SYMPOSIUM ON THE GRAY SQUIRREL

INTRODUCTION

This symposium is an innovation in the regional meetings of professional game and fish personnel. When I was asked to serve as chairman of the Technical Game Sessions of the 13th Annual Conference of the Southeastern Association of Game and Fish Commissioners this seemed to be an excellent opportunity to collect most of the people who have done some research on the gray squirrel to exchange information and ideas and to summarize some of this work for the benefit of game managers and other biologists. Many of these people were not from the southeast and surprisingly not one of the panel members is presenting a general resume of one aspect of squirrel biology with which he is most familiar.

The gray squirrel is also important in Great Britain but because it causes extensive damage to forests. Much work has been done over there by Monica Shorten (Mrs. Vizoso) and a symposium on the gray squirrel would not be complete without her presence. A grant from the National Science Foundation through the American Institute of Biological Sciences made it possible to bring Mrs. Vizoso here. It is hoped that this symposium will set a precedent for other symposia at future wildlife conferences.

VAGN FLYGER.

THE RELATIONSHIPS OF THE GRAY SQUIRREL, SCIURUS CAROLINENSIS, TO ITS NEAREST RELATIVES

By DR. J. C. MOORE

INTRODUCTION

It seems at least slightly more probable at this point in our knowledge of the living Sciuridae, that the northeastern American gray squirrel's oldest known ancestors came from the Old World rather than evolved in the New. If this is certainly the case, then we know that some of the gray squirrel's ancestors spread to the New World a good many million years ago, because there are several fossil squirrels from North America known from the lower Miocene which seem to represent tree squirrels (Bryant 1945, p. 339). If they did come from the Old World, we know that the ancestral tree squirrels must have come across an isthmus or land bridge where the Bering Strait now separates Alaska from Siberia, for Simpson (1947) has shown that many kinds of mammals had crossed the Bering Land Bridge, in both directions, during periods of the middle Cenozoic, and because it now seems quite well established (Simpson, 1947, pp. 657-671) that no other land route was available to emigrants from the Old World.

There is much evidence that during the Pleistocene there were successive periods when the sea invaded and receded, alternately covering and baring the land connecting Siberia and Alaska (Hopkins, 1959, p. 1524). But there is also some evidence that no forests grew on the land bridge during these times (Hopkins, 1959, p. 1527). If that is true, no tree squirrel population could have spread onto and across it, and it seems possible therefore that the most recent crossing of the Bering land bridge by tree squirrels may very likely have been as long ago as Pliocene. After consideration of the slight difference in skull series in the American Museum and baculum characters (Howell, 1938) between the Eurasian red squirrel, *Sciurus vulgaris,* and the North American gray squirrel, *Sciurus carolinensis,* the present writer is of the opinion that the gray squirrel is the closest North American relative of the Asiatic red.

That seems to be nearly all that can be said about the early ancestors of the northeastern American gray squirrel. Tree squirrels have generally left very few fossils, and thus far, at any rate, very little is known about their evolution. However, reasonable speculation is possible about the separation of the gray squirrel species from its nearest southern relative. A growing body of data is being advanced which indicates that during the Pleistocene, the southward extension of the continental glaciers into southern Illinois, Indiana, and Ohio (Flint, 1957, p. 321) inflicted a cold, nearly boreal climate upon the Southeastern Coastal Plain (Blair, 1958; Dorf, 1959, fig. 5). This change of climate appears to have wiped out certain species of vertebrates each of which must have been previously occupying the whole sweep of the Southeastern Coastal Plain, until their only remnants survived at the tip of peninsular Florida and far south into Mexico (Blair, 1958). When the glaciers retreated, permitting the return of what Dorf (1959) calls subtropical climatic conditions, and vegetation, the refugee species must have spread northward from Florida and Mexico and reoccupied the Southeastern Coastal Plain. Two parts of a species kept separate for so long a time as a glacial period may evolve characteristics different enough to estrange the two populations and prevent them from interbreeding when they expand onto the old range and reestablish contact. Then there are two species where there had been one.

Whether this mechanism could work on the gray squirrel depends upon the extent to which this species is adapted to cool temperate climate. Because of the extension of its present range north to the Canadian border toward the northern limits of cool temperate climate (Dorf, 1959, fig. 7), one could consider the gray squirrel too well adapted to cool climate to have been separated into two parts around the gulf at all, let alone pruned back all the way to Yucatan and the tip of peninsular Florida, by Pleistocene glacial climate.

ZOOLOGICAL VALIDITY OF SUBGENERA

Before exploring further for the gray squirrel's nearest relative to the south, we need to reconsider some matters of its presently accepted classification which need revision and which may be obscuring our goal. The problem of what the relationship of the gray squirrel is to its nearest relative has actually not been well studied since 1899 when E. W. Nelson recognized all of the four really good species of the genus *Sciurus* in the United States as distinct subgenera. Nelson (1899) also sorted the Mexican and Central American squirrels into several subgenera, and although this was an excellent work in its time, it may be seen to be very badly out of date with present concepts of how a species is distinguished, by study of the mapped distributions of his alleged species presented by Hall and Kelson (1959, vol. 1).

Nearly 40 years after Nelson's work, and just incidental to revision of the North American ground squirrels, Howell (1938) proposed a general classification of North American squirrels at the level of genera and subgenera. In this classification Howell refused to admit as valid all of the tropical subgenera that Nelson (1899) had recognized (except *Guerlinguetus*), but included them as species in the subgenera *Neosciurus* and *Parasciurus*. Consequently, in Howell's classification the gray squirrel, instead of constituting a subgenus alone, became the type species of a large subgenus including 16 species of Mexican and Central American squirrels. The North American fox squirrel, *Sciurus niger,* instead of constituting a subgenus by itself as Nelson (1899) classified it, became type species of a subgenus including (according to Howell, 1938) five species of the west and the tropics. The only skull character of possibly subgeneric significance upon which separation of these two "subgenera" rests, is the consistent presence in the gray squirrel's alleged subgenus of the vestigial pair of third upper premolar teeth, and the consistent absence of these in the fox squirrel's subgenus. In the absence of a better classification of these tree squirrels, Miller and Kellogg (1955) have followed Howell (1938) in their "List of North American Recent Mammals." Hall and Kelson (1959) also felt obliged to follow Howell's (1938) classification in their "Mammals of North America."

In a recent study of the relationships of the squirrels (Sciurinae) as indicated by the characteristics of their skulls, the writer acquired a familiarity with the degree of distinction acceptable for distinguishing subgenera in dealing with the 37 genera of this nearly worldwide subfamily. In the course of that study the writer could discover no justification, and in spite of the above mentioned implications of possible separation since as long ago as the Pliocene, still cannot find any, for distinguishing the northeastern American gray squirrel, *Sciurus carolinensis,* as a subgenus distinct from the Eurasian red squirrel, *Sciurus vulgaris.* Nor, in fact, have any such characters been proposed. Their skulls and their bacula are alike, and no combination of external and internal features suggests in the present author's opinion (and see Table I) a distinction greater than that of species. It is here proposed that the subgenus *Neosciurus* based on the gray squirrel be dropped. It and the two synonyms of it (*Echinosciurus* Trouessart, 1880; *Baiosciurus* Nelson, 1899) become synonyms of the typical subgenus *Sciurus.*

TABLE I

ESTIMATED DEGREE OF TAXONOMIC AFFINITY BETWEEN THE GRAY SQUIRREL AND ITS NEAREST RELATED SPECIES. NUMERALS 1 TO 4 RESPECTIVELY INDICATE MOST TO LEAST AFFINITY

	niger	*vulgaris*	*negligens*	*alleni*	*aureogaster*
Skull (teeth)	2	1	1	2	1
Body Pelage	3	2	2	1	4
Ear Pelage	2	3	1	1	1
Tail Pelage	3	2	1	1	3
Body Size	2	1	2	1	2
Habitat	2	2	2	1	2
Habits	1	2	3	1	1

The only character of possible subgeneric significance that appears to distinguish the fox squirrel, *Sciurus niger,* and its subgenus, *Parasciurus,* from the eastern gray squirrel and the typical subgenus, *Sciurus,* is the consistent absence of the third upper premolar teeth. The presence or absence of the vestigial third upper premolar teeth is a character which the writer (1959) has found to be diagnostic for polytypic subgenera, genera, subtribes, and tribes of squirrels. In none of these taxa, however, was it found to be the only character of consequence distinguishing so high a taxonomic category. Neither the skulls nor the published illustrations of the bacula of the fox squirrel and other species assigned to the subgenus *Parasciurus* by Howell (1938) show any other distinguishing character of consequence. It is here proposed that the subgenus *Parasciurus* Trouessart, 1880, be dropped. It and the subgenus *Araeosciurus* Nelson, 1899, become synonyms also of the typical subgenus *Sciurus.* With these ill-defined and possibly even unnatural, subgeneric categories so removed, several more species may be recognized as distinct from the gray squirrel at the species level. These nearest relatives include the Palaearctic tree squirrel, *Sciurus vulgaris,* the fox squirrel, *Sciurus niger,* and many apparently too finely split species of Mexico and Central America.

NEAREST MEXICAN RELATIVES OF S. CAROLINENSIS

Which species have already been considered to show the closest relationship to the gray squirrel? The rather diminutive gray squirrels, *Sciurus deppei* and *Sciurus negligens* of the Tropical Zone of eastern Mexico in Tamaulipas and San Luis Potosí are placed nearest to *S. carolinensis* by Miller and Kellogg (1955, p. 239) implying that those authors considered *deppei* and *negligens* to be the closest relatives of *carolinensis.* Hall and Kelson (1959, p. 372) have expressed an emphatically different opinion by placing 10 other species between *negligens* (as a subspecies of *deppei*) and *carolinensis,* and by placing the fire-bellied squirrel *S. aureogaster* next to *S. carolinensis.*

The ranges of *aureogaster* and *deppei negligens* as mapped by Hall and Kelson (1959, pp. 373 and 382) are sympatric, and so located that the range of either one is consonant with the concept of its origin having been by separation from what is now *carolinensis* during a glacial period. Dalquest (1953, p. 89) points out that the small squirrel *negligens,* lives in greater abundance in the Upper Tropical Zone of the eastern slopes of the mountains in San Luis Potosí in eastern Mexico, and is scarcer in the Lower Tropical Zone of the coastal plain to the east. Dalquest (1953, p. 89) describes in *negligens* peculiarities of habit for a tree squirrel, that, together with its small size, suggest specialization both for the tropical forest habitat and for coexisting in this habitat with a larger species of ordinary size. "Shy and retiring, they are relatively inactive as compared with other Tree Squirrels. The animals live in the deep shade, and only rarely are they seen on twigs and small branches. They are commonly [observed] on the ground and seem to spend most of their lives on the lower parts of the trees, less than thirty feet from the ground. One to three ball-like leaf nests, each about a foot in diameter, were found in some trees. Nests were observed six to twenty feet from the ground in dense mango trees. . . ."

Sciurus oculatus alleni of northeastern Mexico has so many of the pelage and other external characters almost identical in every way to those of *Sciurus carolinensis* as to be distinguishable from it at the species level, only by lacking the third upper premolars. In particular the tail hairs of *Sciurus oculatus alleni*, like those of *Sciurus carolinensis* when fully grown out, possess four or five blackish bands consisting of a longer subterminal one and three or four shorter proximal ones. (The tail hairs of *Sciurus niger* and some forms in the southwestern United States apparently closely related to it, generally possess no more than three black bands, and proximal ones tend to approximate the subterminal one in length.) The geographic location of the range of *Sciurus oculatus* is consonant with the concept of separation from *Sciurus carolinensis* during one or more glacial periods of the Pleistocene by the invasion of boreal climate into the Southeastern Coastal Plain.

In the present paper *Sciurus alleni* is regarded as a subspecies of *oculatus* rather than as a species distinct from *oculatus* for the following reasons. In San Luis Potosí Dalquest (1953, p. 86) reports *oculatus shawi* to be occupying oak forests of the mountains west of the Sierra Madre. Dalquest remarks that *alleni* and *oculatus shawi* are "strikingly similar" and sustains *alleni* as a species apart from *oculatus* only on the basis of "slightly smaller size, under parts white rather than buffy, and postauricular spots absent." Baker (1956, p. 214) notes that "In *alleni* from Coahuila there are . . . postauricular spots conspicuous on some specimens but less so on others." (Baker examined 13 speciments of *alleni* and Dalquest but six.) The present writer observes conspicuous light postauricular spots of pelage in some *alleni* material in the United States National Museum. In view of the meager morphological difference between *alleni* and *oculatus shawi*, their correspondence of habitat, and their geographic proximity, it seems probable that their present geographic separation has not been of great duration and that differentiation has not reached a point at which the two populations would fail to interbreed freely if rejoined.

Dalquest (1953, p. 87) reports that *Sciurus* [*oculatus*] *alleni* lives in the oak forests capping the main crest of the Sierra Madre of the Mexican State of San Luis Potosí. The eastern slopes and lowlands of this state from the oak forested crest of this mountain range downward, Dalquest says, are tropical, and *alleni* does not occur there. The tropical forest areas are inhabited instead by the fire-bellied squirrel, *Sciurus aureogaster* (Dalquest, 1953, p. 84) as well as *Sciurus* (*deppei?*) *negligens*. Significantly Dalquest points out that farther north [in the Mexican State of Tamaulipas] where the lowlands east of the Sierra Madre are desert instead of tropical forest habitats, *alleni* does descend into the lowlands along streams and rivers. This certainly suggests that some species, probably *aureogaster* but possibly even *negligens*, is dominant to *alleni* in the tropical habitats and replaces it there.

Dalquest (1953, p. 84) does note that *aureogaster* is "less common at the upper edge of the Upper Tropical Zone than at lower elevations." Thus, even though *negligens* and *aureogaster* do occur together in the Tropical Zone, and seem adjusted by differences in size and habits to coexistence without fatal competition, each is reported as more abundant where the other is less.

Of the three species whose ranges do suggest the possibility of origin by separation from what is now *Sciurus carolinensis*, then, *Sciurus aureogaster* differs most greatly from *carolinensis* in pelage characters, and these are indeed very different. (Nelson, 1899, recognized the two as type species of two subgenera primarily on this degree of difference.) *Sciurus negligens* (as Dalquest, 1953, p. 88, regarded it, declaring that it should remain a species until intergradation with *deppei* is definitely established) or *Sciurus deppei negligens* (as Hooper, 1953, p. 4, considered it, evidently not doubting that intergradation does occur [1]) has considerably less difference in pelage characters from *carolinensis*. It is noted, and it may be significant, that the subspecies (?) of *deppei* and *oculatus* which are geographically closest to the range of the species *carolinensis*, display pelage character evidence of being closest to it taxonomically as well. Both *aureogaster* and *negligens* have become adapted to the tropical forest community, which is in some ways more distinct from the temperate climate habitat of *carolinensis* than is the Upper Sonoran Zone habitat to which *oculatus alleni* is adapted. Thus *oculatus alleni* is essentially like *carolinensis* in pelage characters and in habits and differs from it primarily in the one morphological feature, absence of the third pair of upper premolars. In view of the lack of other notable differences, the tooth character is taken to indicate no more than a good specific difference between *oculatus alleni* and *carolinensis*. The differences, thus, between *carolinensis* and each of the other three species are fewest, and, I think perhaps taxonomically least, in the case of *oculatus alleni*. The similarities in pelage characters, habit, and habitat between *carolinensis* and the geographically nearest form of each of the other three species seem also greatest in the case of *oculatus alleni*. See Table I.

HYPOTHETICAL HISTORY

A recapitulation of the hypothetical history of the separation of the two species will indicate better the reasons for emphasizing habitat in the above comparison of three species in regard to which is most closely related to the species *carolinensis*. When a Pleistocene glacial period intruded what Erling Dorf (1959, map 5) calls "cool temperate" climate on the Southeastern Coastal Plain, it drove what he calls "sub-tropical" climate (Dorf designates the present climate of the Southeastern Coastal Plain north to the Virginia line "sub-tropical" in his map 7) to the southern tip of Florida and south to what is now the Mexican state of Tabasco (Dorf, 1959, map 5). It drove the "sub-tropical" vegetation (which presumably would have constituted the habitat of the gray squirrel stock in the Southeastern Coastal Plain during the interglacial periods) south to these places. (It is primarily the fossil vegetation from which Dorf drew his inferential maps of the climate.) Moving south along with forest types to which it was adapted, the gray squirrel stock could very well have been separated by the Gulf of Mexico into eastern and western populations.

In the most extreme view, it might be conceived that each glacial period so separated the gray squirrel population into two parts and kept them separated long enough to allow them to differentiate beyond the point at which the two populations would interbreed if reunited by the northward migration with their habitat upon the retreat of the glacier. Thus several species might hypothetically have been so produced from the one gray squirrel stock by this one mechanism during the Pleistocene (for example *alleni, negligens, aureogaster* and still another species which has subsequently been competed out of existence in northeastern Mexico).

