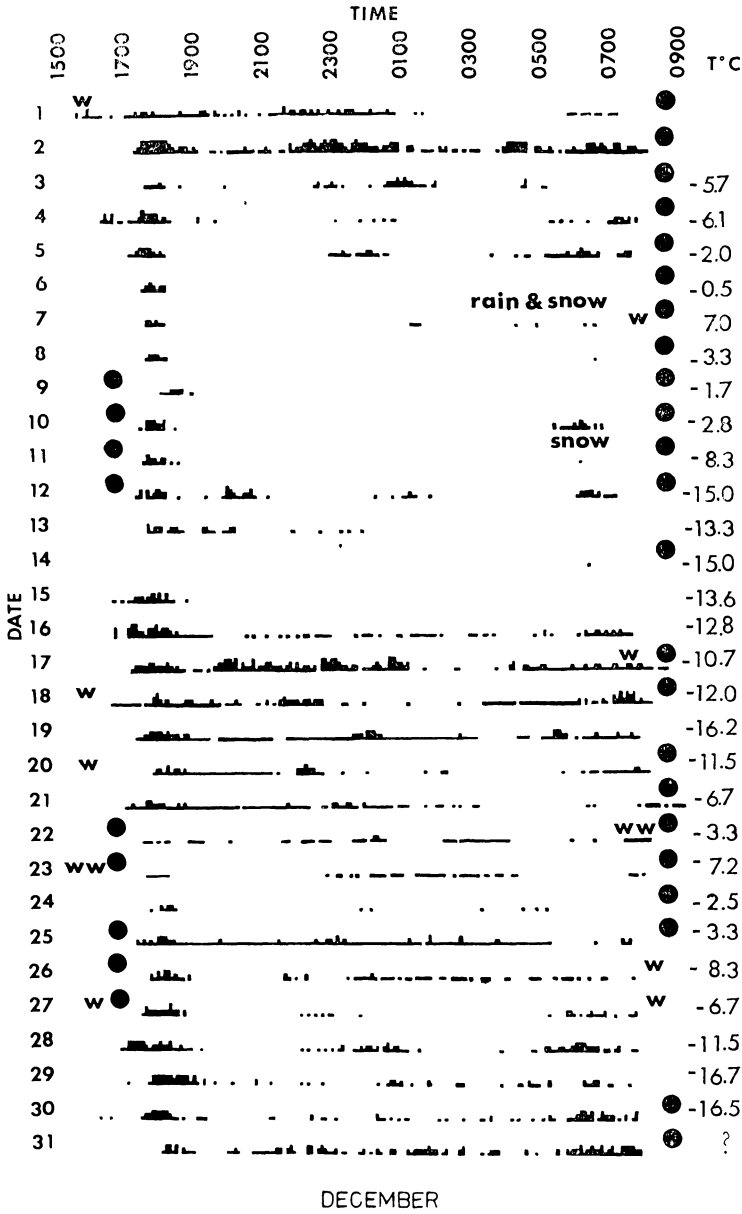
FIG. 20. Pattern of activity of flying squirrels in December 1963 on the Edwin S. George Reserve. Legend as in Fig. 17.
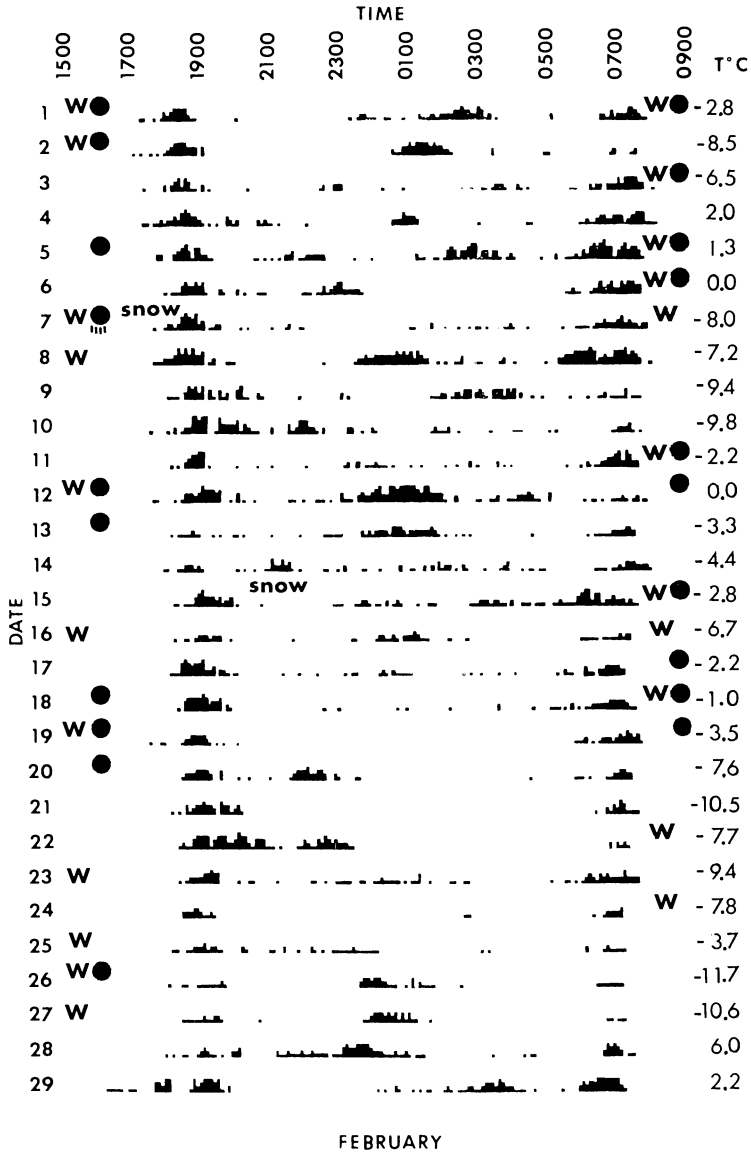
FIG. 21. Pattern of activity of flying squirrels in February 1964 on the Edwin S. George Reserve. Legend as in Fig. 17.
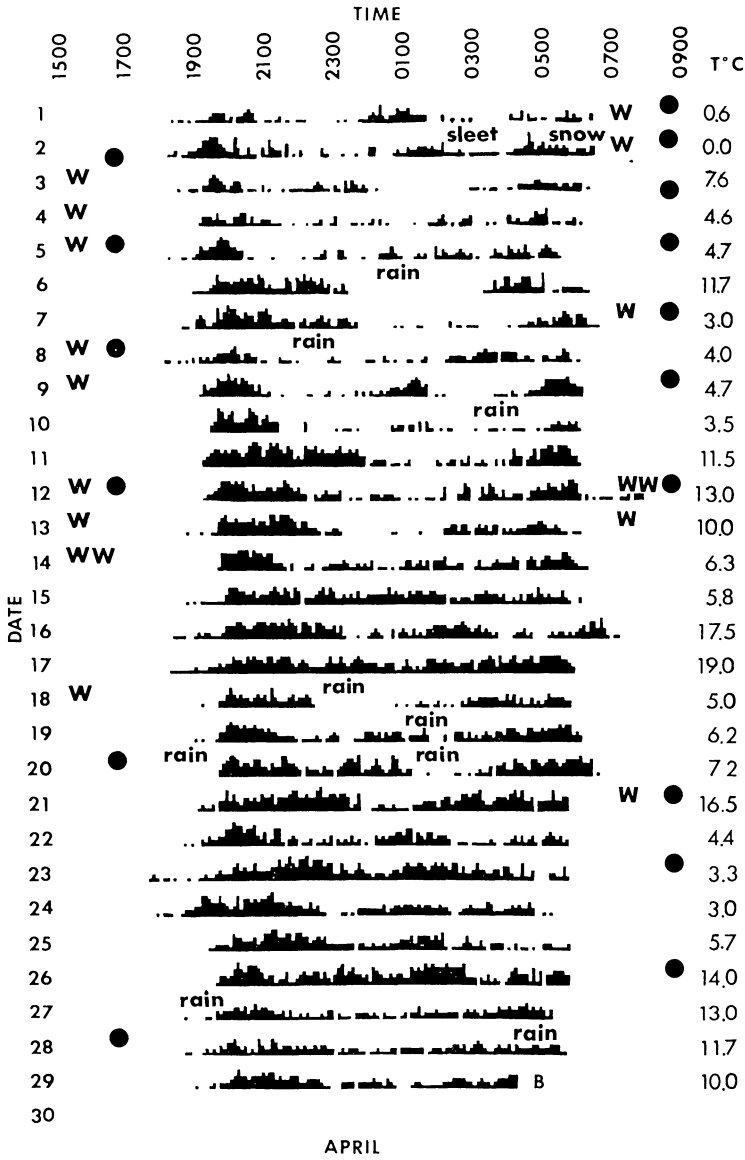
Fig. 22. Pattern of activity of flying squirrels in April 1964 on the Edwin S. George Reserve. Legend as in Fig. 17.

