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ECOLOGY OF MELANISTIC GRAY SQUIRRELS (*Sciurus carolinensis*) AND FOX SQUIRRELS (*S. niger*) IN AN URBAN AREA

By

John George Fogl

A DISSERTATION

Submitted to
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ABSTRACT

ECOLOGY OF MELANISTIC GRAY SQUIRRELS
(*Sciurus carolinensis*) AND FOX SQUIRRELS
(*S. niger*) IN AN URBAN AREA

BY

John George Fogl

The ecology of an urban squirrel population was studied and compared with data on rural squirrel populations. The squirrel population in a 200 acre residential area of East Lansing, Michigan, was composed of fox squirrels (*Sciurus niger*) and the descendants of melanistic gray squirrels (*S. carolinensis*) introduced during the late 1950's and early 1960's. During the 36 month study (June 1977-May 1980), 128 squirrels (81 black and 47 fox) were individually marked with dye and observed for more than 4000 hours. An average of 1.25 feeders per acre were maintained by residents in the research area from which squirrels could supplement their natural food supply.

The distribution of black squirrels in the Greater Lansing area and factors affecting their rapid dispersal are discussed.

Compared to publications on rural gray and fox squirrel populations: 1) the studied urban squirrel densities were higher - winter densities ranged from 1.6-2.4 per acre and fall densities were believed to have been between 2.0-4.0 per acre; 2) average black squirrel litter size was larger (3.16 $\pm$ .16 young/litter), while average fox squirrel litter size was comparable (2.65 $\pm$ .16

young/litter); 3) daily activity levels of East Lansing squirrels were much higher throughout the year; 4) urban squirrel home ranges were smaller (5-10 acres) and showed no difference between males and females.

Road kills and cat predation were the major sources of squirrel mortality in the urban areas studied, though malnutrition and mange were suspected of contributing appreciably during severe winters.

Levels of interspecific aggression increased dramatically during winter, when most interactions occurred at the supplemental feeders. The black squirrels excelled at dominating these feeders and this was believed to have caused the observed weight gain in black squirrels and weight loss in fox squirrels during the Winter of 1979-80. Although the presence of a social heirarchy was not investigated, some form of a complex interspecific dominance heirarchy was suspected to exist.

Winter nesting aggregation size and tree species preference for nest location are investigated.

Recommendations for management and future research on urban squirrel populations was presented.

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INTRODUCTION

The urban environment is not one homogeneous entity, but rather a mixture of ecotypes. These areas can be roughly classified as those dominated by 1) the tall buildings and pavement of business, commercial and light industrial areas having limited green space, 2) the smoke-stacks, noise and debris of heavy industry having disturbed and polluted open areas containing little green space, or 3) the buildings and surrounding grounds of residential areas having varying amounts of green space. Within each of these ecotypes may be found green islands of parks and cemeteries. They are, for the most part, isolated pockets of the rural environment and contain wildlife populations which are only visited by humans and, therefore, only slightly influenced by the human presence.

Within the urban environment exists a number of animal species, invertebrate as well as vertebrate. Those species of greatest interest to the wildlife ecologist, and most often referred to as urban wildlife, are those which also exist in the rural environment and have adapted to the urban environment.

As noted by Edwards (1975:93), the wildlife species most likely to survive in the business and industrial areas of the urban environment would be birds, because winged creatures were most "efficient at tying together the far flung habitat elements" and were "also good for rising above the destructiveness of high density people, dogs and cats... there is no great future for mammalian wildlife in the city proper."

The urban sprawl exerienced by cities during the last 25-30 years has greatly increased the amount of rural and semi-natural land modified for human habitation and activity. Of the ecotypes in the urban environment, the residential area most nearly duplicates the rural environment, thereby making it the most amenable to occupation by rural mammalian wildlife species. The ubiquitous presence of humans and their activities influence this ecotype, the wildlife populations, and the human-wildlife relationship, thus making the urban wildlife populations unique from rural wildlife populations.