In the most conservative view, separation into two populations need not have been produced around the head of the Gulf of Mexico, but the single population must have been cold-adapted enough to maintain its range around the northern rim of the Gulf. At the same time its southern extremity must have reached deep into southern Mexico. Upon the retreat of the glacier and movement of the plant communities northward, it is evident that the vegetation also moved up the east slope of the Sierra Madre Oriental and that the tropical vegetation moved north and replaced it in the lowlands. Desert and grassland then replaced forest in response to diminution of rainfall in lowlands of Tamaulipas and Texas, thus cutting off the "subtropical" forest with its population of squirrels on the mountain. Tropical flora must then have infiltrated the "subtropical"

[1] The present writer cast some further doubt that they do intergrade, in reporting at the annual meeting of the American Society of Mammalogists of June, 1959, that in the collections of the American Museum of Natural History the nine parous female specimens of *negligens* on which functional pairs of mammae could be confidently counted, all had four pair; whereas the 14 of *deppei deppei* and 3 of *deppei matagalpae* all had three pair.

forest and in many instances out-competed the "subtropical." Martin and Harrell (1957, p. 473) find 29 per cent of the trees of their cloud forest, Upper Tropical Zone, to be species that have conspecific relatives or closely related species disjunctly located in the eastern United States. While the flying squirrel and vole apparently would have had no tropical species moving up with the tropical vegetation to compete for their niches, the relict gray squirrel population had a tropical-adapted competitor in the species we recognize now as *S. aureogaster*. If the gray squirrel population occupied the pine-oak forest of the summit as well as the moist, mostly tropical, upper slope, then *aureogaster* has evidently outcompeted and replaced it in the tropical portion, and that gray squirrel population is now identifiable as *alleni*. But if the gray squirrel population being cut off in Mexico had entered only the tropical environments and adapted by further reduction in size and restriction of habits and feeding, to ways that avoided fatal competition with *aureogaster,* then it may survive there still and be identifiable as *negligens*.

DISCUSSION

The evidence regarding the closeness of these forms to *carolinensis* is assembled in Table I, together with similar data for other species. The first four kinds of data represent original observations of museum specimens, but since the field experience of the present author has not included northeastern Mexico, the last three are entirely from literature cited in text. The unit values shown in Table I are not transferable from one line of the table to another, and it would be far from valid, of course, to add these arbitrary figures and compare the totals. Table I does strongly hint, however, that if ecological niches may be considered in this relationship (which they surely should), that *alleni* is the closest relative of *carolinensis*.

From a study of the arboreal flora and vertebrate fauna of a cloud forest area within the moist Tropical Zone area of the eastern slope of the Sierra Madre Oriental in Tamaulipas north of where Dalquest worked, Martin and Harrell (1957, p. 479) conclude 1. that some of the evident relationships between this cloud forest area and the forest flora and fauna of the southern Appalachians and Southeastern Coastal Plain are a result of pre-Pliocene connection by continuous forest ("sweet gum, hard maple, beech, evergreen magnolia, etc." and lungless salamanders) but that 2. some presumably do result from "a cool savanna or open woodland corridor" having extended across the arid Texan barrier during the Pleistocene (two snakes, *Storeria occipitomaculata* and *Rhadinaea laureata;* and barred owl, *Strix varia;* a flying squirrel, *Glaucomys volans;* and a vole, *Pitymys pinetorum*).

From the fact that Dalquest (1953, p. 11) considers *Glaucomys volans* and *Pitymys quasiater* "confined, or nearly" confined, to the Upper Tropical Zone (and Martin, 1955, p. 355, corroborates this in *Glaucomys*), and the occupation of this Upper Tropical Zone by many forest trees of northern affinities, one might expect the nearest Mexican relative of *Sciurus carolinensis* to occur there also. However, if a potentially competing species was already present both in the Upper Tropical Zone (as seems to have been the case), and another in the oak and pine forest capping the sierra (but there is no evidence that this was so), it seems more likely to the present writer that the intruded population of gray squirrel stock would be better adapted to compete more successfully against the species in the oak and pine habitat. Nevertheless, the evidence of Martin and Harrell (1957) suggests otherwise, and inasmuch as the taxonomic evidence of Table I is equivocal, it is uncertain whether *negligens* or *alleni* is the closest relative of *carolinensis*.

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writer is especially grateful to Dr. George H. Lowery, Director of the Museum of Natural Science, Louisiana State University.

SUMMARY

The subgenera *Neosciurus* and *Parasciurus* are regarded as insubstantial, and the eastern gray squirrel is classified in the subgenus *Sciurus* with *Sciurus vulgaris, Sciurus niger,* and many Mexican and Central American species differentiated from it only at the species level. Its nearest relative is shown to be most probably *Sciurus oculatus alleni* and the separation of *Sciurus carolinensis carolinensis* from *oculatus alleni* seems rather satisfactorily explained either by the theory of a boreal climate bisecting the warm adapted biota of the Southeastern Coastal Plain during Pleistocene glacial intrusions, or by the hypothesis that the plants and animals of the Southeastern Coastal Plain including the gray squirrel population, were forced far south into Mexico, and that upon withdrawal of the glacier, fragments of this biota ascended the mountains and became isolated with their squirrel populations by intrusion of desert conditions at lower elevations. Both *Sciurus oculatus alleni* and *Sciurus (deppei?) negligens* could have originated from *Sciurus carolinensis* by one of these mechanisms, but it is uncertain which of the two would have originated the most recently.

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QUESTIONS

Flyger: We don't always find upper premolars present in our gray squirrel.

Moore: This does not surprise me because there is frequently some variation in taxonomic characters.

Shorten: What subspecies of gray do we have in Britain? We have some black squirrels introduced in one or two parts of Britain.

Moore: This is certainly a point in favor of the northern subspecies.

Uhlig: Dr. Mosby, what are the weights of the southern subspecies that you have handled?

Mosby: 450-500 grams.

Moore: I would hesitate to accept weights as a taxonomic character. Scheffer has found considerable decrease in weights of fur seals in recent years.

Sharp: Is there a relative of Tamiasciurus in Asia?

Moore: A Chinese rock squirrel and African ground squirrels appear to be the closest relatives.

Clark: Squirrels may have evolved rapidly because a nasal mite found in gray squirrels at Patuxent is similar to a mite found in an African squirrel (Funisciurus).

Moore: I would say, nevertheless, that these two squirrels are about as far apart as any tree squirrels can be.

Johnson: You say that *Sciurus* has many more species here and only one species in Eurasia. Do you therefore say the squirrels went over there or came over here?

Moore: I have a theory that they came over here but it would take me too long to go into this at present. I hope to publish on this soon.

CURRENT KNOWLEDGE OF TREE SQUIRREL REPRODUCTIVE CYCLES AND DEVELOPMENT[1]

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Knowledge of the reproductive behavior and physiology of a particular species is a prerequisite to its successful management. In those wild species which can adapt to life in artificial surroundings (mink, fox) considerable information has accumulated regarding length of estrus, type of estrous cycle, reproductive development, nutritional balance required for successful breeding, etc., all of which aid in the successful propagation and management. In tree squirrels, however, artificial propagation has been generally unsuccessful. Consequently, much of the information on reproductive cycles in tree squirrels has been acquired by empirical means.

A review of the literature reveals almost complete agreement that tree squirrels have two main breeding seasons per year. Each mating period is rather restricted in time although it vvaries somewhat with latitude and perhaps with age, nutrition, climatic conditions and possibly even with population density.

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In the vicinity of Lafayette, Indiana, the first mating takes place primarily in January and February while the second breeding period occurs in late May and June and possibly into July.

Since our work has dealt almost exclusively with the male squirrel, this report summarizes our knowledge regarding this sex.

REVIEW OF PREVIOUS WORK

When we first considered a comprehensive study of male squirrel reproduction, a considerable amount of information had already been accumulated by Allen (1942) in Michigan and Brown and Yeager (1945) in Illinois. These workers, using subjective impressions, body weight, Cowper's gland palpation, scrotal pigmentation, and testis weights or measurements, attempted to age and classify male squirrels according to sexual development. Conveniently descriptive terminology was evolved, e.g., "in breeding condition," "sexually active," "inactive," etc., although it was known that male squirrels develop sexually in the fall and regress in late summer. Hence, this system did not appraise males accurately in intermediate stages of development and regression because it did not make a physiological distinction between function and non-function of reproductive organs. In addition to adults in indeterminable phases of their cycle, the fact that fall populations contained two groups of juvenile males, one becoming sexually active for the first time, indicated that considerable error could be expected from such a classification.

For the purpose of aging and assessing sexual condition, histological studies of male reproductive organs revealed considerable error in gross methods, and histology as a method promised more accuracy. Accordingly, we described the histological anatomy of testes and accessory glands in relation to ages and seasons (Hoffman, 1952; Kirkpatrick, 1955; Mossman *et al.*, 1955). Five distinct classes of sexual development, comprising two major age classes, were recognized: infantile and prepubertal were considered as juveniles, while functional, degenerating, and redeveloping were classed as adults.

In the light of the histological method for assessing sexual development, a reevaluation of gross methods previously used for that purpose revealed that testis weights and sizes overlap within and between classes of sexual development. The same was true of Cowper's glands, which are often palpated or measured, indicating that these measurements are not reliable for determining sexual activity or even age (Hoffman and Kirkpatrick, 1956). When body weights were correlated with histological indications of sexual activity and age, it was obvious that weights were also poor criteria of age even though this is a measurement frequently obtained by field biologists (Kirkpatrick and Hoffman, 1960).

Measurements of long bones and skull dimensions likewise offer little promise for an easy or accurate aging technique. The weight of the baculum, however, does increase with age during the first year and consequently can be used with some confidence in determining age composition, i.e., juveniles and adults (Kirkpatrick and Barnett, 1957).

RECENT INVESTIGATIONS

With an accurate method for aging and classifying sexual activity, we analyzed a male gray squirrel population in terms of sexual development for all months of the year. For this purpose, we had available 259 animals comprising about 20 males per month. A detailed analysis of this material is in press (Kirkpatrick and Hoffman, 1960), but some generalizations will indicate the seasonal fluctuations in age composition and sexual activity.

Peaks in abundance for the sexual development classes suggested that male squirrels attain sexual maturity at 10-11 months of age regardless of whether they were born in spring or summer. Spring males remain sexually active for 6-8 months while summer males are sexually active for about 3 months. Late summer is a period of sexual degeneration in both groups. The data indicated definite and restricted periods of sexual stimulation of adults and juveniles and well-defined periods of degeneration regardless of the length of time the animals remained functional. This suggested environmental factors operating to regulate and control the sequence of reproductive cycles. Further evidence for an environmental influence is the observation that gray squirrels, transported to the southern hemisphere, reverse their breeding periods to coincide with the change in environmental conditions (cited by Shorten, 1951).

The two most obvious environmental factors are light and temperature. If we plot, in a rough way, the monthly changes in light duration and mean temperatures throughout the year (Fig. 1), it is apparent that both periods of estrus in the female occur primarily during the first 6 months of the year. Some exceptional breeding takes place in July and in December, but as a rule most breeding occurs in January-February and again in May-June. The January-February estrus occurs soon after the minimal daily light duration and during minimal temperatures; coversely, the May-June estrus occurs near the time of maximal daily light and high temperatures. It may be an over-simplification to conclude that estrus and mating activity are induced on increasing daily amounts of light and independent of temperature, but little or no mating takes place when light and temperature are both decreasing (August-December). The age of females could also be a factor in the timing of estrous periods since the proportions of parous and nulliparous females comprising the breeding population at either period are unknown.

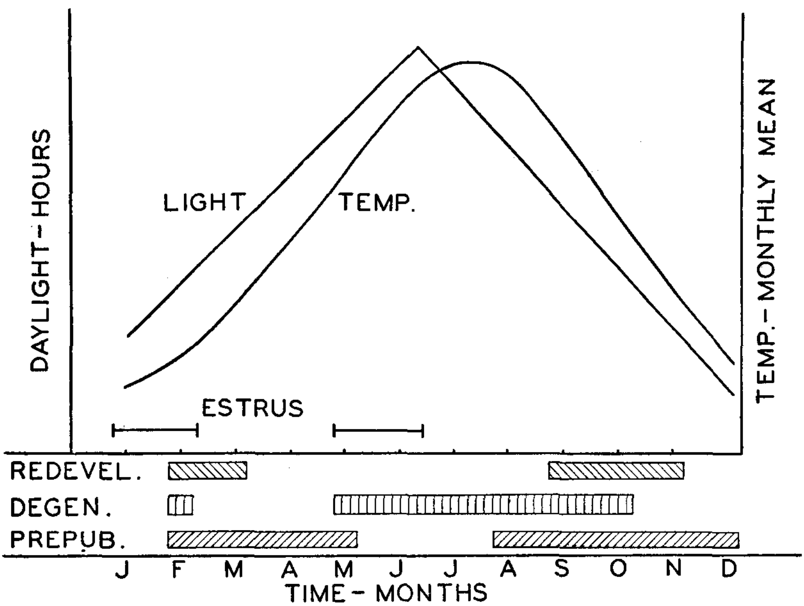

Fig. 1. Reproductive development and regression of gray squirrels correlated with generalized seasonal curves for environmental temperature and light duration.

Different conditions obtain for the male since sexual stimulation of young and adults alike occurs both under decreasing light and temperature and increasing light and temperature. Hence, it does not appear that the environmental factors of light or temperature are solely responsible for sexual stimulation in the male. The major period of degeneration occurs primarily under conditions of a decreasing light and temperature, suggesting that either factor might indirectly suppress sexual activity.

We are considering the possible influence of other endocrine organs on gonad development or suppression. In view of the recognized effect of a hyperthyroid or hypothyroid condition on reproductive vigor in several species of domestic animals, we investigated the thyroid gland (Hoffman and Kirkpatrick, 1960). For this purpose we collected at least 10 males per month, removed and weighed the thyroid glands and assessed thyroid activity by measuring epithelial cell height. In general, an increased thyroid cell height is associated with increased function while a low cell height is indicative of a low level of activity.

When we disregarded seasonal differences, relative thyroid weight and cell height was found to be maximum in the infantile animal (Fig. 2). There was a progressive reduction in values through the prepubertal and functional classes. Hence, signs of reproductive development coincident with somatic development were not correlated with morphological changes indicative of related activity in the thyroid gland. Cell heights exhibited no gross differences among the three classes of adults. Thyroid gland weight in the degenerating and redeveloping classes appeared to be significantly less than that of the functional class but not in those months when all three classes were found in the population. Infantiles and prepubertals showed consistent differences in all months. Thus, once adulthood is reached, thyroid gland activity remains at a certain level regardless of any change in reproductive activity. A high level of activity of the thyroid gland is associated with somatic growth and development but not with reproductive development.

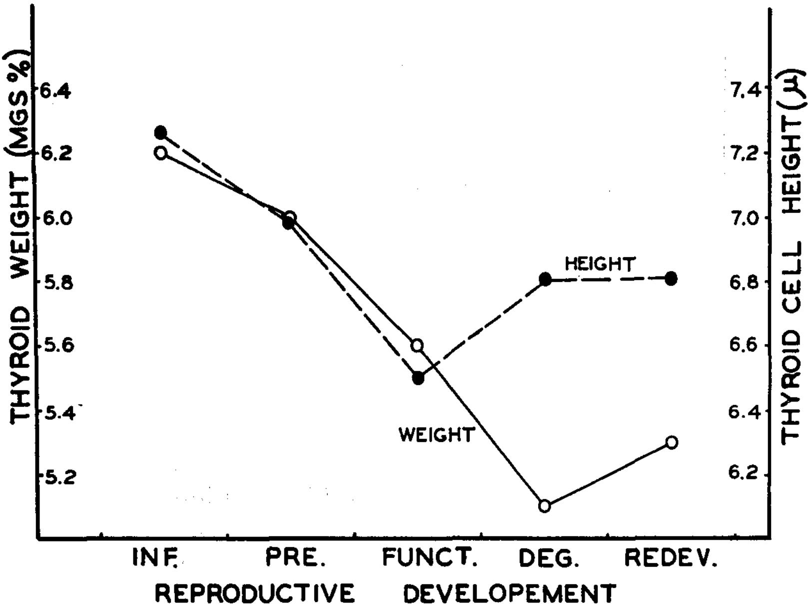

Fig. 2. Mean thyroid gland weight and cell height for all months correlated with reproductive development in male gray squirrels.

To emphasize the effect of season alone and to eliminate the probable influence of somatic and sexual development, thyroid gland cell height was plotted for the functional animals only (Hoffman and Kirkpatrick, 1960). Maximal activity occurred in October-November and the minimum in June-July. Sexual degeneration is first evident in May-June, increasing in July-September. These observations of a low thyroid gland activity associated with a progressive gonad degeneration plus the many references correlating thyroid and gonad function (see review by Maqsood, 1952) suggests that gonad atrophy during the summer is probably due to inadequate support by the thyroid gland secretions. Thus, when certain minimal levels of thyroid activity are reached, reproductive processes cannot be maintained and an irreversible process of sexual degeneration sets in which lasts for approximately 3 months. By this time, environmental factors, i.e., decreasing light and temperature, cause reactivation of the thyroid gland and consequently a redevelopment of reproductive glands.

When the weight of the adrenal gland was plotted throughout the year, two peaks of maximal adrenal weight occurred, one in September-October and one in May-June. However, the relatively heavier weight of glands of juvenile animals was found to bias the curve. When adrenal weights from functional animals only were considered, thus eliminating age and sexual development differences, maximal weight was evident in September-October followed by a dramatic decline to the minimum in November-December. Pituitary weights were found to show a comparable change. Thus we have found no correlation of adrenal or pituitary weight with the male reproductive cycle (Hoffman and Kirkpatrick, Unpubl, ms.).

The available knowledge relative to the sequence of male reproductive development still does not explain the control of the initial stimuli. Both puberty and subsequent redevelopment occur simultaneously and within restricted periods of time, suggesting that a rather precise control mechanism is acting. While environmental factors are probably implicated, according to empirical observations, neither light nor temperature alone appear to be clearly involved with sexual stimulation and as regards the endocrine glands, the relationships are as yet incompletely known.

It is significant that a summer period of inactivity exists when few animals of either sex are capable of breeding. Because the primary breeding periods fall at other seasons, the two littering periods occur only in those seasons when environmental factors of temperature, food supplies, etc., are conducive to successful growth and development of the young. Without a summer period of sexual inactivity, young could be born throughout the year, many at times when their appearance as weanlings would coincide with harsh environmental conditions.