October. On the one rainy night (3 October, A.M.) there was also a wind
and the activity was reduced during the early morning. However, on the
following morning a similar reduction in activity occurred without wind
or rain, but the squirrels remained active throughout the night with no
discernible bimodal activity pattern (Fig. 18).

In November, during some rainy nights (5 November, early A.M.) activity
was reduced, but during others (21 November, early A.M.) no differences
could be detected (Fig. 19).

The decrease in activity during the last week of November may be
attributed, at least in part, to lowered temperatures during the active times.
It was at this time that a trimodal, sometimes bimodal, pattern of activity
began with peaks following sunset, sometimes around midnight, and before
dawn. The majority of the squirrels apparently spent most of their time in
the nest boxes. The occasional bursts of activity apparently represent feed-
ing times. This was confirmed by direct observation.

Mrs. Irene Southworth (personal communication) of Monroe, Michigan,
kept sight records (on file) of feeding times of flying squirrels coming to a
feeding station and peanut butter log; her records (Table 2) agree closely
with the data obtained with the automatic recording devices on the ESGR.

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TABLE 2

OBSERVATIONS OF FLYING SQUIRRELS COMING TO THE FEEDING STATION OF
MRS. IRENE SOUTHWORTH IN MONROE, MICHIGAN

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	No. of nights observed	No. of visits	Duration of visits (minutes)	Average length of visit (minutes)
October, 1963	20	18	15–240	132
November, 1963	25	23	5–210	103
December, 1963	21	14	5–165	27
January, 1964	10	7	5– 15	8.6

December, January, and February: There was no difference in activity
on cloudy and clear nights in December and February, but in January
there was about 25 per cent more activity on cloudy nights than when clear.
During rain and snow activity appeared reduced, e.g., the morning of 8
December, but this type of reduction was apparent during other nights
without any precipitation. Snow during the morning of 12 December and
7 and 15 February had no appreciable effect on activity. On windy nights
the squirrels appeared to be as active as on calm nights (Figs. 20, 21).

Temperature influenced activity, but not always directly. On the night
of 3 December, when a marked decrease in the level of activity occurred, the

temperature did not differ appreciably from that of previous nights, but there appears to have been a cooling trend during the week previous to this with a reduction in average temperature from 10°C to about −4°C during the times when the squirrels were active. This was followed by a slight warming trend, but then the temperature again fell. By 12 December the average temperature during the active period was −13.3°C. This was followed by another slight warming trend and a small increase in activity until 18 and 19 December when the temperature again declined to about −13°C. After this, temperature and activity increased once again. The sporadic times of activity throughout these months were probably spent feeding. Direct observations during various times of night revealed that few if any individuals left the nest boxes. During some nights (e.g., 14 December) the squirrels remained in their nests for the entire night.

March and April: Activity levels during cloudy and clear nights did not differ significantly. Wind alone had no effect, but heavy wind with snow reduced activity (5, 8, 10, 26, 27, 30 March). Rain sometimes had some inhibitory effect (17 and 18 April). A drop in the average temperature from −1°C on 7 March to −8°C on 8 March was not accompanied by a marked reduction in the activity levels, nor was a drop from 1°C on 15 March to −12°C on 16 March. However, a correlation was apparent between the level of activity and the average temperature during active times. The notable exception to this was 16 March when the temperature went down to −12°C.

The general level of activity during March and April was higher than during the three previous months, but the animals still spent much of the time in the nest boxes as evidenced by the trimodal pattern in activity until the last half of April when at least some squirrels were active throughout the night (Fig. 22).

A fair correlation exists between intensity of activity and the average temperature during the active period in the months of January through April (Fig. 23). Throughout the winter there was a bimodal, sometimes trimodal, pattern in periodicity of activity; the squirrels spent most of the time in the nest boxes and came out only to feed. Mrs. Southworth's observations indicate that on some cold nights the squirrels did not come out of their nests to feed.

May and June: The squirrels were active through most of the night. Rain appeared to have some inhibitory effect (3, 12, 15, 17, and 19 June). Wind alone made no difference. The most striking effect on activity was the reduction which could be seen on clear nights during which there was a full or nearly full moon (16, 21, 22 June). This is similar to the phenomenon described by Radvanyi (1959) for *G. sabrinus.*. The inhibition of activity during bright nights may be significant in reducing predation.