Human influence on wildlife in the residential ecotype can contribute to mortality through road kills, to vitality through feeding, and to diversity through the introduction of wildlife species. All of these interactions are illustrated by the history of the gray squirrel in Michigan and subsequent reintroduction of the black phase into a residential ecotype.

During the nineteenth century when most of Michigan was covered with forests, the gray squirrel (including the black phase) was present in large numbers along with the less common fox squirrel that was mostly confined to southwestern Michigan (D. Allen, 1942). Clearing the dense hardwood forests for lumber, firewood and agriculture eliminated much of the natural habitat of the gray squirrel and, with the development of agriculture and the near disappearance of the gray squirrel in the southern part of lower Michigan (some blacks and grays survived in the Detroit area[1]), the fox squirrels of southwestern Michigan apparently moved in. "In woodlots throughout the agricultural region, the fox squirrel found conditions similar in many respects to its former prairie-edge habitat. It extended its range, learned to eat corn, and prospered on soil that had previously nurtured dense forests and the gray squirrel" (D. Allen, 1943).

While the agricultural lands and woodlots of the countryside were better suited to the fox squirrel, increasingly dense tree growths in the wooded parks and residential areas of cities and villages soon became potential gray squirrel habitat. According to Johnson (1973), the black phase of the gray squirrel was introduced into Battle Creek in 1912 and soon became an abundant animal of the urban environment. In the 1940's, some of these Battle Creek black squirrels were trapped and introduced into the Kellogg Bird Sanctuary - Gull Lake area. Thereafter, it apparently became somewhat of a fad to transplant these attractive black rodents into urban environments. A number of southern Michigan cities followed this practice, including Marshall, Holland, Grand Haven and Port Huron (personal observations and personal communications from city officials).

In 1958, eight black squirrels from the Kellogg Biological Station at Gull Lake were released on the Michigan State University campus, with twelve more being set free in 1962 (Baker, 1973). These squirrels

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1. Personal communication from Mr. Henry Glowniak, naturalist, Belle Isle Nature Center, Detroit, and the Detroit Free Press, Detroit Magazine, Jan. 21, 1979, article written under the pseudonym of Barbara Miller.

apparently left the campus area shortly after release and occupied nearby East Lansing residential areas. By 1977, almost 20 years after their introduction, black squirrels had increased their distribution and population, to the point where the blacks comprised from 50-90% of the squirrels in many neighborhoods (personal observation). Lack of information on the resident fox squirrel population at the time of the black squirrel introduction makes it impossible to determine whether the blacks were replacing the fox squirrels or were only adding to it. It is known, however that by 1977 the black squirrels introduced into Marshall, Michigan, had totally replaced the resident fox squirrel population within the city limits.[2]

Investigations of squirrel populations in residential areas of East Lansing and in Toomey Woodlot, a 30-acre natural area situated among the farms on the southern part of Michigan State University, emphasized wildlife differences in rural and urban environments. An obvious difference was the close distance to which one could approach squirrels in residential areas. There also was an evident greater density of squirrels in residential areas. In the urban area, too, both black and fox squirrels were frequently observed at bird feeders. The additional food available during critical times of the year would seem to have probable impact on the behavior and population dynamics of urban squirrels.

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2. Personal communication from Mr. Bart Cook, Grounds Foreman, Department of Parks, Recreation and Cemetery, City of Marshall, Michigan. Verified by personal observation.

It was decided to conduct a study on the ecology of the black and fox squirrel populations in a residential area of East Lansing in order to :

1. determine the present distribution of black squirrels in the Greater Lansing area,
2. compare the behavior patterns and related biology of urban squirrels with similar data for rural squirrel populations, and
3. examine interspecific competition among the black and fox squirrels in East Lansing.