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Kirkpatrick, C. M. and E. M. Barnett. 1957. Age criteria in male gray squirrels. J. Wildl. Mgt., 21(3) :341-347.

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Mossman, H. W., R. A. Hoffman and C. M. Kirkpatrick. 1955. The accessory genital glands of male gray and fox squirrels correlated with age and reproductive cycles. Am. Jour. Anat., 97:257-302.

Shorten, M. 1951. Some aspects of the biology of the gray squirrel (*Sciurus carolinensis*) in Great Britain. Proc. Zool. Soc. London, 121(III) :427-459.

PARASITES OF THE GRAY SQUIRREL

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The American gray squirrel (*Sciurus carolinensis* Gmelin, 1788) has fewer parasites than most other small and medium-sized mammals native to the United States. Even so, the parasites and diseases of this and other tree squirrels are poorly known. Qualitative studies on squirrel parasites are infrequent and none have been comprehensive. Few studies have been made of the biology of squirrel parasites or of the effect of a particular parasite on the host squirrel. References to epizootics among squirrels caused by parasites alone are rare. When die-offs have been reported in the literature, they have not been accompanied by adequate studies on the causative agents. At present any general assessment of the effect of parasites on gray squirrel populations must rely largely on hypothesis and postulation.

Microbiological diseases among squirrels also are poorly understood. We may assume from what is known of other animal populations, however, that tree squirrels are susceptible to a variety of viral, rickettsial, spirochaetal, and bacterial diseases which at times may become epizootic.

Certain of these diseases may be important to man. The virus of western equine encephalitis has been isolated from gray squirrels in California. In California also, human cases of relapsing fever, caused by *Spirochaeta recurrentis* have been contracted by smearing fingers with the blood of *Sciurus douglasii.* It is likely that further studies will disclose many more squirrel diseases that are transmissible to man.

A list of parasites that have been reported from the gray squirrel is appended to this paper. This list, and the references cited in its support, is not complete. The species listed are in general those most likely to be found in this country. These include approximately 48 species of ectoparasites and 30 species of endoparasites. Only a few of these will be found on, or in, a particular squirrel at any given time. Certain of these species, indicated by an asterisk, will be found much more frequently than others. Some occur on squirrels accidentally and will be recovered rarely from them.

ECTOPARASITES

SUCKING LICE

Enderleinellus longiceps Kellogg & Ferris, 1915

Ferris, G. F. 1916. A catalogue and host list of the Anoplura. Proc. Calif. Acad. Sci., 6(6) :129-213.

————. 1920. Contributions toward a monograph of the sucking lice. Part 1. Leland Stanford, Jr., Univ. Publ., Univ. Ser. (1919) :51 pp.

**Hoplopleura sciuricola* Ferris, 1921

Ferris, G. F. 1921. Contributions toward a monograph of the sucking lice. Part 2. Leland Stanford, Jr., Univ. Publ., Univ. Ser., 2(2) :57-133.

Harkema, R. 1936. The parasites of some North Carolina rodents. Ecol. Monographs, 6(2) :153-232.

Morlan, H. B. 1952. Host relationships and seasonal abundance of some southwest Georgia ectoparasites. Amer. Midl. Nat., 48(1) :74-93.

Neohaematopinus sp.

Baker, R. H. 1944. An ecological study of tree squirrels in eastern Texas. Jour. Mammal., 25(1) :8-24.

Morlan, 1952.

Neohaematopinus antennatus

Keegan, H. L. 1943. Some host records from the parasitological collection of the State University of Iowa. Bull. Bklyn. Ent. Soc., 38(2) : 54-57.

Neohaematopinus sciurinus (Mjoberg, 1910)

Davis, G. H. S. 1951. First record of a louse (*Neohaematopinus sciurinus*) from the American gray squirrel in the Cape. Jour. Ent. Soc. So. Africa, 14(1):26.

Fahrenholz, H. 1938. Die Anoplurengattung Polyplax. Ztschr. Parasitenk., Berlin, 10(2):239-279.

Ferris, G. F. 1923. Contributions toward a monograph of the sucking lice. Part IV. Stan. Univ. Publ. Ser., 2(4):183-270.

Harkema, 1936.

**Neohaematopinus sciuri* Jancke, 1932

Scanlon, J. 1960. The sucking lice of New York State. Wildlife Disease, No. 5, 121 pp.

Polyplax spinulosa

Morlan, 1952.

FLEAS

Cediopsylla simplex (Baker, 1904)

Burbutis, P. P. 1956. The Siphonaptera of New Jersey. Bull. No. 782, N. J. Agric. Exp. Sta., 36 pp.

Ceratophyllus gallinae (Schrank, 1803)

Burbutis, 1956.

Conorhinopsylla stanfordi Stewart, 1930

Fox, I. 1940. Fleas of Eastern United States. The Iowa State College Press, Ames, Iowa, 191 pp.

Jordan, K. 1937. On some North American Siphonaptera. Novitat. Zool., 40(2):262-271.

Ctenocephalides felis (Curtis, 1826)

Burbutis, 1956.

Echidnophaga gallinacea (Westwood, 1875)

Morlan, 1952.

Trembley, H. L. and F. C. Bishopp. 1940. Distribution and hosts of some fleas of economic importance. Jour. Econ. Ent., 33(4):701-703.

Monopsyllus sciurorum (Schrank, 1803)

George, R. S. 1954. Siphonaptera from Gloucestershire. 1. Ent. Gaz., 5(2):85-94.

Monopsyllus vison (Baker, 1904)

Holland, G. P. 1949. A revised check list of the fleas of British Columbia. Proc. Ent. Soc. Brit. Columbia, 45:7-14.

Nosopsyllus fasciatus (Bosc d'Antic, 1801)

Burbutis, 1956.

Opisocrostis bruneri (Baker, 1895)

Fox, I., 1940.

Orchopeas caedens (Jordan, 1925)

Knipping, P. A., B. B. Morgan and R. J. Dicke. 1950. Notes on the distribution of Wisconsin ticks. Trans. Wisc. Acad. Sci., Arts & Letters, 60(1):185-197.

**Orchopeas howardii* (Baker, 1895)

George, 1954.

Burbutis, 1956.

Orchopeas wickhami=howardii

Baker, 1944.

Thompson, G. B. 1934. The parasites of British birds and mammals. I. Notes and records. Ent. Monthly Mag., 20:133-136.

Pulex irritans (Linn., 1758)

Shaftesbury, A. D. 1934. The Siphonaptera (fleas) of North Carolina, with special reference to sex ratios. J. Elisha Mitchell Scient. Soc., 49(2):247-263.

Spilopsyllus cuniculi (Dale, 1878)

George, 1954.

Thompson, 1934.

Stenoponia americana (Baker, 1899)
Fox, 1940.

Xenopsyllus cheopsis (Rothschild, 1903)
Morlan, 1952.

MITES

Eulaelaps stabularis (Koch, 1836)
Thompson, G. B. 1935. The parasites of British birds and mammals. IV. Records of mammal parasites. Ent. Monthly Mag., 71:217-219.

**Haemogamasus ambulans* (Thorell, 1872)
Clark, G. M. 1958. *Hepatozoon griseisciuri* n. sp.; A new species of *Hepatazoon* from the grey squirrel (*Sciurus carolinensis* Gmelin, 1788) with studies on the life cycle. Jour. Parasit., 44(1):52-63.

Haemolaelaps glasgowi (Ewing, 1925)
Harkema, 1936.
Morlan, 1952.

Ornithonyssus bacoti (Hirst, 1913)
Morlan, 1952.

Sarcoptes sp.
Mange Mites
Chapman, F. B. 1938. Summary of the Ohio gray squirrel investigation. Trans. N. A. Wildl. Conf., 3:677-684.

Cheladonta micheneri Lipousky *et al,* 1955
Lipovsky, L. J., D. A. Crossley, Jr. and R. B. Loomis. 1955. A new genus of chigger mites (Acarina, Trombiculidae). Jour. Kans. Ent. Soc., 28(4):136-143.

Euschongastia sp.
Morlan, 1952.

Euschongastia jonesi Lipousky and Loomis, 1954
Loomis, R. B. 1956. The chigger mites of Kansas (Acarina, Trombiculidae). Sci. Bull. Univ. Kansas, 37(2):1195-1443.

Euschongastia setosa (Ewing, 1937)
Loomis, 1956.

Trombicula (*Eutrombicula*) *alfreddugesi* (Oudemans, 1910)
Jenkins, D. W. 1948. Trombiculid mites affecting man. I. Bionomics with reference to epidemiology in the United States. II. Control of larval behavior for disease transmission studies. Amer. Jour. Hyg., 48(1): 22-35 & 36-44.

Trombicula (*Neotrombicula*) *autumnalis* (Shaw, 1790)
Keay, Gladys. 1937. The ecology of the harvest mite, ***Trombicula autumnalis,*** in the British Isles. Jour. Animal Ecol., 6(1):23-35.
Loomis, 1956.

Trombicula (*Trombicula*) *cynos* (Ewing, 1937)

Trombicula fitchi Loomis, 1954
Loomis, R. B. 1954. A new subgenus and six new species of chigger mites (genus *Trombicula*) from the central United States. Sci. Bull. Univ. Kansas, 36(2):919-941.

Trombicula (*Trombicula*) *gurneyi* (Ewing, 1937)
Loomis, R. B. 1955. *Trombicula gurneyi* Ewing and two new related chigger mites. Univ. Kansas Sci. Bull., 37(1):251-267.

Trombicula (*Eutrombicula*) *splendens* Ewing, 1913
Morlan, 1952.

Trombicula (*Neotrombicula*) *sylvilagi* Brennan & Wharton, 1950
Kardos, E. H. 1954. Biological and systematic studies on the subgenus *Neotrombicula* (genus *Trombicula*) in the central United States (Acarina, Trombiculidae). Sci. Bull. Univ. Kansas, 36(1):69-123.

Trombicula trisetica Loomis and Crossley, 1953
Loomis, 1956.

Trombicula (Eutrombicula) tropica=alfreddugesi
Goodrum, P. 1940. A population study of the gray squirrel in eastern Texas. Texas Agr. Exper. Sta. Bull. No. 591, 34 pp.

Trombicula whartoni Ewing, 1929
Brennan, J. M. and G. W. Wharton. 1950. Studies on North American chiggers. No. 3. The subgenus *Neotrombicula.* Amer. Midl. Nat., 44(1) :153-197.

Walchia americana Ewing, 1942
Loomis, 1956.

Amblyomma americanum (Linn.)
Morlan, 1952.
Baker, 1944.

Amblyomma maculatum Koch, 1844
Hixson, H. 1940. Field biology and environmental relationships of the Gulf Coast tick in southern Georgia. Jour. Econ. Ent., 33(1) : 179-189.

**Dermacentor variabilis* (Say)
Anastos, G. 1947. Hosts of certain New York ticks. Psyche, 54(3) :178-180.

Hemaphysalis leporis-palustris (Packard, 1869)
Bishopp, F. C. and Helen Trembley. 1945. Distribution of hosts of certain North American ticks. Jour. Parasit., 31(1) :1-54.

**Ixodes cookei* Packard, 1869
Bishopp & Trembley, 1945.

Ixodes hexagonus=cookei
Harkema, 1936.

**Ixodes marxi* Banks, 1908
Bishopp & Trembley, 1945.
Katz, J. S. 1941. A collection of Ohio ticks and their hosts. Jour. Parasit., 27(5) :467-468.

**Ixodes muris* Bishopp & Smith, 1937.
Anastos, 1947.

Bots

Bot fly warbles (larvae)
Chapman, 1938.
Goodrum, 1938.

ENDOPARASITES

Mites

Speleognathopsis sciuri Clark, 1960
Clark, G. M. 1960. Three new nasal mites (Acarina, Speleognathidae) from the gray squirrel, the common grackle, and the meadowlark in the United States. Proc. Helm. Soc. Wash., 27(1) :103-110.

Protozoa

Coccidia
Chapman, 1938.

**Eimeria* sp.
Middleton, A. D. 1932. The grey squirrel (*Sciurus carolinensis*) in the British Isles, 1930-1932. Jour. Animal Ecol., 1(2) :166-167.

**Hepatozoon griseisciuri* Clark, 1958
Clark, 1958.

Hepatozoon sciuri Coles, 1914
Coles, A. C. 1914. Blood parasites found in mammals, birds, and fishes in England. Parasitol., 7:15-61.

Nematodes

Ascaris columnaris (Leidy, 1856) (larvae)
Tiner, J. D. 1949. Preliminary observations on the life history of *Ascaris columnaris.* Jour. Parasit., 35(6) :sec. 2, p. 13.

Ascaris lumbricoides (Linn, 1758) (larvae)
Brown, L. G. and L. E. Yeager. 1945. Fox squirrels and gray squirrels in Illinois. Bull. Ill. Nat. Hist. Survey, 23:449-536.
Katz, J. S. 1938. A survey of the parasites found in and on the fox squirrel and the southern gray squirrel in southern Ohio. Thesis, M.S., Ohio State University.
Rausch & Tiner, 1948.

Boehmiella wilsoni Lucker, 1943
Lucker, J. T. 1943. A new trichostrongylid nematode from the stomachs of American squirrels. Jour. Wash. Acad. Sci., 33(3):75-79.
Rausch & Tiner, 1948.

**Capillaria* sp.
Katz, 1938.
Rausch & Tiner, 1948.

Capillaria americana Read, 1949
Read, C. P. 1949. Studies on North American helminths of the genus *Capillaria* Zeder, 1800 (Nematoda): II. Additional capillarids from mammals. Jour. Parasit., 35(3):231-239.

Citellinema bifucatum (Sleggs, 1925)
Dikmans, G. 1939. Two new nematodes (Trichostrongyloidea) from rodents. Proc. Helm. Soc. Wash., 6(1):1-4.
Hall, M. C. 1916. Nematode parasites of mammals of the orders Rodentia, Lagamorpha and Hyracoidea. Proc. U. S. Nat. Mus. (2131), 50:1-258.
Rausch & Tiner, 1948.
Reiber, R. J. and E. E. Byrd. 1942. Some nematodes from mammals of Reelfoot Lake in Tennessee. Jour. Tenn. Acad. Sci., 17(1):78-89.

Citellinema sleggsi=bifurcatum
Reiber & Byrd, 1942.

Enterobius sciuri Cameron, 1932
Cameron, T. W. M. 1932. On a new species of oxyurid from the grey squirrel in Scotland. Jour. Helminth., London, 10(1):29-32.

**Heligmodendrium hassalli* (Price, 1929)
Chandler, A. C. 1942. Helminths of tree squirrels in southeast Texas. Jour. Parasit., 28(2):135-140.
Rausch & Tiner, 1948.

Longistriata hassalli=Heligmodendrium hassalli
Harkema, 1936.

Microfilaria
Price, D. L. 1954. Filarial parasites in mammals. Jour. Parasit., 40(5), sec. 2:16.
Robinson, E. J. 1954. Notes on the occurrence and biology of filarial nematodes in southwestern Georgia. Jour. Parasit., 40(2):133-147.

Nematoda sp.
Goodrum, 1940.

Physaloptera sp. (immature forms)
Rausch & Tiner, 1948.

Rictularia sp.
Rausch & Tiner, 1948.

Rictularia halli Sandground, 1935
Rausch & Tiner, 1948.

Strongyloides sp.
Rausch & Tiner, 1948.

Strongyloides papillosus (Wedl, 1856)
Reiber & Byrd, 1942.

Strongyloides robustus (Chandler, 1942)
Chandler, 1942.

Trichostrongylus calcaratus Ransom, 1911.
Rausch & Tiner, 1948.

Trichostrongylus calubriformis (Giles, 1892)
Baylis, H. A. 1934. Miscellaneous notes on parasitic worms. Ann. Mag. Nat. Hist., 13(74):223-228.

Trichostrongylus retortaeformis (Zeder, 1800)
Cameron, T. W. M. and I. W. Parnell. 1933. The internal parasites of land mammals in Scotland. Proc. Roy. Phys. Soc., Edinburgh, 22(3): 133-154.

FLUKES

Fluke
Chapman, 1938.

CESTODES

Catenotaenia pusilla (Goeze, 1782)
Katz, 1938.
Rausch & Tiner, 1948.

Cittotaenia pectinata (Goeze, 1782)
Rankin, J. S. 1946. Helminth parasites of birds and mammals in western Massachusetts. Amer. Midl. Nat., 35(3):756-768.

Cysticerci
Schwartz, B. 1928. Occurrence of larval tapeworms in the liver, lungs, spleen, kidneys, omentum and heart of the squirrel (*Sciurus carolinensis*). Jour Parasit., 15(1):67.

Hymenolepis diminuta (Rudolphi, 1819)
Katz, 1938.
Rausch & Tiner, 1948.

Larval cestodes in organs
Schwartz, 1928.

Multiceps serialis (Gervais, 1847)
Bonnal, G., C. E. Joyeux and P. Bosch. 1933. Un cas de cenurose humaine du a *Multiceps serialis* (Gervais). Bull. Soc. Path. Exot., 26(8):1060-1071.
Hall, M. C. 1919. The adult taenioid cestodes of dogs and cats and of related carnivors in North America. Proc. U. S. Nat. Mus., 55:1-94.
Meggitt, F. J. 1924. The cestodes of mammals. [Jena, Frommannsche Buchdruckerei (H. Pohle)], London, 282 pp.

Taenia crassiceps (Zeder, 1800) (larvae)
Freeman, R. S. 1954. Studies on the biology of *Taenia crassiceps* (Zeder, 1800), Rudolphi, 1810. Jour. Parasit., 40(5): sec. 2, p. 41.