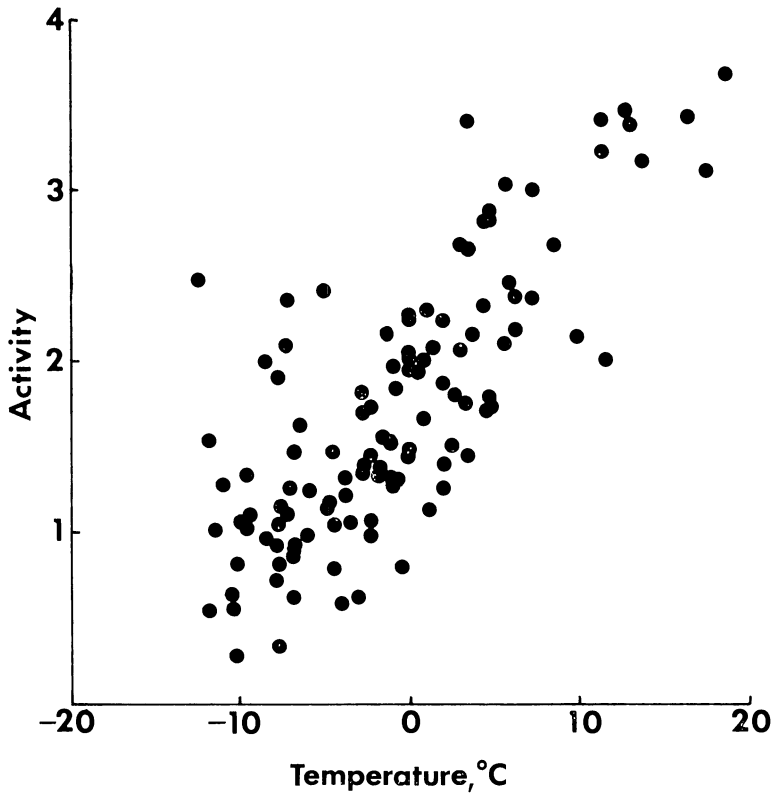The few motorized camera records and the records obtained with the

Fig. 23. Extent of activity of flying squirrels during each night, January–April, plotted against the average ambient temperature during the active period. The measure of activity was based on the number of gate deflections in the nest boxes during the six-minute interval by 30 squirrels in the large outdoor cage at the Edwin S. George Reserve in 1964 ("r" = 14, p < .01; "r" = 14, p < .01; "r" = 19, p < .01; "r" = 20, p < .01 for the months of January, February, March and April, respectively, according to the "corner test") (Mood, 1950).

modified Taylor temperature recorder, both from naturally occurring nests, closely agreed with the results acquired for captive animals.

In general, the onset and end of activity tend to follow the seasonal pattern of changes in photoperiod. During long, cold winter nights two, sometimes three, peaks in activity were seen. These probably represented feeding times.

The records indicate that activity was seldom greatly influenced by rain or wind alone, but these factors in combination were often inhibitory. This is not necessarily inconsistent with the observations of Sollberger (1940) and Hazard (1960), for the measure of activity in the present study con-

cerned the amount of time the squirrels spent entering and leaving the nests; Sollberger and Hazard based their conclusions on direct field observations. My own field observations indicate that although the squirrels came out on windy and rainy nights, they were more difficult to observe then since they moved around less than during more favorable conditions. Also most of their time was spent in sheltered feeding stations or retreats.

Torpor

In the Wild.—Several observations of torpor in flying squirrels were made during the current study. In February, 1951, three torpid flying squirrels were captured when their nest tree was taken down. When the tree hit the ground, the nest cavity broke open, but the squirrels remained curled up when lifted from the nest; they became active when handled a few minutes. On 20 February 1960 several squirrels in an aggregation of 19 that was under study near Sunderland, Massachusetts, appeared to be semi-torpid as they tumbled to the ground from their nest in an old flicker hole when the tree was shaken. On 27 February some of the individuals in the same nest appeared to be on the verge of torpor, since they made inaccurate glides and landed on the ground when the nest was disturbed. Two fell out of the entrance to the nest directly into a stream below the tree. The rectal temperature of another individual was 29.4°C immediately after the squirrel fell from the nest (normal body temperature is about 39°C).

In Captivity.—On 2 March 1963 (ambient temperature −12°C to −1°C, with a low of −17.8°C four nights before) the 30 squirrels in the outdoor enclosure were found to be in two aggregations of 9 and 21, respectively. Their food supply had been depleted, although not for more than 36 hours. The members of the larger aggregation were all active when the nest box was opened for examination. Five in the smaller aggregation were apparently torpid, since they remained curled up when lifted from the nest box. Their eyes were shut and when placed on their feet they stood shivering. They became fully active in less than 20 minutes and ate with the other squirrels. All of the squirrels were active the following day when the nest boxes were checked again.

No instances of torpidity were observed during the winter of 1963–64, perhaps because the weather was milder than usual. Several attempts were made to duplicate the conditions of 2 March 1963 in the laboratory, but the animals could not be induced to go into torpor under comparable temperature and photoperiod conditions even when food was withheld.

On 23 January 1965 members of an aggregation of 10 in the outdoor cage were semi-torpid. The rectal temperature of one male squirrel was 22°C two minutes after the nest box was opened. The thermistor was in-

serted about 0.8 cm in the rectum and was kept there for 31 minutes. During the first 15 minutes the temperature rose at a rate of 0.3°C/minute. By 25 minutes the rate increased to 0.5°C/minute, and by 31 minutes after the measurements were begun the temperature rose at a rate of 1°C/minute until normal body temperature (39°C) was reached (Fig. 24). Again, the food supply had been depleted for about 36 hours before the squirrels were found torpid.

In nature the animals probably enter torpidity after prolonged cold stress when the weather conditions do not permit access to their winter food stores. The phenomenon is likely to be occasional in character, unlike hiberation in *Citellus tridecemlineatus* and other "true" hibernators.

ENERGY BUDGET

In northern climates, especially during the winter, a non-hibernating homeotherm is faced with the problem of replacing body heat lost to the
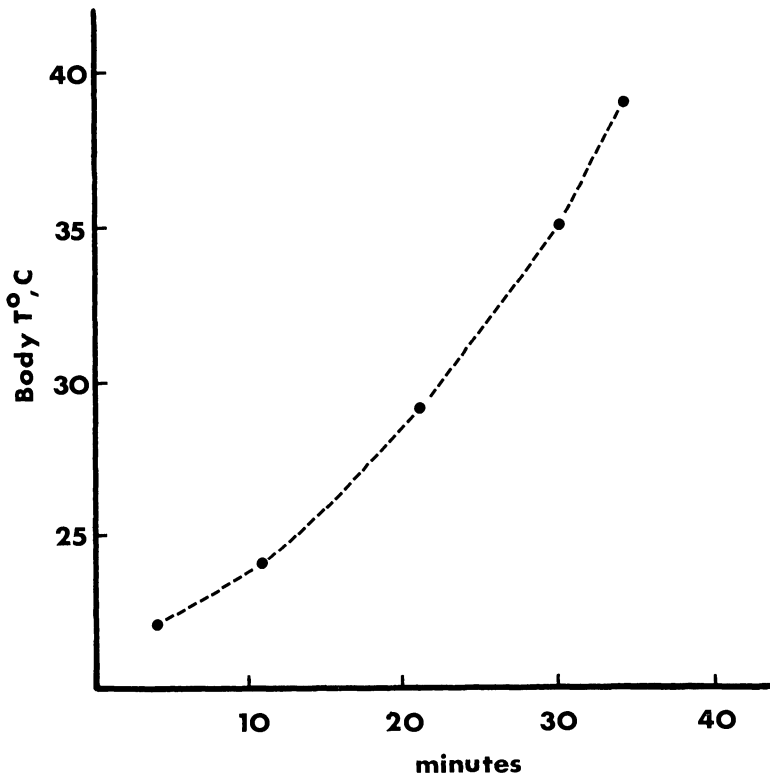
FIG. 24. Rise in body temperature of a flying squirrel aroused from torpor.