LITERATURE REVIEW

The literature rarely refers to the wildlife ecology of urban mammals. In a paper presented at the 32nd North American Wildlife Conference, Davey (1967:57) stated "there are few references in the literature relating to wildlife in urban areas. Wildlife Review, over some 30 years of publication, has yet to find and report papers related to desirable wildlife species in urban areas. The Journal of Wildlife Management Index similarly contains nothing on the subject." In 1969, the 34th North American Wildlife Conference theme was "Conservation in an Urbanizing Society," but failed to contain a single paper regarding urban wildlife. Not until the 1974 symposium on "Wildlife in an Urbanizing Environment" at the University of Massachusetts, Amherst, and the 1975 symposium on "Wildlife in Urban Canada" at the University of Guelph, Ontario, did urban wildlife research receive attention as an area of study within the field of wildlife ecology.

Prior to these symposia, interest in urban wildlife was expressed mostly in the areas of (1) the problems with wildlife in the city, (2) the need for and value of having wildlife within the urban environment, and (3) how urban planners and residents can manipulate the habitat to alter the species diversity in the urban environment.

Problems with Urban Wildlife

Concerning the problems caused by wildlife in the urban environment, Smith (1974) suggested they generally fell into six areas: structural damage, crop damage, ornamental plant and landscape damage, aesthetic degradation, human safety, and disease transmission. To keep these problems at a minimum, he concluded it must be realized that animals responded to favorable habitat conditions by increasing their numbers and we must therefore try to modify habitats so that there is the least amount of conflict, or at the least, realize that damage abatement may be necessary. In discussing the hazards of wildlife to aircraft, Solman (1974) also suggested ecological modification to make the airfield unattractive to birds as the basic way to minimize the conflict with wildlife.

After discussing the disease problems of urban wildlife, Karstad (1975) suggested that it may be preferable to live with the disease hazards and enjoy the esthetic benefits of having wildlife, rather than try to keep the wildlife out. He also suggested that wildlife in the city could be a useful indicator of problems in the environment. For example, the occurrence of salmonellosis in urban wildlife may indicate raw sewage was entering a stream. In connection with disease and parasites in urban wildlife, Locke (1974:111) concluded that "the public needs to be made aware of the causes of mortality among wildlife living in close proximity to human habitation so that fears based on ignorance can be eliminated and, when necessary, control or sanitation procedures can be undertaken to prevent human infection".

Excluding the many health-related studies on rats and mice, the only mammalian species causing problems in the urban environment were squirrels, feral dogs and coyotes. Flyger (1970) dismissed urban gray squirrels as insignificant hazards from a public health standpoint, but conceded their propensity for gnawing caused much damage to telephone cables and houses or buildings which they entered. They were also notorious for damaging gardens and ornamental trees and shrubs. Although feral dogs were not strictly a wildlife problem, they illustrated the problems involved in maintaining an unrestricted, large mammal commensal with man.

Beck (1971, 1973, 1974) conducted extensive studies on the ecology of urban dogs. He found little evidence that strays were an actively self-perpetuating population and hypothesized the stray population was maintained by continual recruitment from released or escaped pets. The readily available supplies of food and water in the city provided dogs, cats and rats nourishment and all seemed to tolerate each other's presence, sometimes being observed eating garbage within a foot of each other. Beck felt that dogs could be used as indicators of urban environmental degradation and could be correlated with trash and pest species. One of the ecological implications of a large population of feral dogs in the urban environment was the potential health hazard caused by the thousands of tons of excrement and hundreds of thousands of gallons of urine left on the streets each year. Besides diseases picked up by children playing in infected dirt, dogs feces was a major factor in the breeding of houseflies, which could then transmit

Salmonella from dogs to man. Also, rats have been observed feeding on dog feces and were most common in alleys with high fecal residues.

Leach and Hunt (1974) reviewed the problem of coyote control in the rural west, concentrating mainly on its history in California, and Gottschalk (1981) reported a number of documented attacks of coyotes upon humans in urban areas. The urban coyote was identified as a new dangerous breed which had lost its fear of humans. Los Angeles County authorities faced an unnaturally large population of coyotes, where the only "natural enemy" was the automobile. The presence and activities of human beings was identified as the major contributor to the coyote problem. Besides intentional feeding of coyotes by well-meaning suburbanites, coyotes also fed on garbage and dried dog and cat food, as well as on an occasional pet poodle or cat. The ubiquitous swimming pools served as water holes. Information on the population levels, reproductive success and movements were lacking in the literature, making it difficult to recommend management procedures.