Taenia hydatigena Pallas, 1766 (larvae)
Baylis, H. A. 1939. Further records of parasitic worms from British vertebrates. Ann. & Mag. Nat. Hist., London, 4(23):473-498.

Taenia pisiformis Bloch, 1780 (larvae)
Brown & Yeager, 1945.

Taenia taeniaeformis (Batsch, 1786) (larvae)
Harkema, 1936.

Taenia tenuicollis Rudolphi, 1819 (larvae)
Baylis, H. A. 1935. Some parasitic worms from muskrats in Great Britain. Ann. & Mag. Nat. Hist., London, 15(89):543-549.
Baylis, 1939.
Serkova, O. P. 1948. Parasite fauna of *Ondatra zibethica* acclimatized in Karelian-Finnish SSR. Parazitol. Sborn. Zool. Inst. Akad. Nauk SSSR (10):189-192.

ACANTHOCEPHALA

Moniliformis clarki (Ward, 1917)
Chandler, A. C. 1947. Notes on *Moniliformis clarki* in North American squirrels. Jour. Parasit., 33(3):278-281.

VIRUS TUMORS OF GRAY SQUIRRELS

By LAWRENCE KILHAM

In the fall of 1951, I received 5 gray squirrels (*Sciurus carolinensis*) which had been shot in Maryland counties adjacent to Washington, D. C. and sent to Dr. C. M. Herman at the Patuxent Research Refuge. The squirrels were covered with skin tumors. These were on all parts of the body, from the nose and toes to the tails and varied from 5 to 100 in number on individual animals. The squirrels appeared to be juveniles. It seemed likely that the tumors might be of virus origin, but for many months I had nothing but failues in attempts to transmit them to squirrels and other animals. Then Dr. Herman sent us another squirrel, a live one. This animal had a few small tumors. They did not furnish much material but I had the good fortune to induce more tumors in the skin of a woodchuck (*Marmota monax*). A peculiarity was that adult squirrels were resistant to transmission. Real success in the study came when we obtained a number of pregnant squirrels. These were kindly supplied by the Maryland Fish and Game Commission which live-trapped squirrels in the suburbs. With some precautions we found that squirrels would give birth and raise their young in captivity. The main thing was to keep them in small cages with plenty of cotton.

Suckling squirrels are very susceptible to the tumor virus. The disease induced in sucklings, inoculated into the skin when 2 days to 4 weeks of age, was unusual in that large tumors appeared at sites of inoculation within 10 days and then, in another 2 weeks, numbers of secondary tumors appeared in situations all over the skin. The general health of the young laboratory squirrels was not impaired. A few, however, became thin, developed labored respiration and when killed, were found to have their lungs studded with small, pearl-like tumors. It is possible to isolate the squirrel fibroma virus from these metastases. The disease is of interest to medical research because virus tumors which have an ability to spread through the body and to kill a certain proportion of animals have features common to true cancer.

The squirrel tumors are similar in many ways to those described by Shope in cottontail rabbits (*Sylvilagus transitonialis*). This relationship is apparent not only by microscopic examination but also by serum neutralization tests. These blood tests are easy to perform. Serum from a recovered squirrel is mixed with the tumor virus and the mixture is inoculated into the skin of a domestic rabbit. A small tumor appears if the serum is from a normal squirrel, but no tumors arise in the presence of immune serum. Domestic rabbits develop these tumors only on the first passage. Cottontail rabbits are completely insusceptible. Young woodchucks are the only other animals which we have found susceptible to the squirrel fibroma virus. Flying squirrels, ground squirrels, mice and hamsters are all resistant.

Squirrel fibromas can be transmitted readily by mosquitoes. Mosquitoes which have fed on a tumor can transmit immediately or several weeks later. Fibromas are ideal tumors for insect transmission. They furnish a bare landing place, raised above the surrounding fur and provided with a rich supply of blood vessels and, incidently, they contain considerable amounts of virus close to the surface. My guess is that mosquitoes are important vectors in nature. We have had no opportunities for field studies, however, and it may be that other arthropods, possibly ones living in squirrel nests, play a role as reservoirs of infection.

SQUIRRELS IN BRITAIN

By Monica Shorten (Mrs. Vizoso)
Great Britain

THE HISTORY OF SQUIRRELS IN BRITAIN

Sciurus vulgaris leucourus Kerr, the British or light-tailed squirrel, is the only known native squirrel of Britain. It forms one of forty-two named subspecies of *S. vulgaris* Linnaeus, the red squirrels which range from Ireland in the west to Japan in the east, and from the limits of tree growth in the north to the shores of the Mediterranean. It is distinguished from other forms by being monomorphic; by the annual whitening of the hairs of the winter coat, ear tufts and tail; and by the small size of the adults (head and body 211-238 mm. tail vertebrae 159-190 mm., condylobasal length of skull rarely exceeding 48 mm.)

This race is believed to have developed since Britain became an island. During the eighteenth century the squirrel appears to have been absent from Ireland and to have reached the verge of extinction in Scotland. Re-introductions made between 1772 and 1876 were successful, and by the end of the nineteenth century red squirrels were abundant throughout Britain. An outbreak of disease then caused a sharp decline in numbers, from which the population has never recovered. At the same time, the introduced American gray squirrel had begun to spread in Britain, and gradually to replace the remnants of the red stock.

Table I

Replacement of Red Squirrels by Gray Squirrels, Forest Year 1956

Gray Squirrels in District	*Forest with Red Squirrels*	*Forest without Red Squirrels*	*Total*	*% Forests with Red Squirrels*
By 1935	3	70	73	5
By 1945	21	43	64	33
By 1955	58	19	77	75
None	66	28	94	70

The gray squirrels introduced into Britain appear to have been intermediate between, or a mixture of, *S. carolinensis carolinensis* and *S. carolinensis leucotis.* The earliest description of an animal resembling a gray squirrel in Britain appeared in 1830; but all major introductions took place between 1876 and 1929. The most important center was that at Woburn Abbey in Bedfordshire. At least thirty releases took place, and all but a few were successful in starting thriving colonies. Few places in England and Wales are now without gray squirrels, and they are also spreading in Ireland and Scotland.

Glis, glis, the Continental or Edible Dormouse, was also introduced into Britain at the beginning of this century. Large, gray in colour, and with a bushy tail, this animal might be confused with a young gray squirrel. It is, however, nocturnal. *Glis* hibernates in cold weather.

HABITS OF THE RED SQUIRREL

The densest population of red squirrels in England today is to be found at Thetford Chase, a 36,986-acre Forestry Commission forest predominantly planted with pine and larch. Even here, foresters estimate that the overall density is not higher than one per five acres.

Dreys built in the coniferous trees, and the litter of chewed cones on the forest floor, betray the squirrel's presence. Seeds from pines, larches, and spruce are the typical diet; but red squirrels also eat acorns, beechmast, and sweet chestnuts; they will take fungi, fruit, pollen-bearing catkins, and eggs, young birds, and insects. Fire-tanks scattered through the forest provide drinking water for squirrels during the dry spells; a well-used runway leading from the foot of a tree to the corner of a tank marks the route that the squirrels take across the open ground.

The season when such runways are in greatest use is the very time that bark is stripped from *Pinus sylvestris* by the squirrels, which attack the cambium layer to get at the sweet sap. At Thetford such damage is found between late April and late July. The top ten feet of the main stem of trees between 10 to 40 years' age are most frequently damaged. Weakened tops may then be blown out, and the growth of the tree is distorted. Damage to the bark leaves a permanent scar which does not heal, though it may be masked by later growth. A fault is left, which appears when planks are cut at the sawmill.

European larch, Norway spruce and lodgepole pine (*Larix decidua, Picea abies, Pinus contorta*) are sometimes damaged by red squirrels, but *Pinus sylvestris* is most often attacked. Hardwood trees are not usually affected. In the days of its abundance the red squirrel caused concern because of this damage, and bounties were offered to encourage its destruction. Today it is relatively scarce in Britain, and is not considered to be a pest. In 1956 only thirteen out of 270 forests containing red squirrels sent in reports of damage caused by these animals.

HABITS OF THE GRAY SQUIRREL

Little work has been done in Britain with free-living marked gray squirrels; their status as a pest of forest and farm has discouraged most attempts. Gray squirrels are being marked and released within an area of twelve square miles in southern England in an attempt to study movements and to follow the history of individual animals through successive seasons.

Some types of problem facing those who are concerned with squirrel control may be answered by this kind of research. The Pest Officer needs to have advice on the following questions:

If a crop of young trees, cereals, or fruit is to be protected against damage by squirrels during the few months of the year when serious attacks are made, at what season and over how large a surrounding area can control be most economically applied to ensure protection? If a farmer whose wheatfield adjoins squirrel-infested woodland destroys all dreys and kills squirrels during the winter months, will his crop be damaged the following summer? Is there one period of the year particularly devoted to travel by squirrels? If so, it would be wasteful to let this period intervene between control measures and the season when damage is anticipated.

Until experimental work began, we had little idea whether squirrels in a woodland or parish remained within the same area all their lives, came and went seasonally, or stayed for a short while only before being replaced by other transients. We had no idea how far an individual might travel, what routes it would be likely to follow, what times of year it would choose to move, or what factors influenced movements. The work is still in progress, and it is too early to draw conclusions; but some interesting facts have emerged.

Marked animals have been shown to travel three or four miles in a month; June is the month when most movements are recorded, and is also the month when cage-trapping is most successful. Within a sixteen-acre wood, cage-traps were set at six-weekly intervals for several years. Some squirrels mainly females which had reared young, were trapped regularly there. Others, usually males, were only taken during one or two trapping periods each year. Young born on the area during the spring were often not taken in traps after the following summer, or not for several years. Although subject to normal control methods everywhere outside the experimental area, marked squirrels survived for up to five years in spite of the bounty offered for their tails.

Individuals are marked by removal of toes, using a system which gives almost 2,000 variations. Black dye is also applied to the tails, males and females being marked differently.

The gray squirrel has shown itself to be hardy and adaptable. It will colonize many different types of habitat, but prefers mixed woodland with a predominance of oak.

Two types of leaf nest are built, the solid domed winter breeding drey and the open leafy summer drey. Winter dreys may be used for a number of years, but summer dreys soon fall into disuse. Dens in hollow trees are used less regularly, and young are rarely found in them.

The most serious type of damage inflicted by gray squirrels is that caused by removal of bark and damage to cambium on young hardwood trees between April and late July. Sycamore * and beech † are most often attacked, but a variety of tree species, including conifers, may suffer. The growth of sycamore as a crop may be virtually impossible in an area where there are many gray squirrels.

TABLE II

DAMAGE BY GRAY SQUIRRELS IN FORESTRY COMMISSION AREAS, 1954-55

				Among Forests with Damage			
	Number	*Forests*	*Forests*	*Forests with*		*Forest with*	
	Forests	*with Gray*	*with*	*Beech*		*Sycamore*	
Year	*Surveyed*	*Squirrels*	*Damage*	*Grown*	*Damaged*	*Grown*	*Damaged*
1954	469	213	87	96	44	72	50
1955	538	217	68	96	41	72	37

A pilot survey of farms growing susceptible crops near woods where gray squirrels were present provided the following information:

TABLE III

DAMAGE BY GRAY SQUIRRELS TO FARM CROPS, 1956-57

	No. of Farms with Crop	
Crop	*Grown*	*Damaged*
Wheat	48	26
Oats	35	12
Barley	38	12
Walnuts	1	1
Cobnuts	10	8
Cherries	4	3
Apples	18	9
Pears	6	3
Plums	6	3
Strawberries	8	3
Peas	4	1
Potatoes	6	1
Beans	5	0
Roots	9	1

SQUIRREL CONTROL

From 1945 to 1955 inclusive, hunters were provided with free cartridges for use against gray squirrels. From 1953 until 1955 a bounty of one shilling was offered for the tail of every gray squirrel killed; hunters could choose between cash and cartridges. From 1956 until 1958 the reward was doubled, and then the bounty was withdrawn. Although the publicity associated with the bounty scheme undoubtedly sharpened awareness of the squirrel as a pest, and helped to advertise methods of hunting and trapping, it did not provide an incentive strong enough to raise the control exerted by man to a level which balanced the increase in numbers due to breeding within a year.

When leaves are off the trees, woods can be cleared of dreys. A party of three men, together with a trained dog, can clear about 50 acres in a day, shooting every squirrel disturbed. A set of aluminium alloy tubes, each 5 foot 6 inches long, giving a total extension of sixty feet, and with the last section shaped like a V, is used to dismantle the nests. Every squirrel that leaves is shot, and any young found are humanely destroyed. Dens thought to harbour squirrels are smoked out, and then plugged.

* *Acer pseudoplatanus.* † *Fagus sylvatica.*

Spring traps, set in tunnels along likely routes, may catch squirrels traveling on the ground. Bait greatly improves the success of this method, but the choice of sites for the traps is also important.

Cage traps are most effective in late spring and early summer, when food supplies are running short. Acorns and whole maize are used as bait, and traps are prebaited for four or five days before setting. Using this method, a trapper can produce a score of squirrels from a wood apparently uninhabited by them. It is a more efficient method of control than shooting.

In England and Wales it is illegal to use poison against squirrels. There is evidence that they are susceptible to the effects of warfarin, the anti-coagulant widely used against rats.

The introduction of the gray squirrel into Britain has faced us with problems which are not felt in America. In Britain the squirrel causes appreciable damage, is not regarded as a prized game animal, and is not often eaten. It is, in fact, an unpopular animal.

DAMAGE CAUSED BY THE GRAY SQUIRREL IN BRITAIN

By MONICA SHORTEN (MRS. VIZOSO)

INTRODUCTION

The American gray squirrel (*S. carolinensis* Gmelin) has for many years been recognized as a destructive animal in the broadleaved woodlands of Britain. Growing concern has been caused as the range of the species has increased, and at the same time the expanding acreage of young broadleaved crops at the vulnerable pole stage has afforded greater risk of serious damage.

Although primarily pest in woodland plantations, the gray squirrel also attacks cereal crops and orchard fruit in Britain. It is reputed to take eggs of game birds and poultry, although the evidence on this charge is rather conflicting.

In order to gather information on the distribution, type and severity of damage caused by gray squirrels to forest trees, a questionnaire has been circulated annually since 1954 to every forest area supervised by the Forestry Commission. Damage by squirrels to farm crops has not been surveyed on a wide scale; except in years when squirrels are very abundant such damage tends to be overshadowed by the damage caused by rabbits, woodpigeons, and other species. A pilot survey has been used to show the order of frequency in which farm crops are attacked by squirrels. Damage to eggs and young birds by *S. carolinensis* has not yet been critically surveyed; there is a little information in connection with the woodpigeon and the common partridge.

Results of the annual survey of damage to forest trees will be considered in this paper.

DISTRIBUTION OF DAMAGE

Gray squirrels were reported to be absent from more than 50% of Forestry Commission areas in each year. Where they were present, light damage was reported from 19 to 30% of the areas, and severe damage from 0.4 to 11% of them. The total number of forests in which some degree of damage by gray squirrels occurred was 87/469 in 1954, 68/538 in 1955 and 45/551 in 1956. In each of these years there was a bounty scheme in operation, whereby one shilling was paid for the tail of each squirrel killed.

Damage was most commonly reported from forests in southern Wales and southern England, and in west Scotland.

To justify classification as "severe," damage must be such that it affects the final value of a crop to an appreciable extent. Scrub, amenity trees, trees marked for thinning, or isolated trees of small importance may themselves be severely damaged without warranting the classification "severe" to describe damage on the area.

TABLE I

GRAY SQUIRREL IN FORESTRY COMMISSION FORESTS—DAMAGE SURVEY RESULTS, 1954-56

Area	*Total No. of Forests*			*Squirrels Absent (%)*			*Squirrels Scarce (%)*			*Squirrels Numerous (%)*			*Forests with Squirrels*			*% with Light Damage*			*% with Severe Damage*			*Forests with Damage*		
	'54	*'55*	*'56*	*'54*	*'55*	*'56*	*'54*	*'55*	*'56*	*'54*	*'55*	*'56*	*'54*	*'55*	*'56*	*'54*	*'55*	*'56*	*'54*	*'55*	*'56*	*'54*	*'55*	*'56*
England	220	246	259	35	40	40	50	56	56	15	4	4	142	149	155	44	34	20	12	2	0	67	49	31
Wales	81	90	93	28	39	39	59	52	54	13	9	2	58	55	57	21	31	19	9	4	2	17	19	12
Scotland	168	202	199	92	94	91	7	6	8	1	1	1	13	13	17	23	8	12	0	0	0	3	1	2
TOTAL	469	538	551	55	60	58	36	36	38	9	4	3	213	217	229	29	30	19	11	2	0.4	87	68	45

SUSCEPTIBLE TREE SPECIES AND AGE GROUPS

Table II illustrates the frequency with which various tree species are attacked by gray squirrels. The number of areas recording damage to a species is expressed as a percentage of the total number in which that species was grown, within the group of forests where squirrel damage occurred at least once in the two years concerned. Some forests had to be dropped from this sample because they did not return a complete stocklist of the trees grown.