environment by metabolic heat production. To do this food is converted through metabolic processes into heat. Even if ample food supplies were available, the animal would be able to do this only within the limitations of its surface area/size relationship and insulation, ambient temperature, and time available to fulfill other necessary biological functions. In previous sections, physical and behavioral resources available to *G. volans* were discussed. In this section an attempt will be made to analyze these resources quantitatively in light of calculated energy requirements of the animal as they arise under natural circumstances.

McNab (1963), who made one of the first attempts to construct an energy budget for a mammal, stated that there is a need for "studies of the bioenergetics of homiotherms [*sic*] that have value under natural conditions" and that the role of "metabolism must be expressed as a function of the physical events that comprise natural conditions." His model is based on the variables of time, temperature, and rate of metabolism.

In the calculation of a partial energy budget for *G. volans,* a more descriptive approach will be used, mainly because formulas given by McNab seem to over-complicate the situation. The annual "cost of living" for Michigan populations of *G. volans* will be estimated on the basis of continuous records of activity of the squirrels and weather for an entire year, and on known energy requirements at various temperatures based on laboratory data. In addition, behavioral patterns such as aggregation and nest-building as they occur under natural conditions will be taken into consideration (Fig. 25). Because data are incomplete for some phases of the animal's behavior and physiology, extrapolations have been made when necessary.

McNab and Morrison (1963) found that during activity *Peromyscus* increased its metabolic rate to about twice that of the basal rate. In flying squirrels slight activity brought about as much as a three-fold increase, and increases of up to eight times the basal metabolic rate were observed while the animal was in the respiratory chamber (Fig. 3). Under natural conditions, when the animals glide and climb, much greater increases must occur. In humans, untrained individuals may increase their O_2 consumption 14.5 times the basal rate in strenuous work, a trained athlete as much as 21 times (Brody, 1945). Flying squirrels do not remain vigorously active continually while they are out of the nest; also, during vigorous activity the effectiveness of the insulation of the pelage is likely to decrease (Hart and Heroux, 1955). For the purpose of calculating the energy budget I have assumed that the insulative effectiveness of the pelage is reduced by one-fourth because of activity and that, on the average, activity in the wild results in a four-fold increase in the metabolism over the basal rate.

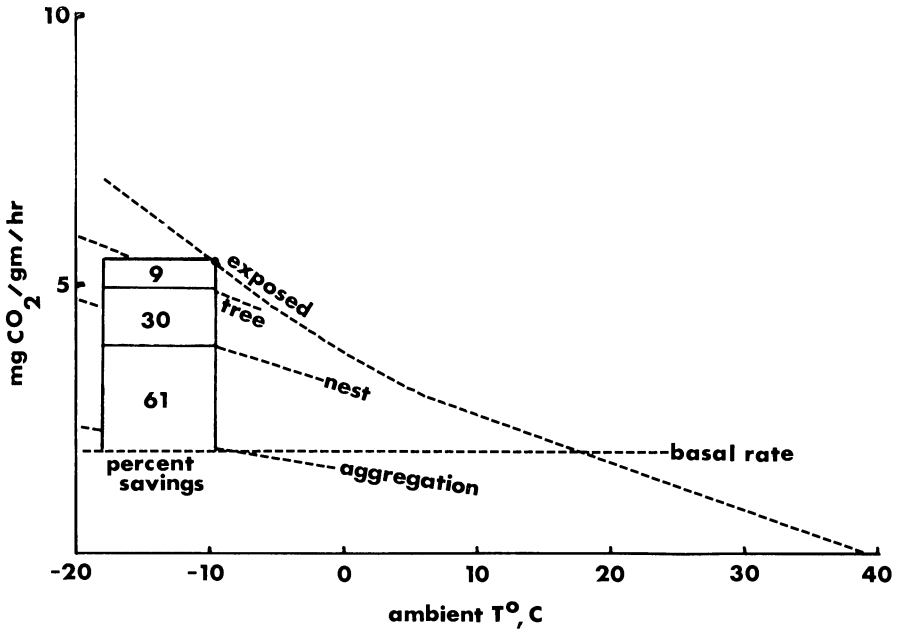In order to determine the low temperatures at which a flying squirrel is

FIG. 25. Minimal metabolic rates (extrapolated to body temperature) of flying squirrels at various ambient temperatures while (1) exposed, (2) in a tree cavity, (3) in a nest in the tree cavity, and (4) in an aggregation in a nest. The bar graph represents per cent savings of energy derived from each of the factors, constructed on the basis of the metabolic rate values under each condition extrapolated to $-10°C$ (see text).

able to balance the heat loss through transfer by heat produced as a by-product of muscular activity, the following calculations need to be made. Extrapolation of the metabolism-temperature curve indicates that a flying squirrel at $-14°C$ would have to expend 19.8 cal/(gm. hr.) or 13.6 cal/(gm. hr), in excess of basal requirements, 6.17 cal/(gm. hr.). If the insulative effectiveness of the pelage is decreased by one-fourth during activity, to maintain homeothermy heat production must increase by one-fourth to compensate for the additional loss. Thus, $1.25 \times 19.8 = 24.75$, which is roughly equal to a four-fold increase of basal metabolic rate ($6.17 \times 4 = 24.68$) (assumed average rate during activity). As long as this amount of heat is produced through activity no additional heat production should be necessary down to ambient temperatures of $-14°C$ unless the pelage insulation decreases by more than 25 per cent as a result of activity. Below $-14°C$ with the one-fourth decrease in the insulative effectiveness of the pelage, energy expenditure would probably have to be increased at a curvilinear rate starting at about 0.50 cal/(gm. hr. °C), in addition to the amount needed for muscular work.

The activity records for 30 squirrels under natural climatic conditions are summarized in the previous section (Figs. 17–22); it is assumed that these records reflect the active time of natural populations under comparable weather conditions. During inactivity, the squirrel is insulated by nesting material and by the wood enclosing the nest cavity (see section on Physiology of Nesting Behavior). In cold months the squirrels were found to aggregate in the wild (average of six animals in a nest). The energy budget is calculated for a squirrel of average weight (70 gms) nesting alone in the warm months (April through October) and as a member of an aggregation of six in the cold months. Continuous temperature records and other climatic data were collected on the ESGR during the same year that activity was measured and that year (July 1963–June 1964) was assumed to be "typical" for the purpose of calculating the energy budget.