Value of Urban Wildlife

Surveys have shown a strong desire among city dwellers for contact and experiences with wildlife. Dagg's (1970, 1974) surveys in Waterloo, Ontario, indicated most householders liked having birds, squirrels, chipmunks and rabbits on their property, but not other mammals because of the damage they caused. Dawson et al. (1978) found a relatively high awareness and interest in wildlife for most respondents in their Albany, New York, survey: 54% maintained one or more habitat improvements around their home, 73% participated in non-consumptive (photography, etc.) and 36% in consumptive (hunting, etc.) wildlife-related activities. In Taylor, Michigan, a suburb of Detroit, Cauley (1974) found that 76% of the people interviewed liked and enjoyed seeing wildlife on their property, only 4% disliked wild animals, and no one actively discouraged the presence of wildlife. Attempts to attract wildlife were made by 32% of the residents and 80% put food out for wildlife some time during the year. A survey of cemeteries in the Greater Boston area by Thomas and Dixon (1973) revealed they were being heavily utilized by urbanites for a number of outdoor recreational activities including some which were wildlife related. Davis (1974) stated that the National Wildlife Federation Backyard Wildlife Program demonstrated people's hunger for leadership in urban wildlife management on a small scale. Over a quarter million reprints were distributed concerning methods to attract wildlife into the backyard.

Others interested in urban wildlife have addressed the educational and political value of wildlife in the city. Euler (1975) suggested that the role of the Ontario Ministry of Natural Resources, Wildlife Branch, in managing urban and non-game wildlife was to educate the public toward a more realistic view of the natural world and make them aware of wildlife management practices. Howard (1974:17-18) stated that "man has a moral responsibility to manage nature once he has disrupted it" and "the essential need is for man to recognize that he is part of nature, and that he must meet nature at least halfway." DeGraaf and Thomas (1973) realized that an urban electorate uninformed about natural processes and resource problems could create problems for biologists and other resource managers. Dagg (1970) pointed out that urban public voting power could affect wildlife conservation throughout the world.

Perhaps the most thought provoking and controversial value of wildlife in the urban environment was the effect wildlife may have on the developmental biology of human children. Valerius Geist (1975) hypothesized that the retention of natural environments during the ontogeny of children was beneficial to them. He presented data from a number of studies on the phenotypic development of the brain and Intelligence Quotients in relation to environmental manipulation. Geist noted that "in its phenotypic development during ontogeny, an individual needs not only a nutrition that is excellent, but also a socially diverse and intellectually challenging milieu." He argued that "the availability of nature is an excellent prerequisite to high intellectual and physical development of humans during ontogeny, a prerequisite many middle- and upper-class families clearly are exposed to, since they reside more often than not close to or in areas with diverse plant and animal life... therefore a neglect to provide in urban areas rich natural environments in areas where people of low income are found reduces the potential of children found there to develop intellectually or physically to the same extent as children from economically more privileged parents." Conceding that "no one study demonstrates conclusively that retention of natural environments for the benefit of children during ontogeny is beneficial to them," he concluded "the circumstantial evidence makes such a conclusion all but inescapable."

Wildlife in the city could also influence the awareness of world wide environmental problems. Again Geist (1975) observed that "the stimulation of interest in natural events, objects and environments generates an interest in, appreciation of and ultimately respect for the land from which we derive our sustenance." He suggested that perhaps the best way to curtail the trend of environmental degradation would be to "provide in urban areas, where most of our citizens live, some islands of environments that support a rich plant and animal life. It stimulates persons, rouses curiosity and in the longrun helps to create a citizenry aware of the values of the land."