TABLE II

THE RELATIVE FREQUENCY OF DAMAGE TO VARIOUS TREE SPECIES

	No. Areas in Which Present	*No. Areas in Which Damaged*		*% Area With Damage*		***Parts of Tree Usually Attacked***
		1954	*1955*	*1954*	*1955*	
Acer pseudoplatanus	72	50	37	70	51	Crowns
Fagus sylvatica	96	44	41	46	43	Butts
Quercus robur, Q. petraea	87	18	11	21	14	Upper Stem
Betula spp.	60	9	7	15	12	Upper Stem
Fraxinus excelsior	68	7	11	10	16	Upper Stem
Castanea sativa	47	4	2	9	4	Upper Stem
Larix leptolepis	71	5	3	7	4	Upper Stem
Pinus sylvestris	83	5	2	6	2	Upper Stem
Populus spp.	52	2	1	3	0	Tops
Carpinus betulus	10	5	3	–	–	Tops
Acer platanoides	10	3	0	–	–	Tops

Sycamore (*A. pseudoplatanus*), beech (*Fagus sylvatica*) and possibly hornbeam (*Carpinus betulus*) are shown to be most susceptible to attack by gray squirrels. The slightly lower percentage of attacks on beech shown in this table is due to a preference on the part of the squirrels for a particular age range in these trees.

Previously it had been believed that gray squirrels would not attact coniferous trees. Although the instance are few in number, this habit can no longer be attributed solely to the British red squirrel since trees have been damaged in forests where red squirrels have been absent for four years. Although the gray squirrel prefers a habitat of mixed mature trees, with oak predominating, it also nests and feeds in pine and larch plantations: provided that food-bearing hardwoods are present on the borders or in the vicinity of the plantations. In addition to *Pinus sylvestris,* and *Larix leptolepis,* gray squirrels are reported to have attacked *Pinus contorta, Pinus nigra, Pinus pinaster,* and *Thuja plicata.*

The most susceptible age for trees likely to be damaged by gray squirrels is between twenty and thirty years. Sycamore, however, was reported to be damaged in more than 50% of the areas where it was grown from the age of five years up to sixty years or more. Beech was shown to be most vulnerable between eleven and forty years of age, and hornbeam between twenty and thirty years. Oak between twenty and thirty years of age was damaged in 26% of the forests where it was grown; but sycamore of this age group were attacked in 81% of forests.

TYPE OF DAMAGE

The type of damage referred to here involves the stripping of bark from main stems of trees during the summer months. Shreds of outer bark which are left at the foot of the tree provide a means of distinguishing between damage done by squirrels and that caused by rabbits on the tree butts.

The cambium layer appears to be the attractive tissue, and often this is girdled. Although squirrels may not always girdle a stem completely in one season, they will often gnaw tissue adjoining the scar in the following year.

Where damage is done to the upper parts of the tree, it is usually found on the main stem just above a branch fork. If the stem is girdled, the parts of the tree above the damaged area may die, and growth of the laterals will increase, producing a deformed tree. Sycamores are sometimes almost denuded of bark in the crowns, and young beech trees are often killed by girdling on the butts. When plantations are attacked before thinning, damage is usually found on the best trees in the crop.

Squirrels will also take outer bark from some tree species, which is then used as nesting material. Such activity is not considered to be harmful, and should not be confused with the damage described here.

A pure crop of young beech (10 years and upwards) planted at 65 trees per acre over 40 acres in a squirrel-infested locality was damaged to such an extent that half the crop was rendered useless, and 99% of the trees were affected to some degree.

The season of the year during which damage occurs runs from late April until July. This is the same period as that in which red squirrels strip bark from *Pinus sylvestris,* and is thought to be determined by the condition of the sap and by a relative scarcity of food for squirrels. This last statement may seem puzzling, but precisely during these months it is most easy to lure squirrels into traps with use of bait.

Some foresters believe that damage is more severe in dry summers, and that sap is licked because water is hard to find. Instances where trees have been stripped of bark in the immediate vicinity of streams would seem to weaken this theory.

DISCUSSION

Whether the search for tree sap is a habit of particular individuals, or a generalized type of behaviour amongst the squirrel population, is not known. Observations are difficult at this season, when squirrels are shot at sight in the plantations. A forester encountering a marked squirrel would want to know why the animal had been released after capture.

The surveys have only been in progress since 1954, and during that time there has only been one marked variation in the general abundance of squirrels. 1955 was a poor year for the gray squirrel, and practically no breeding took place that spring. During the damage season, the population was judged to be at about one-third of its normal level. Reports of damage were fewer than in the preceding year, and there was a lower proportion of severe damage. Until August 1956 squirrels in Commission forests remained relatively scarce.

TABLE III

NUMBER OF SQUIRRELS AND INSTANCES OF DAMAGE ON NINETY-THREE AREAS

Number of Forests Reporting:	*1954*	*1955*	*1956*
Squirrels Numerous, Damage Severe	14	1	1
Damage Light	24	9	8
Damage Nil	1	1	0
TOTAL	39	11	9
Squirrels scarce, Damage Severe	9	4	0
Damage Light	37	44	26
Damage Nil	8	34	53
TOTAL	54	82	79

As shown in Table III, there appeared to be a connection between the level of the squirrel population and the amount of damage suffered. Even with a bounty of two shillings for the tail of every squirrel killed, however, damage occurred in thirty-five of the forest areas.

Measures applied to protect trees from bark injury caused by rabbits or by deer, such as fencing and the application of repellents, cannot be used to prevent squirrel damage. Since it is illegal to use poison against squirrels in England and Wales, the only methods that can be used are trapping and shooting.

Foresters naturally feel that surrounding landowners should also kill squirrels, to prevent constant re-invasion of the plantations; but the provision of incentives to persuade those not affected by squirrel damage to participate in control is likely to be an uneconomic proposition.

A COMMENTARY ON THE BEHAVIOR OF FREE-RUNNING GRAY SQUIRRELS*

By WARD M. SHARP
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When I accepted Dr. Vaughn Flyger's invitation to participate in this meeting and to discuss behavior in the gray squirrel, I did so with the feeling that I would not be expected to enter into an exhaustive treatment of the psychology behind squirrel behavior, nor do I expect to present the entire behavior pattern of the gray squirrel. Just as we do not understand the behavior patterns in our domestic animals, so we do not claim to know much about wild animals in their native habitats. Although I have been deeply interested in the scenting ability in bird dogs, I am at a loss because one cannot measure scent trails which the dog detects without difficulty. Gray-squirrel behavior is even more baffling, but one can record and report his observations. One can be quite certain after years of field experience that the gray squirrel possesses more than blind instinct. Its knowledge, its instincts, and its supernatural something make it more than just a "dumb animal."

Free-ranging gray squirrels are those squirrels living in the wild, choosing their inherent ecological niches, coping with the annual fluctuations of food supplies, living with and forecasting the weather throughout the year, reproducing their populations, and avoiding their enemies. Free-ranging is the living in and surviving in the elements of their climate and their habitat. In captivity the gray squirrel's initiative to seek food, to elude pursuit, to respond to breeding periods, and to live by their cunning is suppressed.

In order to understand behavior in the squirrels of the genus *Sciurus* one must re-examine the genera within the subfamily *Sciurinae*, the family *Sciuridae*, of the order *Rodentia*. Miller and Kellogg (1955) list seven genera—*Marmota, Cynomys, Citellus, Tamias, Eutamias, Sciurus,* and *Tamiasciurus*—which belong to the *Sciurinae;* and all are to be found in the United States. In the eastern United States we encounter the woodchuck or ground hog (*Marmota monax*), the eastern chipmunks (*Tamias*), the gray and fox squirrels (*Sciurus*), and the red squirrels (*Tamiasciurus*). The representative genera cited all have many behavorial traits in common. A language, a tendency towards gregariousness, and an inclination to become subdormant to dormant in cold seasons are traits in common among these genera.

The genera of the subfamily *Sciurinae,* which live in ground dens and feed exclusively upon grasses and forbs, have less need for specialized behaviors than have the tree squirrels. Because tree squirrels have adapted to a specialized arboreal habitat, they have developed special patterns of behavior and thus have achieved high survival qualities. Their food habits, their den habits, and their survival habits contrast with their cousin genera living in ground dens where food in season is always available in habitat niches that afford optimum site requirements. Since our tree squirrels of the eastern United States are not true hibernators they have had to adapt themselves for living in all four seasons. Food storage is necessary to survival during the winter months. The chief foods of gray squirrels are the nuts and other fruits of trees. The result is a specialized feeding habit complicated by frequent mast failures. Gray squirrels have thus been compelled to develop survival mannerisms not needed in the grass and forb feeding genera of the *Sciurinae.*

The Language of the Gray Squirrel: All of the above genera have one call in common which they use to warn others of the approach or presence of a natural enemy. For example, woodchucks often signal a warning at the approach of a dog. Anyone who has hunted woodchucks with a well-trained

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woodchuck dog will have been exasperated on many occasions by their sharp, whistling signals. The woodchuck less commonly warns of the approach of man. In remote, isolated regions where man is seldom seen golden-mantled marmots will signal man's approach by their warning calls.

The gray squirrel has a language consisting of several calls which may be relegated to five categories as follows: the call of apprehension, the call of fright, the after-feeding call, fussing calls, a variety of clucking calls, and the squeal of death. In apprehension of another animal when a squirrel cannot determine the intruder's motives a barking call is uttered in rapid succession. This is a challenge to tease and to draw out the intent of the intruder. A concealed hunter is frequently teased into moving, thus satisfying the squirrel that the intruder has unfriendly intentions. The cat-call is the language of fright when the potential enemy has been identified and a warning is emitted. The presence of a hawk provokes the call of fright. The feeding call is emitted just prior to or upon the completion of feeding. Squirrels moving in to a food supply first feed and then perch on a limb and bark. This feeding call is similar to the barking call of apprehension, except that its tone and rapidity are modulated. The clucking and sucking sounds are emitted usually when two or more squirrels are closely associated. Mating chases are characterized by a variety of chucking or sucking calls. The fussing or growling call is most frequently heard when another squirrel, upon seeing a hunter, runs into a tree den already inhabited by another squirrel. A female, weary and tired, may emit this call when molested by a persistent male.

BEHAVIOR IN YEARS OF FOOD SCARCITY AND ABUNDANCE

1. *Behavior in the wake of a food shortage:* In 1956 the dearth of mast in many parts of Pennsylvania resulted in a movement of the squirrel population from the Cameron County study areas, where the mast crop was a complete or almost complete failure (Creed, 1957). Squirrels began deserting the study areas by early August and, by early September, squirrels were seldom seen in our beech-maple-birch study area. This exodus began before the mast would have filled out had there been a crop. Squirrels tagged in March had moved from the beech-maple area as far as 62 miles by November. Although this area had supported 56 squirrels in the late winter and spring of 1956, only three were present in December and January the following winter.

Do gray squirrels have the ability to detect years of food shortage months in advance of the time that it will be needed? Schorger (1949), in discussing gray squirrel migrations in early Wisconsin, cites reports where squirrels migrated out of areas of mast failure in advance of the season in which the nut crop would normally mature.

2. *Behavior in the wake of food abundance:* The Barrens Grouse Study Area in Central Pennsylvania experienced mast failures in 1956, 1957, and 1958. The squirrel population declined on the 1,470-acre area to about 6 squirrels.

A heavy mast crop for 1959 was evident by late June, but the acorns would not be filled before late July and early August. Squirrels began to appear in early July. Since the area had a scarcity of den trees, the squirrels resorted to building leaf nests. The population had increased noticeably by mid-July. Can gray squirrels in passing through an area determine the maturing food potential?

TERRITORIALITY AND GREGARIOUSNESS

Territoriality and gregariousness of the gray squirrel are here treated under the same heading because the two are related. The gray squirrel is not so gregarious as the prairie dog or the golden-mantled marmot. In the first place the arboreal habitat of the gray squirrel prevents it. But gray squirrels do desire the presence of others and, in a sense, are gregarious. As many as four have been found using a nesting box during the winter in Pennsylvania. Since they are somewhat gregarious, they do not demonstrate territoriality.

I have observed no indication that a territorial habit prevails in free-ranging gray squirrels. Rank in their social hierachy may suggest this, but this type of dominance prevails among all groups of social animals. A female may defend the den tree in which her young are located. A female may, in some manner, entice her young to sources of food once they are sufficiently active to leave the den tree. I have observed at least three cases in which young were brought to artificial feeding sites. One was at a residence, and in two separate cases young came to a basket-type feeder.

Observations have led me to believe that without a gregarious tendency a gray squirrel population would be less able to survive. One squirrel attracts or directs others to a newly found food source by its after-feeding calls. Food cached by a squirrel may be used by others inhabiting the same forest community.

When squirrels evacuate a range because of a dearth of mast, the entire population appears to be alerted to this unrest. Such united action must indicate some sort of social tie. Since their departure is timed, there must be a means of communication. Although the number of gray squirrels appeared normal in Cameron County in March and April 1956, by late August the population had virtually vanished. One of these squirrels moved a distance of 62 miles, two others 40 and 42 miles. Where others went we do not know. In 1958 when there was an abundance of food the squirrels did not move, but there was a late November ingress that increased the population (Kriz, 1959).

HIBERNATION

Gray squirrels do not hibernate as do the chipmunk or woodchuck, but they do fast for varying periods. During very cold weather a squirrel may eat only an acorn then return to its tree den for the remainder of the day; if the weather is cold and windy, it may not reappear for several days. Gray squirrels in nesting boxes in midwinter have appeared to be in a deep sleep. They would not move until the observer reached into the box, located their heads by the hand, and tightened his grip. Their first struggles occurred as they were lifted out of the box. In warm weather an adult rarely remains in the box but escapes while the investigator climbs the tree.

Fasting experiments were conducted at Penn State by subjecting some squirrels to *ad libitum* feeding, others to a starvation diet. When underfed for a period, the squirrels did not lose weight rapidly. Prolonged scanty feeding caused loss in weight. But when these emaciated animals were subjected to *ad libitum* feeding, their weight gains were rapid. A squirrel may regain a weight loss of five ounces within a week. This could be attributed to an adaptive habit necessary in the survival of squirrels when they are exposed to feast or famine conditions in nature.

FOOD CACHES AND COMMUNAL FEEDING

Feeding habits of the gray squirrel: The gray squirrel is tolerant of others at a source of food. A number of squirrels may feed amicably in a hickory tree. Their habit of caching food at random is a communal behavior, and the food stored on the forest floor by one squirrel which was later bagged in the hunting season may later be utilized by other squirrels that winter in the area. Red squirrels on the other hand are strongly territorial in nature, and in most cases defend a source of food against intrusion. (Gordon, 1936), and (Robinson and Cowan, 1954).

SMALL RODENT CACHES

It was thought at one time that small rodents in the forest competed for the food supply of forest game. The white-footed mouse was believed to be a keen competitor. Our studies in Pennsylvania since 1949 have not confirmed this hypothesis. Much evidence has been disclosed to show that gray squirrels rob food caches of the white-footed mouse and the chipmunk when their caches are placed under the leaves in the upper 2 to 3 inches of the forest duff. Food supplies buried by gray squirrels are not immune from the raids of these small rodents. But food supplies buried by chipmunks, which hibernate, are frequently raided by squirrels during the winter. I am of the opinion that some of the deep scratching done by wild turkeys may uncover caches of wild-cherry stones, beech-nuts, or acorns concealed by woodland mice, chipmunks, or even gray squirrels.

PRACTICAL USE OF BEHAVIOR MANNERISMS OF THE GRAY SQUIRREL IN ITS MANAGEMENT

Behavior in hiding: When the leaves have fallen in the fall and when squirrels have become wild from hunting pressure, their tendency to hide from the gunner is most noticeable. Even under these wild conditions a gray squirrel will not remain hidden for more than 15 minutes if the hunter is well concealed and if the squirrel has been actively feeding.

We have put this information on hiding behavior into use by incorporating its significance into our time-area counts. Each stop along the route of the time-area count should not exceed 20 minutes. Squirrels which have not been subjected to gunning pressure will become active in about 10 minutes. The difference in the results secured by investigators using the time-area count is that some of them may stop and remain exposed, but others conceal themselves during the stop. To stop in an exposed, open location along the route of the time-area count often results in a low count when compared with the concealed stops.

I use the 15-minute stop method in hunting to approach several squirrels which are too wild to permit stalking. I survey the area and walk boldly within gun range and conceal myself. If I am well concealed, the squirrels in the vicinity become active within about 10-15 minutes. Care must be exercised that I am concealed from all squirrels, for one animal watching the concealed hunter may defeat the purpose of the stalk and foil his chances for a shot. This technique is of little value if the hunter approaches at a time when activity is ready to cease. This is especially true in late morning or late evening hours.

The use of rank in live-trapping operations: The successful live-trapping of gray squirrels is based on their behavior mannerisms. Sharp (1958), in the art and technique of live-trapping gray squirrels, describes the use of a wire basket filled with ear corn. The basket is hung on the trunk of a tree about 6 feet above the ground. Four traps are set on the ground around the tree. Dominant squirrels chase the subdominant from the feeder. These squirrels go to the ground and are first to enter the traps.

The lay-off period in trapping: Gray squirrels will enter traps readily to remove ear corn. But after about three days of trapping, the population refuses the corn in the traps. Traps are then turned bottom-up and prebaited for about three days or until the corn is being removed readily, at which time trapping is resumed until trap-shyness again becomes evident. In Pennsylvania one can trap at least 80-90 percent of a population within a three weeks period by taking advantage of rank and by softening their fear to trap-shyness by lay-off periods.

Pre-baiting and conditioning: Much time may be wasted in live-trapping operations by failing to condition squirrels to live-trapping operations. Uhlig and other investigators have informed me that they had no success with ear corn. Our Pennsylvania studies have revealed no difficulty in enticing squirrels to feed on ear corn. Perhaps there is a regional difference, but I feel that the difficulty lies in a conditioning process. This problem in enticing squirrels to feed on ear corn can be alleviated by establishing feeding stations. A feeding station will serve the needs for each 28 to 30 acres of squirrel habitat (Sharp, *op. cit.*).