In constructing an energy budget from these types of data, I recognize three main activity levels of the animals:

(1) Active time—time during which the squirrel is active.
(2) Solitary inactivity—time spent alone in a nest.
(3) Aggregation inactivity—time spent in an aggregation.

The salient points of the data can be expressed as:

$$C_T = C_A + C_I$$

where C_T, C_A, and C_I represent, in order, the calories expended during total time, time during which the animals were active, and time during which they were inactive. C_A and C_I can be further defined as:

$$C_A = t_1 M_1 + K_1 \sum_{\text{over all values of } \triangle} t_{1\triangle} \triangle$$

in which:

t_1 = total active time during which temperatures exceed T'
T' = lower critical temperature of activity
M_1 = metabolism during assumed average activity
K_1 = rate of increase in metabolism at various temperatures during $t_{1\triangle}$
$t_{1\triangle}$ = total time during which temperatures are lower than T'; or the number of hours in each increment, e.g., $T' - 1°C$, $T' - 2°C$ .... $T' - \triangle °C$
$\triangle$ = observed range of temperatures below T'

$$C_I = t_2 M_2 + K_2 \sum_{\text{over all values of } \triangle} t_{2\triangle} \triangle + t_3 M_3 + K_3 \sum_{\text{over all values of } \triangle} t_{3\triangle} \triangle$$

in which:

> t_2 = total inactive time during which temperatures exceed T''
>
> T'' = lower critical temperature of the animal nesting alone
>
> M_2 = metabolism during inactivity during t_2 = M_{basal}
>
> K_2 = rate of metabolism increase during $t_{2\Delta}$
>
> $t_{2\Delta}$ = total time during which temperatures are lower than T'', or the number of hours in each increment, e.g., T'' − 1°C, T'' − 2°C .... T'' − Δ°C
>
> Δ = observed range of temperatures below T''
>
> t_3 = total inactive time during which temperatures exceed T' ''
>
> T' '' = lower critical temperature of the animal nesting as a member of an average size aggregation
>
> M_3 = metabolism during inactivity during t_3 = M_2 = M_{basal}
>
> K_3 = rate of metabolism increase during $t_{3\Delta}$
>
> $t_{3\Delta}$ = total time during which temperatures are lower than T' '', or the number of hours in each increment, e.g., T' '' − 1°C, T' '' − 2°C .... T' '' − Δ °C
>
> Δ = observed range of temperatures below T' ''

The values in the above equations will vary between species and within species; there may be variations among populations. In other species there may be additional states that must be considered or the situation may be simplified. Following are observed or calculated critical temperature and metabolism values for a 70-gm G. *volans* in southern Michigan.

> T' = 14°C
>
> T'' = 4°C
>
> T' '' = −9°C
>
> M_1 = 4(M_{basal}) = 1727 cal/hr
>
> M_2 = M_3 = M_{basal} = 432 cal/hr
>
> K_1 = 0.50 cal/(gm.hr.°C)
>
> K_2 = 0.50 cal/(gm.hr.°C)
>
> K_3 = 0.12 cal/(gm.hr.°C)
>
> (K_1, K_2, and K_3 probably become curvilinear rates at low temperatures)

Calories expended during each month of the year were calculated on the basis of activity and temperature records. Average temperature for each hour during each 24-hour period was considered. For the purposes of calculation, whenever the squirrels were active it was assumed that metabolism increased to four times basal rate as long as temperatures were above −14°C. Caloric expenditure for inactive periods was determined from laboratory data (see section on Physiology of Nesting Behavior, and summary on Fig. 25) and varied according to temperature and the size of the nesting group, i.e., whether the animal was living alone or in an aggregation during that

time of year in the wild. On a monthly basis the calculated energy expenditure of an average flying squirrel in southern Michigan appears in Fig. 26; on an annual basis:

$$C_{Total} = 6,890 \text{ Kcal}$$

Although torpidity was not observed during the year that activity records were taken, this phenomenon should be included in the budget. The adjustment factor for this would be:

$$C_I = C_N + C_{T_0}$$

where C_N is the caloric utilization during inactive time in the nest and C_{T_0} the caloric utilization during the time spent in torpidity under given temperature conditions.

Errors in the calculation may arise in the estimation of the level of activity and the determination of the resultant metabolic rate during the times the animal is out of the nest (the amount of heat loss during activity).
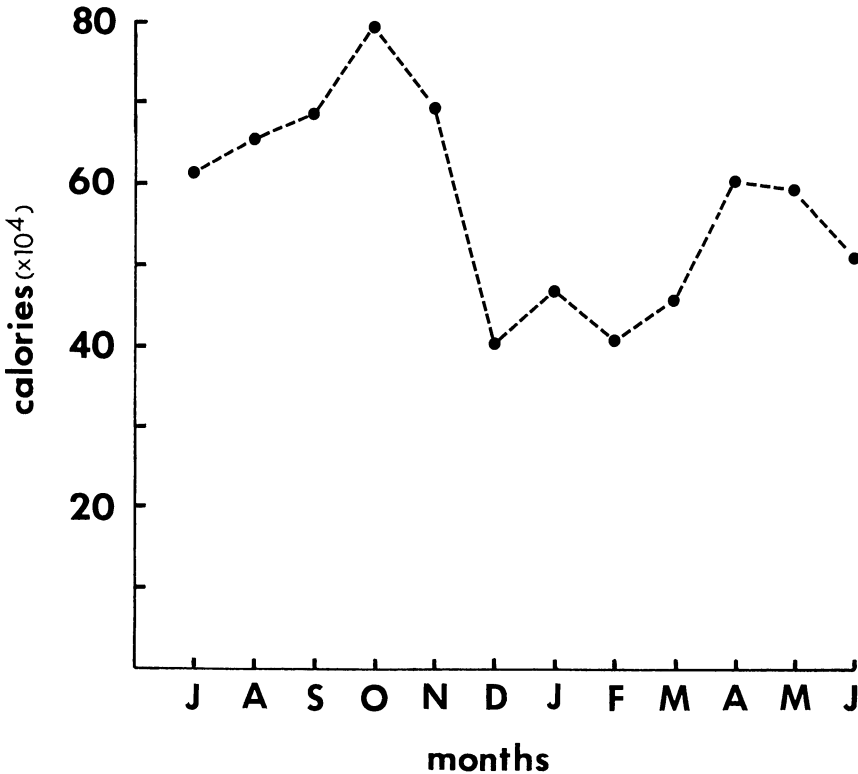
Fig. 26. Monthly totals of calculated energy expenditure of an average flying squirrel in southern Michigan from July 1963 through June 1964 (see text).

A more nearly accurate estimate of this will be attempted at a later time. Also, the levels of activity vary during the night and during different times of the year, e.g., during October and November when the squirrels are storing food the activity is much more intense than in May and June although the environmental temperatures may not be very different. The activity records show this to some extent, but more accurate measurements are needed. Additional energy requirements during pregnancy and lactation should also be taken into consideration.

With better estimates of the number of nuts and acorns stored by wild populations, one can arrive at a more nearly accurate evaluation of the energy available in the form of food stores. The estimate based on the performance of captive animals was a maximum potential of 15,000 nuts per animal (see section on Food Storing) under conditions of ideal temperatures and an abundant food supply.

If an average squirrel lived entirely on hickory nuts, its annual food consumption based on the energy budget, would be 892 nuts*. Under natural conditions and comparable temperatures caloric intake would probably be greater since activity would be more intense, e.g., through increased climbing and gliding. Nevertheless, there appears to be more food stored than is needed in most years. This should compensate in part for pilfering of the food stores by other squirrels, by mice, and by birds.

Caged squirrels ate 2 hickory nuts (15,356 calories*) a day at 23°C, with a 15-hour photoperiod; at 2°C the food consumption increased to 3.5 nuts (26,873 calories) a day with a 10-hour photoperiod. This means that during the nine hours of darkness while the squirrels were active, the average energy expenditure at 23°C was about 2.3 times greater than the basal metabolic rate; at 2°C the average energy expenditure during the active time (14 hours) was about 3.7 times greater than the basal metabolic rate. Thus, the actual energy expenditure in the laboratory approximates the calculated expenditure in the field under comparable temperature conditions.

Although more information is needed to construct a complete energy budget, it is quite clear even with a limited amount of information that the savings incurred through various behavior patterns (e.g., nest-building, lability in activity cycles, periodic torpidity, and seasonal aggregation) place the animal in a much more favorable relationship with its environment in the winter in northern climates than one might have expected. As was indicated previously, while in a nest, animals in an aggregation of six remain

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* The meat of an average hickory nut used in the experiments weighed 1.1 grams. If they had the same food value as closely related "pecans" (Spector, 1956), these hickory nuts averaged 7678 calories per nut.

within their zone of thermal neutrality as long as ambient temperatures are over −10°C. Below that temperature, energy expenditure rises more slowly 0.12 cal/(gm. hr. °C), than that of an exposed animal, 0.50 cal/(gm. hr. °C). Thus, from the standpoint of heat loss, the aggregation acts as a larger, better insulated animal.

Survival through the most rigorous winters in the northern states at a reasonable energetic cost would require aggregations of at least two animals. The overwintering success is thus seen to be dependent on population density. Social behavior leading to aggregation not only has survival value in terms of populations persisting from year to year in the northermost parts of the geographic range, but also reduces the average cost of living in all winters, which may be an important factor even in the central parts of the geographic range during years when food supply is reduced.

Perhaps the most important factor in the overwintering success of flying squirrels, and probably other non-hiberating, supra-nivean rodents, in the northern climates is their ability to remain relatively inactive through the cold months. Apparently, reserves of fat which accumulate as the animals feed on their food stores allow the squirrels to remain inactive for several days without either feeding or going into torpor (see activity records for December-March). If the unfavorable weather persists and the fat reserves decrease, the animals may go into torpor and thus reduce their energy expenditure. Periodic test arousals enable the animals to feed as soon as weather conditions permit it. As a result, energy expenditures can be kept down and are about the same during the cold months as in summer (Fig. 26). The greatest costs, as indicated by data from the caged animals, are accrued in the months of October and November when activity is normally increased because of food storing. The caged squirrels had very few food items available that were suitable for storing. Yet, during the storing season there was a general increase in activity in spite of the scarcity of storable food items. The observed increases in energy expenditure by the caged animals during the spring (March–May) may have resulted from courtship and copulatory activities.

Considering that nest construction, seasonal aggregation, lability of activity cycles, and torpidity are highly important in the energy budget of the flying squirrel, it would appear that without these adaptations, provided the energy budget is a reflection of its present energetic limits, this species would be confined to climates considerably milder than are found in much of its present geographic range. Although for many species food does not appear to be a short-term limiting factor, the total expenditure of energy by an animal and subsequently its food intake, must have physiological limits. Even with an unlimited food supply, the animal cannot spend an excessive amount of time feeding. Thus, survival is limited to areas where

the expenditure of energy required to maintain homeothermy can be met without unduly infringing on other essential functions in the life of the animal.

ANALYSIS OF PAST AND PRESENT DISTRIBUTION

In order to evaluate the influence of various environmental factors on the distribution of a species it is necessary to compare elements of the environment within various parts of the species' geographic range. This includes an analysis of various vegetative associations and climatic factors and the determination of the dependence of the species on these factors. Such a determination, although based on many assumptions, at least emphasizes the aspects of the biology of a species which need further study.

PRESENT DISTRIBUTION.—The present range of the southern flying squirrel *Glaucomys volans,* covers most of eastern United States, extending north to include much of Minnesota, Wisconsin, Michigan, and parts of Ontario, New York, Vermont, and New Hampshire. The western boundary is formed by the prairie region. Isolated populations of *G. volans* are also known from deciduous and mixed conifer forests in the mountains of Middle America from Mexico to Honduras (Hall and Kelson, 1959). Its range includes the following life-zones as defined by Merriam (1899): Canadian (northern Lower Peninsula of Michigan); Transition (parts of Minnesota, Wisconsin, Michigan, Ontario, New York, Vermont, New Hampshire, Massachusetts, and other eastern states in high altitudes); Upper and Lower Austral. It is absent from all other Canadian regions and from the Transition of Northwestern Minnesota, Quebec (along the St. Lawrence River), and southern Maine* (Hall and Kelson, 1959).

G. volans is found in various habitats. In mature hardwoods of Minnesota it inhabits associations of basswood, sugar maple, elm, and oak, and also associes of oak-aspen. It is also reported to occur in counties within the "birch-pine-spruce-fir belt" (Gunderson and Beer, 1953).

In Michigan I found *G. volans* in oak-hickory associations, and in aspen stands with scattered oaks. In Massachusetts their habitats were variable, e.g., red maple—oak-white pine association, oak-maple and beech-maple

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* When writing this section I was perplexed over the fact that no specimens of *G. volans* had been reported from southern Maine. The isotherm which occurs at the northern boundary of this species in Vermont and New Hampshire also extends into Maine. Recently, however, I discovered some specimens at the American Museum of Natural History (AMNH 166835 and 166836) which had been collected by G. H. Heinrich in November 1951 in Dryden, Maine (Franklin Co.). This is the first record, to my knowledge, of *G. volans* in Maine. The isotherm at the locality where these specimens were collected conforms with that at the northern boundary of the species in Vermont and New Hampshire.

forests, scrub oak woodlands, gray birch-oak-hemlock mixtures and aspen stands with scattered oaks.