INFLUENCE OF BEHAVIOR MANNERISMS ON POPULATION LEVELS

Had the gray squirrel acquired territorial behavior similar to those of the red or pine squirrel (*Tamiasciurus*), their numbers would not have been comparable to their present abundance in good habitats. Their population in a 30-acre woodlot of optimum habitat would have been limited. But since by nature they are tolerant, the 30-acre woodlot becomes common ground for the entire population, and the area could conceivably support one or more squirrels per acre (Flyger, 1956).

The habit of caching food at random over their common territory is a community sharing effort. Where 30 squirrels cache mast over the forest floor of a 30-acre habitat, and where 15 of the population are removed by hunting, the remaining 15 have the chance to resort to the winter's food supply laid away by the effort of 30 animals. But where the population is not reduced, they may be short of food by late winter.

A shortage of late winter foods is offset by the late winter and early spring shuffle. Ten years of spring trapping operations in Pennsylvania has disclosed that there is an annual movement of the squirrel population, especially in March and April. This movement is neither emigrating nor migrating. I have called it a *"floating"* population since it may proceed in a circuitous route, the squirrels wandering no further than a radius of one to one and one-half miles.

When gray squirrels are emigrating or migrating, they appear to move in one general direction. The mass exodus of gray squirrels from Cameron County in 1956 was in a southerly direction (Creed, *op. cit.*). The feeding call can be of particular value to the population under these circumstances. When one animal finds a niche where there is food, its barking may attract others which may otherwise pass by the food source.

The gray squirrel has been and continues to be the leading small game species in many states. In Pennsylvania it has held second place to the cottontail rabbit in importance over the past several years. Had the gray squirrel developed territorial and other traits of nonsocial animals and had it been without any type of social unity within the population, its numbers surely would have declined to the point of extinction from early gunning pressure. Since 1890 its habitat was virtually destroyed by lumbering operations; yet the gray squirrel has survived and has continued to be an important small-game species.

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QUESTIONS

Uhlig: The squirrels in small woodlots took corn but in large forests they had to learn about this. Mr. Johnson has had experience using raisins as bait.

Johnson: Once they found what corn and wheat were they took this bait.

Clark: Have you ever heard of someone being attacked by a female when handling young?

Sharp: No.

Shorten: Once.

Clark: I had a squirrel attack and bite me when a young squirrel from a nest box was being handled by me.

Uhlig: A squirrel ran over me on a similar occasion and bit me twice on a finger.

Bakken: I have noticed a restlessness of squirrel in March and April. Females being found 200 yards or more outside of their range. Could this be due to food availability?

Shorten: I have found this and believe it is partly due to young becoming independent; but both young and adults move about, especially in June.

Bakken: I have some evidence to show that a squirrel has her first litter in a den and that the female frequently moves this litter to a leaf nest shortly after the eyes open.

Uhlig: I feel the leaf nest counts can be used to determine densities but this is open to much controversy.

Moore: My observations have been mostly on fox squirrels building nests in long leaf pines and I found that many of the oak leaf nests in the wild were made by immature squirrels and were badly made.

Lwellyn: Could it be that adults have already appropriated the dens and have their own nests?

Moore: In my study I don't think this occurred. There were plenty of dens available.

Uhlig: I don't believe that anyone has shown an inverse of leaf nest relationship to dens, except perhaps in England.

Shorten: Certainly in England.

Clark: I believe that high temperature and fleas play a part in the use of dens.

Uhlig: What about nests built in October? They are not related to temperature.

Sharp: Leaf nests are a good index to the squirrel population. Squirrel may move into a good food area and construct nests.

Uhlig: It's rough but a good index for management.

Moore: I had 6 to 8 nests per squirrel for fox squirrels in Florida so I am skeptical of their value as a fox squirrel density index.

Sharp: In ridge and valley sections of Pennsylvania, squirrels are relatively sedentary but in birch, beech maple area they move much.

SQUIRREL MANAGEMENT AND RESEARCH

By HANS G. UHLIG
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When Dr. Flyger requested me to participate in this symposium he practically provided me with an outline. The subjects he suggested that I cover included:

1. How well can we manage squirrels?
2. How is it done?
3. What needs to be known in order to better manage this species?

It is obvious that were I or anyone else able to provide adequate answers to these questions, there would be little need, except for academic interest, for continuing this symposium. However, let us put some facts and ideas together and see how we come out.

The first two points are too closely tied together to separate them. Following Leopold's definition that "game management is the art of producing sustained crops of game for recreational use," I feel we now have sufficient knowledge to manage squirrels within reasonable limits. My "reasonable limits" are simply to provide the public with a huntable population without trying to control annual fluctuations or the so-called periodic cycles.

In fact, we can probably maintain the present status of squirrel hunting without doing anything except continuing our present regulations and recommending the usual management procedures. However, I believe we are here today as biologists to improve these procedures and increase, if possible, this one natural resource.

I do not believe we can accomplish this through the annual manipulation of regulations. If anyone doubts the small effect that regulations have on squirrel populations he should consult the works of Durward Allen (1943) on fox squirrels in Michigan; John M. Allen (1952) on fox and gray squirrels in Indiana; or Uhlig's (1955) work in West Virginia. Given reasonable protection squirrels are well able to hold their own. Daily and seasonal bag limits appear to be of little importance. Daily bag limits are self-regulatory, and seasonal limits are unenforceable. Hunter psychology, however, may be of prime importance. It appears that hunters who kill four squirrels when the bag limit is five, will go home much happier than the hunter that kills the same number when the bag limit is six. Hunters are no different than fishermen. In fact, they are often the same people. They are content if they can brag about reaching the seasonal bag limit, or even slightly exceeding it. Season length, as long as it doesn't interfere with the major part of the breeding season, is also of little importance since studies show that two-thirds to three-fourths of the squirrel take occurs during the first week. Actually there is only one regulation that I believe bears looking into and that is the opening date. It will be discussed later.

Regulations are one side of the picture, habitat maintenance or improvement the other. While we have some information as to basic food and cover requirements, detailed information along these lines is woefully short. Colin (1957) determined that in the lowland hardwoods of Alabama high populations were where there were four or five den trees per acre, and a fair population was present on another area when there were ten mast trees per acre. Specific information of this type is lacking.

Despite this lack, should a squirrel project start in a state that has not had one, it is more likely that the project would start out with research concerning bag limits, season lengths, life history, or in general, follow the pattern already set by others that have met with eye-catching success. While this "follow the leader" type of research may result in improved techniques applicable to the local situation, it more often ends in repetitious and reconfirming data, adding nothing in the way of new data or concepts. Research time is too valuable for reapplication of techniques. May I repeat, we have now sufficient knowledge to manage squirrels within reasonable limits, provided we are willing to search the literature, apply what we know, and then possibly set up research projects to determine the outcome in terms of population manipulation.

What needs to be known in order to better manage the species? While it is obvious that a general knowledge of the life history and habits of the squirrel are essential for proper management, it is also obvious when the literature is reviewed there are some shortcomings. With this third question, I am firmly put on the spot. Undoubtedly all of you have ideas as to what additional information you would like to have regarding the squirrel. Perhaps we could even make a list and assign problems to each of you present. I am sure that such a list would be a lengthy one, reaching from the presence of protozoan parasites in squirrels to more detailed woodland management measures that we might recommend. However, in order to keep such research along management lines, I believe we might subject each of these proposals to the following questions:

1. Does the problem concern an important limiting factor in squirrel management or hunter recreation?
2. Would any solution be of such an economic or practical nature that it would be widely adopted by interested parties?

Undoubtedly there are many interesting problems that would be eliminated by these two questions, but remember we are speaking now of managing squirrels, not in research that is strictly of academic interest. Rationalize all you want, a line can be drawn.

One factor that I feel needs to be known deals with regulations. I, for one, had previously concluded that the opening hunting season date was of utmost importance in managing squirrels. Because of the second litter squirrels, I had concluded that the season should open late, October 15th, when the maximum population was available. However, such states as Ohio, Kentucky, Missouri, and parts of Virginia with early seasons continue to have satisfactory harvests. Possibly their harvest may have been better had the seasons been delayed, or possibly wastage due to warble infestation, killing of lactating females, may have been less. On the other hand, studies have shown that in general, squirrels are underharvested. I, therefore, raise the question, is an early season actually harmful, is it poor management, or does it provide the hunter with additional recreation without, in the long run, harming the population?

There is a question regarding den boxes as a special management measure. While it is my belief that this is a good management tool, we have yet to determine their true effect on a population. Possibly North Carolina has the answer already.

I believe we need a great deal of information concerning squirrels' habitat, maintenance, or improvement in different forest types, in extensive forests and in small woodlots. Cooperative projects between the U. S. Forest Service and State game agencies could lead to cutting practices that would result in thousands of acres of better squirrel habitat. A girdled den tree might be of equal value to squirrels as a live tree and be more acceptable to foresters. How many mast producing trees do we need in different forest types, and of what size to maintain a squirrel population and still be consistent with good forest management?

Possibly research could point out management measures in small farm woodlots that would benefit squirrels. Whatever they are, they must be practical and economical, otherwise their acceptance would be doubtful. If they bring about a profitable return to the landowners, so much the better. There are thousands of acres of small woodlots throughout the country that will never be managed for timber production. How can such areas be managed for wildlife or for quirrels in particular? The usual management measures such as the prevention of fires and over-grazing, leaving three or four den trees per acre or ten mast trees per acre may be all we have to offer.

Essentially, what I am saying is that squirrel research that will eventually lead toward practical management must be practical in itself. We need a good and practical censusing technique to aid us in the many phases of research concerning management. Other than this I would limit research by state game departments, for the most part, to squirrel food and cover requirements or management. For when these factors are met, all other factors, such as the effect of hunting, predators, and weather will fall in their proper places. When practical and economical management measures are developed agencies concerned with land management will be even more willing to use them as recommendations to the people that own the land.

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THE GRAY SQUIRREL—PAST, PRESENT AND FUTURE

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Accounts of the dramatic decline of the American bison and the extinction of the passenger pigeon are well known to conservationists and laymen alike. Using these species as examples, the defenders of nature have described eloquently what happens when man encroaches excessively—sometimes necessarily, sometimes needlessly—on the wildlife resources of the country. Frequently we term species as "compatible" or even "plastic" when they are able to adjust themselves to changes that man has made in the landscape and, at the same time, can withstand a reasonable amount of annual harvest. The bobwhite quail, the fox squirrel, the eastern cottontail and even the white-tailed deer have been so classified and may be expected to remain important game species for some time to come. We term other species as "incompatible" or even "non-plastic" when they do not adjust well to the changing patterns of land-use. Some of these, like the gray wolf and the grizzly bear, are titled "wilderness species" and special effort is made to set aside refuges to maintain suitable habitat for them. The following passages will present data to show that the gray squirrel (*Sciurus carolinensis*) also has been notably unsuccessful in adjusting to changes to its forested habitat brought about by man.

In the days of early settlement, the gray squirrel occupied the vast, mature forests of nut-bearing hardwoods (chiefly oaks and hickories) in what is now eastern United States and extreme southern Canada. The species ranged as far west as the vicinity of the one hundredth meridian, where the Great Plains barred further spread, except for short distances in narrow stands of timber along streams (for Kanass, see Packard, 1956:6; for Nebraska, see Swank, 1907:80; for North Dakota, see Bailey, 1926:45; for Manitoba, see Soper, 1946:142). The gray squirrel also was barred where coniferous forests were dominant to the northward, on the higher eastern mountains, and on parts of the Gulf Coastal Plain.

Early writers have described the great abundance of gray squirrels from the Atlantic Seaboard to eastern Iowa. Occasionally, large numbers would band together and move from one place to another. Seton (1953:14-19) summarizes many early observations on movements; in another account, he (1920:57) calculated that one great emigration in Wisconsin, reported by Hoy in 1842 as lasting four weeks, must have included almost a half-billion gray squirrels (also see Cahalane, 1947:400). While on such journeys, squirrels were known to invade habitats normally inhospitable to them and even to swim large bodies of water, including the Mississippi River, as at Prairie du Chien, Wisconsin (Fryxell, 1926:60). The causes of mass movements are unclear; Schorger (1947:402) and others point to shortages of food. At any rate, whether moving cross-country or not the gray squirrel, like the now extinct Carolina paraquet, was credited with doing severe damage to corn and other crops of the pioneers. Damage in Massachusetts was sufficiently serious in 1740 to warrant the payment of a bounty of four pence per gray squirrel (Crane, 1931:270). Cahalane (1947:400) relates that in 1749, the treasurer of Massachusetts paid out 8,000 pounds sterling for the destruction of 640,000 squirrels. Hunters had phenomenal luck; Seton (1953:21) records that in Kentucky 12 hunters accounted for almost 10,000 squirrels in a week's time. In other states kills of similar magnitudes resulted, often through community efforts to rid farming areas of troublesome gray squirrels.

The hunters took their share but in the early days their harvest probably made little impression on the over-all squirrel population. Rather, it was the use of the axe, saw and torch by land-clearing pioneers and later by lumber crews that shattered the realm of the gray squirrel. The clearing and lumbering began in the east and spread slowly westward toward the prairies. In Ohio clearing started as early as 1788 (Chapman, 1939:2), although in the northern part of that state the gray squirrel dominated in dense forests until at least shortly before 1850 (Hicks, 1939:418). At the time of the Civil War a marked decrease in the number of gray squirrels was observed generally (Cahalane, 1947:400). This decline continued and in the early years of the twentieth century some conservationists even feared that the species might become extinct. Uhlig (1956:2-4) vividly described the destruction of gray squirrel habitat in West Virginia. He estimates that before the arrival of Europeans there were 15 1/2 million acres of forested lands in the state. This area was still 90 percent intact in 1880, but by 1910, only 1 1/2 million acres of virgin timber remained. The chestnut blight also added to the decline, in this state and elsewhere, of high quality gray squirrel habitat; the blight was found in West Virginia in 1911, and by 1930 had removed this important squirrel-tree. In 1956, Uhlig (*op cit.*:66) found 64 percent of the state was forested but that less than 45 percent of this area consisted of hardwood types of sufficient stand-size to be good range for gray squirrels.

The hardwood forests of river plains and swamps of the southern states were less severely treated by clearers and lumbermen, possibly because southern pines were sought more eagerly, and bottom lands were isolated and uninviting. Even so, the southern habitat also declined; by 1915, gray squirrel populations in eastern Texas began to show signs of marked reduction (Anon., 1945:127). Hunting also became an increasingly greater decimating factor in these often-narrow, stream-side habitats.

As the virgin hardwoods declined and gave way to a mixture of farmland, brushland and second-growth forests, gray squirrels and other forest game were replaced by farm game, including fox squirrel, bobwhite quail and eastern cottontail (Chapman, 1939:2). The primitive habitat of the fox squirrel in Michigan, according to Allen (1943:33), was the prairie margin. In less than 30 years, he reports, the fox squirrel replaced the gray squirrel in cut-over oaks, hickories and other hardwoods over the entire lower half of the southern peninsula of Michigan. In most places where the gray squirrel formerly was dominant the fox squirrel is now the familiar tree squirrel.

Even so, habitat in many areas is improving for gray squirrels. Submarginal farms and areas that have been heavily logged may revert, in time, to forests of types attractive to gray squirrels. Such has happened in Ohio (Hicks, 1938:418) and elsewhere, especially in the eastern states. Yet, second-growth timber, of which elms may be dominant, often supports fox squirrels and few or no gray squirrels. Furthermore, the increasing use of nut-bearing hardwoods for pulp and various chemical products may mean that in many areas, trees will be cut (with little selection) prior to maturity and, consequently, much potential habitat for gray squirrels will not develop. At the northern and northwestern peripheries of its distribution, the gray squirrel may even be extending its range, where oaks now grow along formerly open streams, where the animal has been introduced into planted groves in prairie towns (as in North Dakota, Hibbard, 1956); and where nut-bearing trees have replaced conifers removed in lumbering operations. Although prairie-border states, such as Kansas (Packard, 1956:8), have more acres of timber today than in pioneer days, the trees often are of species unsuitable for gray squirrels.

Fortunately, gray squirrels have become established in groves of nut-bearing shade trees in city parks on schoolgrounds and in back yards in many communities. The literature is filled with references to gray squirrels in urban areas —from Ontario (Judd, 1955:296, and Snyder, 1923:59) and New York (Nichols, 1958) westward to Ohio (Dennis, 1930), Kansas (Cockrum, 1952:113) and North Dakota (Bailey, 1926:45). Currently, these urban groves seem to be principal habitats for gray squirrels in several states, chiefly those in the western part of its range. The value of this specialized habitat was made clear to me during nine year's residence (1946-55) in eastern Kansas. I saw more gray squirrels within the city of Lawrence than on all of my numerous field trips outside of its limits in that state.

The available facts show that, with less publicized fanfare, the gray squirrel has shared somewhat the fate of the American bison and the passenger pigeon. Some comfort may be derived from the following statements: (1) The species still occurs in most parts of its pre-settlement range, although its distribution often is discontinuous and spotty; (2) Favored habitat is becoming re-established slowly, especially along streams; (3) The gray squirrel has become resident in groves of nut-bearing shade trees in numerous communities, especially in city parks; (4) If we wish to have more gray squirrels, more long-range programs to manage slow-growing, nut-bearing hardwood forests need to be formulated, keeping in mind that the gray squirrel can be an important wildlife product. In the face of a progressively higher human population in the United States in the years to come, many conservationists may consider that survival, except in token numbers, of the gray squirrel and many other animals and plants may very well depend largely on how compatible these species will be with man's "inevitable" changes in the landscape.