Osgood (1938) noted that there has been a "marked decrease in numbers" of *G. volans* subsequent to the occurrence of the gray squirrel *(Sciurus carolinensis)* in Vermont. Flying squirrels were reported from Rutland and Windham counties, in the Champlain Valley, and along the foothills of the Green Mountains. According to Osgood this would be equivalent to the Transition Zone with an association of white pine, basswood, elm, butternut, and hickory.

In more southern parts of the range they have been reported from beech-maple forests in Pennsylvania (Sollberger, 1940) and in oak-hickory and black oak-sweet gum-red maple associations in southern Illinois (Layne, 1958). On peninsular Maryland near Pocomoke, I observed them in cut-over cypress swamps where the most abundant plants were white cedar *(Chamaecyparis thyoides)*, red maple *(Acer rubrum)*, and loblolly pine *(Pinus taeda)*; within several hundred yards were more upland type woodlands (mostly oak *(Quercus)*. In Georgia they have been observed in both hardwood forests and turkey oak-pine associations along the coastal plain (Golley, 1962). In Florida, J. C. Moore (1947) found them in turkey oak-pine associations, in bay head and in xeric hammock (live oak).

Thus, it appears that the species is not closely confined by plant associations. Neither is it limited by food species.

The northwestern part of its range extends about 300 miles farther north than the northernmost hickory, *Carya ovata* (Harlow and Harrar, 1958). In the northeast this hickory is found about 100 miles north of the southern boundary of Maine, but *G. volans* has not been observed in that state*. The northern limit of the distribution of white oak, *Quercus alba*, is 200 or more miles farther north than the known range of *G. volans*, but in Minnesota this oak does not extend as far north as does the squirrel (by about 200 miles). This absence of a correlation between the distribution of *G. volans* and the distribution of potential food trees undoubtedly reflects the lability in the type of food requirements of this species..

PAST DISTRIBUTION.—*G. volans* occurred in Pennsylvania and Virginia in late Pleistocene (Guilday and Bender, 1960; Guilday, 1962). Pleistocene records of the northern flying squirrel, *G. sabrinus*, have been reported for Virginia (Guilday, 1962), California (Merriam and Stock, 1925; Stock, 1925), and for Maryland (Gidley and Gazin, 1938). In Virginia and Maryland, the areas from which the fossils were collected are currently unoccupied by the latter species. In Virginia the fossils of *G. sabrinus* were associated with other species now inhabiting the Canadian Life Zone, but are no longer found in the areas from which the fossils came (Guilday, 1962).

Guilday postulated that the fauna associated with the flying squirrel material existed during early post-Wisconsin (about 11,000 years ago) and predates the post-Pleistocene warming period. According to Martin (1958), the area where Guilday's fossils of *G. sabrinus* were found was covered by a boreal forest (a favorable habitat for this species, but not for *G. volans*) about 18,000 years ago. Martin postulated a northward recession of the boreal forest about 10,700 years ago, after the Valders Re-advance. According to his maps (of the ice sheets, forest types, tundra, and taiga 10,700 and 18,000 years ago, and for the present) *G. sabrinus* could have inhabited eastern United States only in areas more southerly or at lower elevations than the areas occupied at present, i.e., south of the Great Lakes region and at low elevations in the Appalachian region. All of these areas are now occupied only by *G. volans*. The range of *G. sabrinus* must have receded in a northward direction and to higher elevations, e.g., in the Catskill, Adirondack, Berkshire, and Appalachian regions, within the last 10,700 years. In the Connecticut Valley in Massachusetts, for example, only *G. volans* inhabits the lowlands; *G. sabrinus* occurs at higher elevations, often quite isolated from adjoining populations.

During glaciation, *G. volans* was probably excluded from northern United States and may have spread into Middle America. *G. sabrinus* apparently sought refuge in southwestern and possibly southeastern United States and, as the climate became warmer, *G. sabrinus* was replaced by *G. volans* in the eastern states, except in the isolated areas of the Canadian Life Zone that still persist at higher elevations (Hall and Kelson, 1959).

SPECULATIONS.—On the basis of the more southerly distribution of *G. volans,* as compared with *G. sabrinus,* and the differences in the morphology of their bacula (the latter having a baculum remarkably similar to some of the *Hylopetes* of Asia), Burt (1960) postulated that *G. volans* became separated from the parent stock in Asia earlier than *G. sabrinus*. Since *G. volans* is absent from the west coast of North America, and does not appear in the Pleistocene deposits there, it seems likely that this species followed a path east across what is now northern Canada, then south along the east coast of the United States. This route appears to have been followed at that time (Miocene and Pliocene) by other forest-dwelling forms such as *Gomphotherium* and *Mammut* (Hibbard, personal communication). During the Miocene there was also a spread of *Amphicyon,* from the Old World, which might have followed a similar route (Wilson, 1960). Like the forest mastodons (Hibbard, personal communication) and *Pitymys* (Blair, 1958), *G. volans* probably reached Middle America during the Pleistocene. According to pollen studies of Potzger and Tharp (1954), Texas (northeast of Austin) has had alternately spruce-fir and alder-chestnut forests; this suggests that

favorable climates and habitats existed between what is now southwestern Texas and northern Mexico. Similar habitats could have extended south to Honduras. Depending on how extensive these forests were, they could have served as avenues for the spread of *G. volans* into Mexico and Middle America. The subsequent separation of the populations of *G. volans* in Middle America from those in North America occurred with the alternation of moist and dry periods in the central part of the United States.

It is likely that the dry periods resulted in the restriction of favorable habitats to high elevations on the west coast and subsequently populations of *G. sabrinus* in southern California (San Bernardino Mountains) became isolated from more northern populations. This does not account for the distribution pattern on the east coast, however, where the populations of *G. sabrinus* are relatively isolated, but Transition forests extend to lower elevations than the squirrel (e.g., Mt. Tom Reservation, near Holyoke, Massachusetts). In the Mt. Tom Range, although no major differences could be detected in the flora of the areas from which the two different flying squirrels were collected, the areas with *G. sabrinus* were often observed to have temperatures 10° to 20°F lower in winter than areas in which *G. volans* were found.

In Michigan and Massachusetts the northernmost boundary of *G. volans* as drawn by Burt and Grossenheider (1964) agrees fairly well with the 20°F (−6.7°C) isotherm of average January temperature (Climate and Man, 1941); in Wisconsin and Minnesota with the 12°F (−11°C) isotherm of average January temperature. Throughout the entire extent of the northern boundary the average number of frost free days is about the same (about 140). Although both of these measures reflect aspects of environmental temperature, it is difficult to determine what aspects of temperature might be stressful. Moreover, there may be large differences in temperature in local microclimates which do not necessarily agree with national weather maps. And certainly flying squirrels do not occur in every habitat that is included in a range map.