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BEHAVIOR OF GRAY SQUIRRELS

By ARNOLD BAKKEN

The numerous and varied members of the Sciuridae form a widely distributed and successful family of rodents of which four members, the red, flying, fox and gray squirrels, are represented throughout much of the deciduous forest biome of eastern North America and adjacent areas. The presence of all four of these forms in the same woods or even woodlot certainly is an argument for their diversity in that closely related species tend to differ in their behavior, ecology, or habitat requirements or become spatially separated. While these species differ in their behavior, ecology, and biology to varying degrees, numerous similarities persist. When we restrict our attention to the Sciurini, it is apparent that the cranial skeleton is very conservative (Moore, 1959) which is an argument for the stringency of anatomic requirements for tree squirrels. A somewhat parallel similarity in behavior pattern would therefore not be unexpected. The gray and fox squirrels are the most closely related, are more similar in their life history than the other forms, and seem more sympatric than allopatric in distribution. While both species are specialized as tree squirrels, studies of either or both have demonstrated not only similarity in their nesting, feeding, and habitat requirements but great diversity and adaptability in these same requirements. Apparently the two species have a broad enough resource base so that they can jointly occupy the habitat without the inception of disoperative competition. The behavior of the fox and gray squirrels is very similar, and surprisingly similar in many aspects to that of the European red squirrel. It is to be expected that the behavior of the gray squirrel would be similar to that of other tree squirrels whenever similarity would enhance survival and would be distinct where behavior among fox and gray squirrels with some distinct differences in breeding behavior.

Activity of gray squirrels, measured as number of squirrels observed per unit of observation, follows an annual sequence. Such activity figures are affected by changes in population size, population dispersal, visibility, weather, and differential activity of the sexes. The high point in activity was noted in September in Indiana (Allen, 1952) and in October in Wisconsin (Bakken, 1952). It seems that not only is the population at its highest point but observed individual activity attains a maximum during autumn (Moran, 1953) hence the population appears much higher than is actual. It is common for 30 to 40 squirrels to be killed in a woods in autumn which supports only a half dozen or so during the rest of the year (Allen, 1952). Lesser peaks occur at other times of the year.

When examining diurnal activity it is immediately apparent that both fox and gray squirrels are active to a limited extent throughout all daylight hours but that greater numbers are active during certain periods (Seton, 1929; Hicks, 1942, 1949; Goodrum, 1937, 1940; Baker, 1944; Allen, 1943; J. A. Allen, 1952; Brown and Yeager, 1945; Uhlig, 1955; Shorten, 1954; Moore, 1957). This diurnal activity may attain three peaks per day, as noted by Shorten (1954) for the introduced gray squirrel in Britain, or two peaks as frequently reported in this country. An analysis of activity by seasons indicated high morning and evening activity, with perhaps an early afternoon peak in spring, several peaks leading to a late afternoon high in summer, continuing high activity culminating in very high late afternoon activity in autumn, and the compression of all peaks into one principal peak of activity in the morning or at midday during winter. Activity during any one day will be variable due to disturbances or meterological conditions and may be strongly affected by our methods of recording data, as pointed out by Moore (1957). Gray squirrels seem to be active at lower light intensities than are fox squirrels (Packard, 1956).

Activity patterns are also modified by differential activity of the sexes (Chapman, 1938). Males were trapped more frequently than females during winter and also observed more often than females from January through March

(Bakken, 1952). More females than males were observed April through September. If differential activity and trappability coincide, time area counts or indices based upon trapping should be corrected for time of year prior to calculating the population estimate.

No consistent responses have been noted by the writer nor reported by other workers on the part of squirrels to temperature, relative humidity, precipitation, wind speed, wind direction, barometric pressure, sky cover, or snow cover. Responses of gray squirrels to weather factors have not been studied as intensively as have those of fox squirrels, but in general gray squirrels respond to the complex of factors through temperature extremes, high winds and deep snow cover are independently acting factors reducing activity. For example, winds at intermediate temperatures were generally endured or ignored while high winds, particularly if associated with low temperatures, reduced activity in exposed areas such as travel in the upper branches of tall trees. However, food supplies may alter this response as squirrels continued budding during spring despite cold and wind coupled with intermittent precipitation. Usually the squirrel would station itself on the lee of the tree and put its tail to the wind, or seek food in more sheltered areas such as the leeward of slopes and shrubs, or under conifers, shrubs and deciduous trees where wind and precipitation appeared lessened. In like manner rain, snow, and sleet were endured or ignored by those squirrels out feeding. Heavy precipitation reduced but did not halt squirrel activity. Squirrels did not rush into a shelter or den immediately upon the onset of a shower as humans typically do but continued their activity for some time.

During winter and spring squirrels tended to seek sunny areas or to sun themselves, behavior which was particularly evident well into summer among captive young. No distinct tendency for the avoidance of sun during hot weather was noted, as this response appeared directed more toward temperature. On warm days squirrels would frequently stretch out atop limbs facing outward about two feet from the junction of limb and tree, the tail elevated and extended over the back as a "shade" or allowed to hang limply. Less frequently squirrels would lie draped across branches or spread-eagled atop shaded nest boxes, on cool rocks, wet ground and shaded lawns during high temperatures. Considerable panting on the part of resting squirrels was frequently observed on hot days.

The foods utilized and the feeding habits of gray and fox squirrels are broadly similar to virtually identical and follow similar annual trends (Barber, 1954; Bakken, 1952). Both species are naturally restricted to the eastern deciduous forest and its outliers and utilize the seeds, fruits, or buds of a tremendous variety of plant species, but possess enough plasticity in food requirements to permit the successful introduction of one or the other into Colorado, British Columbia, Saskatchewan, North Dakota, England, South Africa, and elsewhere beyond the range of their original habitat.

Utilization of foods varies with availability, their importance with abundance. Vegetable foods constitute most of the diet, but meat or insects are eaten when available. Seasonally important foods may include acorns, hickory nuts, beech nuts, walnuts, maple samaras, elm seeds, fruits, some berries and agricultural crops such as corn. From a behavioral viewpoint the most interesting item is the response of the population to locally abundant food supplies resulting in feeding aggregations to be discussed later in this paper.

If the books to which we were exposed as children were to serve as an accurate criterion, the gray squirrel spends its entire life span sitting on its haunches with tail arched, manipulating an acorn in its forepaws. While a large proportion of the squirrel's daily round of activity does consist of ingestive behavior and it does possess dextrous forepaws with high manipulative capacity, this happy picture is somewhat less than complete. Foods are normally picked up by the sharp incisors and manipulated by the forepaws while the preferred portions are extracted (corn) or the hard shell removed (acorns, hickory nuts, etc.). One squirrel which had lost a forepaw and distal two-thirds of the forearm wedged food between this stump and the remaining forepaw for manipulation but still handled food as well as her more fortuante brethren. Similar observations have been recorded by Shorten (1954). Some foods such as large chunks of frozen meat too heavy to handle, lard wedged into bird feeders, and small cereal grains such as bird scratch feed are eaten directly from the substrate. A distinct tendency to carry larger food items such as acorns or corn cobs to a feeding perch, usually a stump, low crotch or low limb, has been described by several students of squirrel behavior. The distance and rapidity with which materials are removed from a feeding station is rather surprising in that large ears of corn have been transported over 100 yards in less than five minutes on several observed occasions and corn cobs have been found along squirrel travel lanes at least one-fifth mile from the feeding station. Once hunger has been satiated intermittent burial of food items occurs, a tendency that seems dependent upon the quantity of food available and not restricted to the fall of the year.

Captive squirrels will feed upon a wide variety of foods and chew the green leaves of maple, elms and oaks avidly when these are given. Insects are captured intact or picked up in a damaged condition from roadways, car radiators, etc. (Layne, 1954). An interesting sidelight is that this animal, supposedly an expert appraiser of nuts and acorns, does not seem able to distinguish black oak from white oak acorns. Squirrels have been repeatedly observed to open and discard as many as fifteen acorns before eating one. Examination of the remains indicated that the discarded acorns were those of the black oak, the ingested acorn white oak.

Little is known of the mineral needs of squirrels. Observations of the gnawing of bones and antler by rodents are common. I have observed squirrels licking calcareous sandstone, concrete, calcareous and non-calcareous rocks, and the undersides of cars, particularly those that have been driven over streets treated with salt. However granulated table salt is completely ignored by wild squirrels.

While shelter-seeking behavior of squirrels in response to meteorological factors appears ill-defined, hiding or "freezing" appears to be the common response to disturbances. At any rate the gray squirrel is very adept at keeping the trunk of the tree or large limb between it and the observer or hunter. On occasion he may not move around the trunk but "freeze" in position. When remaining immobile in this manner gray squirrels are remarkably difficult to observe and are frequently noticed only when a gust of air moves a portion of their tail, a happenstance that has been responsible for putting many a squirrel into the stew pot. Sometimes flight into tree cavities, depressions, or crotches, and less frequently into leaf nests occurs. Under such conditions as release from a trap or restraining device a squirrel may flee for a considerable distance and to a particular refuge area. Most students of this species in the field can recall instances of having run after a squirrel for some distance before it disappeared into a specific and certainly not the closest refuge.

Squirrels in captivity have been observed to race into nest boxes at the first indication of human disturbance and have remained therein during the feeding, watering, or cleaning process. No attempt was made to escape even when the nest box was disturbed, rolled over or lifted out of the cage. On the basis of these observations it seems that the hiding reaction of captives was stronger than the escape or flight reaction.

The eliminative behavior of gray squirrels has not been studied extensively. As far as wild young are concerned, it is virtually unknown though we may infer that the female cleans the nest or transports the excrement to the exterior as the nests and young are clean, dry, and free from odors (Lange, 1920) but often harbor numerous fleas. Captive young placed in nest boxes eliminate and urinate indescriminately at first. A tendency toward the placement of urine and feces in distinct, usually separate, areas later became evident in nestling young. After captive young were capable of moving about and leaving the nest box they rapidly developed distinct areas of their cage for defecation and urination, areas which usually did not coincide for the different cage inhabitants. Urination in a particular site appeared more strongly developed than did defecation as squirrels were frequently allowed the freedom of the room and were seen to return to the top of the cage to urniate while feces apparently were dropped at random or in association with nervousness or investigative behavior.

Adult animals in captivity also developed distinct sites for defecation and urination within their cages. In the wild elimination was observed in trees and on the ground but no definite dung heaps or urinating areas were noted. Elimination appeared to be enhanced by tension or excitement with the area where a squirrel had eliminated or urinated probably serving as a transitory scent spot as other squirrels traversing this area for periods up to two hours afterward, perhaps longer would stop and sniff before continuing.

Care of the young is undertaken only by the female. During the later stages of pregnancy and for a time after the birth of the young the adult female develops a territory immediately surrounding the den tree which is defended against both sexes and all ages (Robinson and Cowan, 1955; Bakken, 1952). The areal extent of the territory varied between individual females but was generally about 15 to 30 yards in diameter with rather distinct boundaries. On only one occasion were two female gray squirrels rearing young known to share a tree and different cavities were used in this case. This arrangement appeared to be transitory as one female moved to a nearby vacant cavity about a week after the discovery of this joint occupancy.

In captivity pregnant females may kill all other cage residents prior to giving birth to the young. In my experiments elimination of other squirrels may represent the territoriality noted under natural conditions in which females would attack "trespassers" if they would overtake them. Shorten (1954) has reported that the female may become very aggressive but not kill other occupants in cages larger than those that I used.

If the young are handled or the nest otherwise disturbed the female usually moves the young, or if captive she frequently kills them. Moving of nestling young even in the absence of disturbances appears to be a common and, I believe, typical procedure as almost all litters carefully observed were moved one or more times. One female has been observed to move her offspring from the same den tree to the same second nesting site for five summers. During this past summer she reared her litter for the first time in a different den tree, but as I was away much of the summer no observations could be made of her moving the litter. The young usually are moved shortly before they are ready to leave the nest. The hypothesis that this movement might be precipitated by the abundance of fleas is attractive for shortly after this move, which is frequently to a leaf nest, some combination of molting and moving or other factors results in a marked reduction in the flea infestation.

Following the departure of the young from the nest the female watches over the litter to a certain extent. The young apparently respond to low pitched calls given by the female in or near the den tree and have frequently been observed to enter the tree cavity following such calls. Young following a female, usually in the den tree, and the grooming of the young by the female in the den tree are not uncommon occurrences.

While gray squirrels are not organized into distinct social groupings, as are prairie dogs, they have evolved a rudimentary social organization which as we would anticipate appears to have some survival value. The sensory perceptions of gray squirrels upon which their social organization as well as their awareness of their surroundings would be dependent have not been adequately studied. It seems that touch is very important within the den or nest and in informing the squirrel of the substrate, but hearing, smell, and sight are probably more important outside the nest. Smell probably serves as the principal means of detecting food as reported for the fox squirrel (Cahalane, 1942), or of determining its quality though weight of items handled may be of value as well. Smell may also serve as a means of sex and species recognition as the sniffing of branches on which elimination had occurred and the sniffing of den entrances or tree trunks harboring territorial females was frequently noted. Females apparently were followed and frequently found during mating chases through the sense of smell.

The eyes of squirrels are well developed (Walls, 1942), have a wide field of vision, and are perhaps the most important single source of sensory information outside the nest with hearing next in importance (Flyger, 1956). The number of different signals, postures, and calls observed is certainly suggestive of this interpretation.

The calls of gray squirrels and the conditions under which given are listed in Table 1. The signals and postures apparently used in recognition or communication with the conditions under which these were observed are given in Table 2. The characteristic buzzing call was heard only during a mating chase, its frequency one buzz per bound. Similar calls have been reported by Robinson and Cowan (1954). The "intense alarm" call was usually given when the squirrel was racing to some point of refuge and upon attainment of the refuge was replaced by the "general alarm" call with its associated signal. This in turn might be followed by the "warning" call for periods up to 20 minutes after the apparent stimulus had departed. These latter two call were frequently answered in kind. The significance of the calls associated with groups is undetermined.

Concerning the signals and postures (Table 2), the "intimidation" signal was observed most frequently, and lasted usually 2 to 3 seconds except when given by territorial females in which case it might last for 8 to 10 seconds. Normally this was given from the ground rather than from elevations. In contrast the next most frequently observed signal, the "general alarm" signal, was given from a vantage point to the surrounding area and appeared to be a variation on the above. More detailed descriptions of these communications may be found in my thesis research (1952).

Calls and signals, such as the "general alarm" call and the "alarm" signal, sometimes resulted in allelomimetic behavior on the part of all age groups. Allelomimetic behavior among males was evident upon their hearing the buzzing call of other males during the mating chase, though the same behavior was elicited by the screams of the female in which case the response could hardly be regarded as allelomimetic. The highest degree of allelomimetic behavior was noted among post-nestling juveniles.

As population densities increase the number of contacts between squirrels correspondingly increases with the result that above a minimum density of about three, preferably more, squirrels per acre these interactions become sufficiently frequent for analysis. Above this density the independent activities of squirrels usually coincided sufficiently to result in aggregations wherein elementary social organization was discernible. Ranking appeared based upon agonistic behavior and varied with age and sex (Flyger, 1956). Dominance was established only during mating chases, at feeding stations, and by females near the den tree. Dominance apparently was re-established at succeeding encounters usually by signals and chases, rarely by actual contact or combat. The more frequently observed chases I have summarized in Table 3.