Yet, the constancy of many temperature measures, e.g., average annual, $6.4°C \pm 0.8°$ ($43.5°F \pm 1.5°F$); average January, $-9.4°C \mp 2.8°$ ($15°F \pm 5°F$); average July, $20°C \pm 1°C$ ($68°F \mp 2°$); and average annual minimum, $-31.6°C \pm 4°C$ ($-33°F \pm 7°F$) along the northern boundary of the range of this species is remarkable. In areas where the energy budget studies were conducted the squirrels can probably exist during most winters without much more of an energy expenditure than during summer (discussed previously). If the calculated energy budget is truly a budget, i.e., not just an account of energy expenditure, and this species were disposed to extend its range northward without any changes in behavioral or physiological characteristics, its energy expenditure during the winter *would be* greater

than during the remainder of the year, with the result that food supply might act as a limiting factor. In years of food scarcity the species might become food limited and realize a decrease in population density. This in turn would be less favorable from the standpoint of energetics because aggregations would be smaller and the population would lose this additional increment in its pattern of heat conservation. Although some of this stress could be alleviated by increasing the amount of nesting material, it is at such times in areas of low temperatures that populations of *G. sabrinus,* which appear to be better adapted for cold climates, would probably be more successful than *G. volans.*

In somewhat warmer climates (i.e., still far enough north so that *G. sabrinus* is not subjected to heat stress), the two species would probably do equally well except that in areas where the ranges of the species meet, *G. volans* tends to breed earlier (Muul, unpublished data). The competition experiments between the two species suggest that non-reproductive individuals were about equally aggressive. Field observations indicated that in *G. volans* females with young were successful in procuring and retaining the most favorable nest sites of those available to the species as a whole. In the laboratory, reproductive females of *G. volans* appeared to be slightly dominant (or at least as aggressive) over females of *G. sabrinus* that had young. In the laboratory none of the female *G. volans* with young were evicted from their nest boxes by female *G. sabrinus* with young when only a single nest box was available to both species (during a period of at least 3 days). It is, therefore, possible that in areas that both species could potentially inhabit, *G. volans* occupies the limited numbers of favorable nest sites earlier during the reproductive season (because it breeds earlier) than *G. sabrinus,* leaving the latter species to occupy the less favorable nest sites. This type of competition may be the reason why populations of *G. sabrinus* are confined to higher elevations or farther north than those of *G. volans.*

Thus, with the climates becoming warmer since Wisconsin glaciation, *G. volans* has apparently been able to invade areas previously occupied by *G. sabrinus* and eventually replace the latter (e.g., Virginia and Maryland; see section on Past Distribution).

SUMMARY

In Michigan and Massachusetts the southern flying squirrel, *G. volans,* nests primarily in woodpecker holes and other cavities in trees, 5–40 or more feet from the ground; oak, aspen, and red maple are most frequently used. Nests usually are less than 100 yards from water and often in isolated trees, but within gliding distance from others. Finely divided inner bark

(aspen or cedar) most commonly serves as nesting material, and the amount varies seasonally, depending on the age of the litters and sizes of winter aggregations. The openings of the woodpecker holes are from 1½ to 2 inches in diameter.

Secondary nests and retreats, reached by the squirrels along well-established routes of travel and escape, serve as cover from predators, for sheltered feeding stations, and for defecatoria.

There appears to be interspecific competition with red squirrels, *Tamiasciurus hudsonicus,* for favorable nesting sites if entrances to the nest cavities are large enough to admit the larger squirrels. In competition with the northern flying squirrel, *G. sabrinus,* as measured in the laboratory, no clear-cut dominance of either species was apparent. Intraspecific competition in the wild favors reproductive females which gain occupancy of the most favorable nesting sites, which appear to be in great demand during the breeding season.

During the cold months (November–March) the average number of adult squirrels in a nest (N = 39) was 5.7; during the warmer months (April–October) the average was 1.3 (N = 58). The aggregation tendency of 30 squirrels kept in a large outdoor cage correlated with temperature.

Temperature-related physiological measurements indicated that the basal metabolic rate was about six calories/(gm. hr.) and the lower critical temperature between 19° and 20°C. The rate of heat loss down to 6°C was 0.29 cal/(gm. hr. °C) increasing to 0.50 cal /(gm. hr. °C) below 6°C. The insulative properties of the tree cavity, nesting material, and members of winter aggregations were also determined by physiological measurements. Extrapolated to −10°C, the insulative value of the wood enclosing the nest cavity was calculated to save 9 per cent of the total thermoregulatory energy at this temperature, the nesting material saves 30 per cent, and the other members of an aggregation of six animals save 61 per cent.

During the cold months the squirrels appeared to depend on stored food materials, during warmer months they were omnivorous and showed an appetite for live insects (beetles and moths). In areas where hickory nuts and acorns are available, the former were preferentially utilized, but during a year of hickory nut crop failure the squirrels used acorns. Food items are stored on the ground and wedged between branches and rough bark in trees.

Laboratory experiments indicated that photoperiod, independent of temperature, is the cue that triggers the intensive period of food storing, characteristic of fall. The storing activity of animals on a long photoperiod (15 hours) was delayed until the daylength was changed. Accelerated diminishing photoperiod resulted in animals showing an accelerated storing response. Experimental evidence indicates that repetitive storing is avoided

by behavioral responses to an odor marker deposited on food materials during the storing process; this directs the animal's efforts to the accumulation of new food items.

According to observations in the field and year-round monitoring in a large outdoor cage, the onset and end of activity follows seasonal changes of photoperiod, whereas the intensity of activity is correlated with temperature. Precipitation, cloud cover, and wind did not always affect the level of activity singly, but wind and precipitation together often had an inhibitory effect. During the winter the squirrels remained in their nests, coming out only for short periods after dusk and just before dawn; sometimes a short peak of activity was also seen in the middle of the night. Torpid animals were seen in the wild and in confinement, but no prolonged hibernation was observed.

An energy budget was constructed in an attempt to estimate energy exchange in this species as it would occur under natural conditions. Energy expenditure was calculated from continuous activity records and continuous weather information for a year, in light of laboratory-derived energy requirements at various temperatures. Insulative properties of typical nest trees, nesting materials, and other members of seasonal nesting aggregations were also taken into consideration. Such calculations indicate that this species is not in a stress situation from the standpoint of energy exchange (heat loss) during the winter, but because of the various behavioral characteristics it expends as little energy in winter as in summer.

No correlation could be found between the northernmost distribution of this species and the northernmost distribution of various trees that serve as food sources, nor with tree associations in which this species is found in other places. Analysis of the paleo-ecological changes indicates that this species has spread northward in late Pleistocene time as climates became warmer. At present, the northern boundary of the species correlates with various isotherms. If the species extended farther north, it could no longer stay within bounds of its energy budget unless other behavioral characteristics were developed. The northern species, *G. sabrinus,* apparently cannot spread farther south because in areas now occupied by *G. volans,* the latter species breeds earlier and thus acquires the limited breeding sites.

ACKNOWLEDGMENTS

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