The interactions between individuals in the population occurred both in random encounters between all sex and age groups and whenever their independent activities coincided forming loosely knit casual aggregations, of which feeding and nesting aggregations were the most common. The number of interactions could be markedly increased by providing artificial feeding stations. Male-male, female-female, or mixed sex interactions consisted primarily of threats and chases and were strongly influenced by age, adults dominating yearlings and juveniles (Bakken, 1952), and by sex, males tending to dominate in most encounters (Flyger, 1956). Short combats between males were infrequently observed during mating chases. The most distinctive female-female interaction occurred between pregnant or lactating females when they engaged in signaling matches at the periphery of their territories or, less frequently, chased to the territorial boundary. Reversal in the chase was observed twice. Although territorial females were intolerant of the approach of any squirrel to the den tree, an analysis of the observed chases indicates that intolerance was most frequently directed toward yearling males. If overtaken the pursued animal was severely bitten at the base of the tail and on five occasions was tossed a half yard or more by the violence of the attack. Shortened or deformed tails are one of the most common deformities of fox (Brown and Yeager, 1945), red (Layne, 1954), and gray squirrels and are most evident at the

TABLE I

CALLS OF GRAY SQUIRRELS

Calls	*Sex*	*Age*	*Description*	*Associated with*
Associated with Mating Chases:				
Buzzing	Male	Yearling and adult	Stridulating insect or partly stifled sneeze	Hunting for or chasing the female during mating chase
Associated with Warning or Alarm:				
Intense alarm chuck	Both	All	Rapid kuk, kuk, kuk	Imminent danger
General alarm chuck	Both	All	Drawn out ku-u-uk ca. one per two seconds	Danger
Warning chuck	Both	All	Slower, short kuk, kuk kuk, kuk; or kuk, kuk kuk, qua-a-a-a	Immediate past danger; usually follows general alarm call
Attention chuck	Female	Adult	Low chucking, barely audible at 30 feet	Given to young as a warining (?) call
Juvenile scream	Both	Juvenile	Soprano scream; mouth at maximum gape	Handling in cone or removal from nest; probably signifies fear
Female scream	Female	Yearling and adult	Lower harsh scream, like combined scream and snarl	At males around her while cornered in mating chase (Warning?)
Associated with Groups:				
Mew	Both	Adult and (?)	Resembles meow of a cat	(?)
Rapid chucking	Both	All (?)	Kuk, kuks rolled together	Sometimes given before entering nest
Whistling	(?)	(?)	Resembles ground squirrel whistling	Sometimes given by occupants after nest is entered
Purr	Both	Young	Low purring like a cat	Play

Table II

Signals and Postures of Gray Squirrels

Description	*Sex*	*Age*	*Given to*	*Associated Situation*	*Associated Behavior*
Tail Signals:					
Associated with Intimidation or Warning:					
Rapid, stiff fore-and-aft jerks	Both	All	All sex, age and species groups	Feeding encounters and mating chases; directed toward other squirrels	May be followed by short ground chase
Rapid, flexible fore-and-aft waving	Both	All	Surrounding area	Disturbance; not directed toward other squirrels	Warning call may or may not be given (warning?)
Associated with Mating Chase or Inter-Sex Signals:					
Short, rapid fore-and-aft flips	Male	Yearling and adult	Yearling or adult female	Given by male when first seeing female; during the breeding season	Male moves to feeding female
Slow waving, 1 to 4 in a series	Male	Yearling and adult	Yearling or adult female	Follows preceding signal and movement	Male follows female in slow ground chase
Slow fore-and-aft waves through wide arc	Male	Yearling and adult	Yearling or adult female	Female cornered during mating chase	Lead male faces female
Circular waving	Male	Yearling and adult	Yearling or adult female	Same as above	Same as above
Postures:					
Tail pressed over back and at one side of head	Both	Juvenile	Strange objects	Variable	May jump away several times during approach
Tail pressed over back	Both	Yearling and adult	....	Danger or disturbance gone	Posture while on limb giving warning call
Foot stamping	Both	All	....	Variable	Variable

Table III

Chases Observed Among Gray Squirrels in Forest Hill Cemetery

Month	*Mating*	*Slow Ground*	*Short Ground*	*Territorial*	*Spiral Tree*
July	–	1	–	3	1
August	–	5	3	7	7
September	–	–	2	–	1
October	–	–	1	1	4
November	–	1	2	2	3
December	–	1	–	–	5
January	8	1	1	–	2
February	8	1	–	1	2
March	4	–	1	3	6
April	5	9	1	9	–
May	2	7	3	6	3
June	2	3	2	3	–
Total	29	29	16	35	34

Breakdown by Sex and Age of the Last Three Chases Listed Above *

Month	*Male/ Young*	*Female/ Young*	*Female/ Female*	*Male/ Female*	*Female/ Male*	*Male/ Male*
July	1	6	1	2	3	2
August	–	4	4	–	–	1
September	–	3	1	–	–	–
October	–	–	1	–	1	–
November	–	–	–	–	–	–
December	–	1	–	1	–	3
January	–	–	–	–	–	1
February	2†	–	–	2	–	1
March	1	1	–	1	4	1
April	–	–	4	–	2	–
May	–	1	1	–	–	–
June	3	4	–	1	1	1
Total	7	20	12	7	11	10

* Includes only chases involving marked squirrels; many more were seen than are listed.
† Either late summer litter young or yearlings.

time when females are territorial. As caged females killed other cage occupants shortly, before parturition and in each case the tail was badly bitten, virtually severed near the base, the circumstantial evidence would suggest that attacks by intolerant females may be the origin of this deformity. Intolerance by the female was limited to several weeks immediately before and after birth of the young.

Tenuous individual ranking or dominance of squirrels was established through the interactions described above. Numerous observations of individually marked animals indicated that rank or dominance varied greatly with sex and with age and had a marked influence upon home range. Varying estimates of home ranges are given by Goodrum (1940), Flyger (1956), Robinson and Cowan (1954), Baker (1944), Wingard (1950), and others. Varying population densities and ecological conditions undoubtedly account for variations from 2.0 acres per male reported by Flyger to approximately 50 acres per male reported by Robinson and Cowan. My data (Table 4) indicate that home range increases with age and is larger for males than for females. There is much overlapping of home ranges as a rule, densities of five per acre without noticeable dissension being reported by Flyger. The extent to which ranges of dominant males exceed the norm is not shown by any tabular compilation. The dominant male in my Madison study area for example had a range well in excess of 50 acres, the number two male a range of 44 acres. Variation in the size of the female ranges was not so great.

Table IV

Average Home Range in Acres in Relation to Sex and Age of Gray Squirrels in Forest Hill Cemetery (1949-1951)

Age	*Male*	*Female*
Juvenile	5.0 (12)*	3.8 (10)*
Yearling	10.7 (19)	7.1 (23)
Adult	24.1 (14)	9.9 (21)
Total Squirrels	(45)†	(54)†

* Number of animals on which average is based.

† As some squirrels were seen throughout the study, they are represented in more than one age category. The above breakdown of ranges in relation to age category is based upon 30 marked males and 40 marked females.

Group activity in the gray squirrel population consisted essentially of loosely knit aggregations of several squirrels doing the same thing, *i. e.*, feeding or nesting, at the same time and location which were more dependent upon high squirrel densities than upon any other single factor.

Feeding aggregations were formed in response to a local abundance of some food and can be induced by the addition of feeding stations. Under these conditions ranking of individuals is apparent (Flyger, 1955), the spacing of individuals feeding upon the ground being maintained by a limited number of signals or chases. The ratio of signals to chases was on the order of four to one. Little contagious behavior was noted in a feeding aggregation as squirrels only a few feet apart would feed on different items for example. Once squirrels began to feed they remained fairly stationary separated from one another by three to four feet as a rule though the spacing might be only a foot or more when they fed upon rain-concentrated elm seeds in the spring. A spacing of about a yard was noted when they fed in the trees upon bur oak acorns or hickory nuts in August. Bur oaks, walnuts, and hickories were a magnet to the squirrel population with over ten individuals noted in one tree when the crop was being utilized. It might be interjected that many of the older records of squirrel abundance, such as fourteen shot from one tree, etc., usually appear associated with late summer feeding aggregations.

As food production in a natural area is not uniform, casual aggregations of squirrels will be noted in autumn burying acorns under heavily yielding trees and feeding in these areas during the winter. Spacing apparently is maintained under these conditions by signals only or by signals followed by chases. Under conditions of heavy snowfall subnivean tunnels were excavated and used by several different squirrels during one day or longer. No distinct possessive responses by the excavator were noted over a period of several days though dominant squirrels might prevent others from using a particular tunnel for a half hour or so. Frequently squirrels were observed feeding in separate depressions or tunnel entrances in the snow at distances of about a yard with no evidence of strife.

Nesting aggregations were frequently observed and might be encountered at any time of year though they were more apparent during the non-breeding period. Gray squirrels primarily utilize tree dens, mainly in oaks in Wisconsin, and leaf nests, also nest boxes, garages, farm buildings, holes between walls, accessible attics, and spaces in stone walls when necessary. Tree dens are thought to be the best dwelling with most reproduction occurring therein (Chapman, 1938a). The den entrance may be gnawed back particularly if it is below the "desirable" level of about three inches in diameter, but gnawing is not a criterion of den occupancy. In addition to tree dens, leaf nests, either covered or platform type, and composed of twigs with leaves attached or of leafless twigs lined with leaves have been described. Most leaf nests are constructed during the summer and autumn presumably by juveniles (Uhlig, 1956) and located in seasonally favored food trees. Many of these nests fall apart during the winter.

Several squirrels at a time may occupy either a tree den or a leaf nest, as many as seven having been driven from a tree den in winter and five observed to enter a den during a ten-minute period in late autumn. During the spring it appears that pregnant females evict other members of a winter nesting aggregation which may be mixed in sex and age. At this same time the platform type of leaf nest appears along with nesting aggregations composed of non-breeding females, males, and last season's offspring. Males may form temporary nesting aggregations at this time; four marked males have been identified out of a group leaving a shallow, normally unoccupied tree cavity. Characteristic calls were sometimes associated with entry into tree dens. It is probable that individual squirrels have more than one den or nest available to them and that the composition of any aggregation therefore varies from time to time.

The most conspicuous and spectacular aggregation of squirrels is the mating chase which occurs from late December to early August in Wisconsin. Thirty-four mating chases were observed by the writer varying in length from a half hour to over a day and in number of participants from three to fourteen. A typical chase proceeded about as follows:

The female, feeding on the ground in early morning, was noticed by a male feeding nearby who gave a typical short fore-and-aft tail flipping signal, moved to the female and sniffed her anal region. As the female bounded away the male followed in a slow ground chase. Behavior of this type could be observed almost any morning but would result in the circumscribed mating chase more rarely. Other yearling or adult males feeding nearby would repeat the process during intermittent feeding. When the males exceeded three in number the female usually bounded away to a tree or some other point of refuge, and the chase was on. Those males who had not been following the female closely gave the characteristic buzzing call when they seemed momentarily lost. Other yearling or adult males within a radius of about 100 feet apparently heard this call and ran also buzzing, to the area and joined the chase, which developed a tempo varying directly with the number of males involved. The female ran from tree to tree with the males in close pursuit and remained in crotches, on the ends of limbs, or in a tree den for variable periods of time, dependent apparently upon how readily she could prevent the close approach and attempted mounting of some male. When the female was cornered thusly she periodically emitted a characteristic screaming snarl, the best audible indication of the occurrence of a mating chase. This snarl appeared to function as a warning, for males tended to remain more than two feet from her for nearly a minute afterwards. As soon as the female left one refuge all the males would join the chase again with the one nearest the escape route becoming the lead male. If he overtook the female he would grasp her flanks with his forefeet and attempt mounting. This male's temporary position at the head of the pack was usurped by the dominant male when the female was again brought to bay.

Frequent signaling, intermediate chasing, and infrequent combats appeared to determine which male would be nearest the female when she was cornered. Dominance apparently was re-establisehd during each chase with different males appearing dominant during succeeding chases. However during any one chase a definite chase order was rather quickly established and would be frequently repeated. Most of the jockeying for position appeared to occur between the males intermediate in rank with the subordinate males, mainly yearlings, often sitting quietly in the tree or on the ground feeding at intervals. Stamping of the hind feet, biting bits of bark, chattering of the teeth, and two characteristic tail signals were conspicuous elements of the behavior of the male nearest the female.

The mating chase was intermittent, some lulls persisting for over half an hour during which the casual observer would only note an aggregation of apparently resting squirrels. Movement of the female to another portion of the tree would bring all males into the chase again, whereas when cornered her screams directed toward the nearest male appeared to evoke only increased alertness but no concerted movement among subordinate males.

This spectacular aggregation apparently disbanded slowly whenever one male had established dominance over the other males. Where fewer numbers of squirrels were involved dominance appeared to be established in a shorter time. Copulation was observed only after the other squirrels had left the area.

The development of behavior patterns in young has been reported by Shorten (1954) for the gray squirrel and by Eibl-Eibesfeldt (1951) for the European red squirrel. The similarity of behavior in the young of these two species is quite striking. Growth, development of fur, and weight curves have been presented by Uhlig (1955a) and Shorten.

The young within the nest or den apparently burrow underneath one another, move around the den cavity to an increasing extent, and may climb to the entrance shortly after the eyes open. Prior to the opening of the eyes these animals will open the mouth to its maximum gape and emit the juvenile scream when taken from the nest into the light unless very carefully handled. This was the only careseeking (et-epimeletic) behavior observed and was answered by the general alarm call by squirrels within about 40 yards. They normally do not leave the nest until over two months of age, appearing at the base of the den tree and in its immediate surroundings first at about 9 to 10 weeks of age. The litter group is noticeable in or near the den tree for about five weeks after emergence from the den, dispersing after about 40 days.

The young squirrels in a litter group stay close together near the den tree with allelomimetic behavior very prominent. They frequently race as a unit to the tree and up the trunk for two or three yards, though no stimulus was apparent, and indulge in group play, such as wrestling or mock combat, racing and bouncing about the base of the tree. During this time the constant closeness of the littermates is the most noticeable characteristic of this aggregation. The first indications of independent behavior in wild litters have coincided with the onset of agonistic behavior in captives of similar ages. Independent movements of siblings in a small but expanding home range have been noted thereafter.

A behavior pose characteristic of young, and also described by Eibl-Eibesfeldt for the European red squirrel, can perhaps best be termed investigative behavior. The young squirrel would approach cautiously some new object, stretching the body and extending the tail over the back and to one side of the head while doing so. Usually it would leap backward several times before approaching close enough to smell the item. This type of hebavior disappeared slowly and was occasionally noted among yearlings.

Nest building behavior of captive young squirrels was observed by mid-July.

The data suggested that male squirrels may have a stronger tendency to build nests than do females. Green maple, oak, and elm leaves were avidly chewed by the captives, carried about, and eventually deposited in a shapeless mass either in or alongside the nest box. Unorganized attempts to place this material into a semblance of a nest were numerous. One captive male become very grasping, removing facial tissues, sheets of paper, handkerchiefs, in short anything flat, from our hands and secreting them behind a studio couch. When given free rein a tremendous labor was accomplished and a recognizable nest was produced. The nest building behavior of captive juveniles reinforces Uhlig's (1956a) suggestion that fall leaf nest building activity is primarily traceable to this age group.

It appears that the critical period in the socialization of the young squirrel may occur between the time the eyes open and the animal leaves the nest. Young removed from the nest or picked up after falling out of a tree at about 6 weeks of age respond well to human handling whereas young trapped at the base of the tree do not.

Before turning our attention to what may be accomplished, we must recognize that almost all behavioral data on squirrels have been gathered incidental to ecological or management-oriented research. This must be corrected. The Sciuridae, particularly the Sciurini, are primarily generalized, diurnally active rodents with a wide range of adaptations from fossorial to arboreal and behavioral organization varying from territorial to social, and as such represent what I believe to be the best source of data of comparative mammalian behavior. These forms are accessible, living in sufficiently high densities to render our results statistically verifiable and are, on the basis of body size and diurnal habits, fairly convenient to handle and observe. The diurnal activity pattern is probably of greatest significance. What other tribe of mammals has these attributes?

As far as the gray squirrel is concerned it would probably be most instructive to record signals, postures, sounds, etc., simultaneously on movie film alone or on movie film and tape recorder so that the individual features of a behavioral sequence could be individually examined as in the Blauvelt technique, and the sounds could be analyzed using oscilloscopes as has been done with birds. A great deal of work is being done in this area at present. The enchanced insight thus procured should enable us to study more adequately the effect of food supplies and their dispersion upon individual and social behavior as well as upon interactions with other species, as has been suggested by work with rats (Barnett et al., 1951).

Tinbergen (1953) cautions that good behavioral studies, either comparative or experimental, must be preceded by the broadest possible observational approach. Sciurids can certainly be observed more readily than rats or other nocturnal forms, and since behavior patterns may have taxonomic significance (Marler, 1957; Lehrman, 1956) it would seem that in the sciurids we could cover comparative ethology (Eibl-Eibesfeldt and Kramer, 1958) in a family or tribe wherein behavior varies from territorial to hierarchial. We can use the tree squirrels to obtain insight into the position of the individual in the population, or the role of intra-species conflicts in its population dynamics (Collias, 1944, 1950), or the social aspects of population dynamics (Calhoun, 1952). Sciurids would seem a good species to use in the development of techniques and field experiments (Emlen, 1950), and also since they become so abundant in urban areas they are seemingly an excellent mammal for use in the needed experimental studies of trap-revealed home range (Hayne, 1949). The work of King (1955) and Anthony (1955) on captive and free populations of prairie dogs provides an instructive suggestion of what might be done with sciurids, though Shorten appears to be the only one to compare extensively populations under these two conditions. We must also develop standard conditions under which to study dominance hierarchy as proposed by Baron *et al.*, (1957) for cats.

From a more practical management viewpoint, further behavioral studies could provide us with better census techniques through the correlation of trap, sight, leaf nest, and hunting data, such as those of Davis (1955), Flyger (1956), Uhlig (1956), and Friley (1955), with population elimination experiments, such as those of Shorten (1955). Behavioral studies should provide a good source of mortality or life table data to add to those of Linduska (1947) and Flyger (1956).

When the above have been accomplished we can experimentally (and much of this can be done in the field) measure behavioral development and socialization, and the effect of stresses (Christian, 1950), feeding habits and preferences (Baumgras, 1944) upon dominance hierarchies and population patterns. Scott's (1950) thoughtful presentation suggests many lines of inquiry.

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QUESTIONS

Mosby: We have been much concerned with shock as a density dependent factor.

Bakken: I have lost only one squirrel from shock because I visited my traps frequently.

Marshall: I have had squirrels die frequently, even when the traps were visited every six hours.

Bakken: I visited mine every three hours at the most. I found a cemetery an excellent place to work. It was easy to make frequent visits to my traps.

Lwellyn: Is temperature an important factor?

Bakken: Yes, a very important factor.

Uhlig: In extensive forests I found 1-2% of squirrels going into shock but in small woodlots up to 20% died from shock.

Marshall: I had up to 50% of the animals in Georgia die from shock.

Clark: It may be a function of temperature and method of handling.

Mosby: What's the clinical symptom of shock?

Clark: The gross clinical symptoms of shock are few. Congestion of blood in the mesenteric and hepatic veins is one of the few consistent phenomena.

Mosby: We may have perhaps referred to shock but really had something else.

Lwellyn: I have found that leaving squirrels (in shock) out in the warm sun they frequently recover. Running traps twice a day and not leaving squirrels overnight reduces shock to a minimum.

Bakken: I have found squirrels entering traps after dark. I had to spring my traps in the evening.

Uhlig: Perhaps nocturnal movements are caused by human disturbance such as hunting.

Shorten: After 3 trap rounds a day, no captures were made after dark, in Britain.

Lwellyn: Have you tried control lighting?

Hoffman: The facilities needed are too great to be practical.

Flyger: On several occasions I had squirrels moult at odd times of the year when kept indoors under artificial lighting.

Uhlig: Do you think the bearing of young in Indiana was different than Illinois?

Hoffman: No, I don't.

Uhlig: Yes.