Urban Habitat Manipulation

Davey (1967:58) noted that "most sociologists, architects, landscape architects, and city planners today stress the importance of diversity in our cities... they visualize... a stabilized, self-restoring neighborhood and community - a climax city, in ecological terms... these urban-oriented professionals can use information on wildlife management." A number of problems with urban habitats which tended to decrease species diversity have been identified by biologists. Edwards (1975) noticed a definite need for a shrub layer in the urban forest, and Stearns (1967) felt that the small size and discontinuity of units, generally without corridors, and the absence of diversity were the major problems in urban wildlife habitat.

Geist (1975) suggested the protection of river flood plains as parks to increase the diversity of wildlife, and the building of highway underpasses where major animal trails cross to reduce highway wildlife kills in urban areas. Maffei's (1978) study showed that properly managed urban golf courses could supply the diversity of habitats necessary for survival of wildlife through the use of uncut fields, marshes and water hazards, high roughs, unmanaged fringe areas, coniferous and mixed hardwood stands, and the careful use of insecticides to minimize hazards to wildlife.

Whatever the specific improvements in urban habitat, Stearns (1967) observed that they must provide a variety of food sources such as annual and perennial plantings or planned neglect for regrowth of wild and weedy food plants, adequate water both summer and winter, adequate cover and travel corridors between habitat units such as conifer stands and unmowed grass areas, protection from humans as through the use of thorny shrub species and hidden fencing, and population control by predators, weather or other means to prevent habitat deterioration.

While an awareness of the need for and the value of having wildlife within the urban environment has been established, and the problems related to wildlife in the city have been discussed for some time, recommendations for managing those rural species drawn into urban areas by beneficial habitat manipulation have been based upon knowledge of rural populations. Maestro (1974) raised some questions about the applicability of knowledge on rural species to populations present in urban areas. "The home range requirements of most species have been documented in the 'wild', but can we consider these requirements to hold in an open-space system in the middle of a 10,000 acre newtown? ...what are the effects of human disturbance, noise, domestic pets, barriers to movement patterns such as roads, and narrow connecting links in the open-space system? ...how do their home range and habitat requirements compare to their counterparts in the wild?". Geis (1975:83) also noted that "the usual approaches to enhancing wildlife populations based on experience in rural areas often do not apply in urban situations... further research on factors defining urban wildlife populations and their management is needed."

Urban Wildlife Studies

Studies on bird populations in urban areas are common compared to mammal studies. Thomas and DeGraaf (1975) briefly mentioned the essentials of seventeen urban bird studies, but only noted three authors who had studied gray squirrels and raccoons in urban areas. A few other urban mammal studies have since been reported.

Beck's (1971, 1973, 1974) study on feral dogs, though an excellent urban ecology study, may not be considered wildlife research by some, in that it is not on a "wild" rural species which has adapted to the urban environment.

Ryan and Larson (1976) studied chipmunks in a residential environment near Amherst, Massachusetts. They found chipmunks heavily utilized man-supplied food sources, so much so that the normal period of chipmunk inactivity during late July and August was clearly lacking. They concluded that "artificial feeding and physical features in urban residential grounds appear to influence the seasonal pattern and spatial distribution of eastern chipmunk activity".

In their study of an urban deer herd in Winnipeg, Manitoba, Shoesmith and Koonz (1977) noted that over a half million people and 200 white-tailed deer cohabitated in the greater Winnipeg area. While the deer herd was flourishing, the available habitat, largely private land, was dwindling. The deer herd existed in a number of small concentrations closely associated with parks or wooded areas, of which the Charleswood deer herd was the largest concentration and the one most intensively studied. The Charleswood deer herd was found to be largely sedentary, marked individuals having "all been re-observed or recovered within the city limits and within 2-3 km of their initial capture site. Man-made barriers such as fences, buildings and heavily used streets probably prevent much exchange of deer" with other nearby areas. The densities of city deer were found to be as high as or higher than densities anywhere in Manitoba. One of the major reasons for this was the close association of winter cover to readily accessible food sources. Native foods were "not present in sufficient quantities to support the present deer herd if they had to rely on native foods alone." During winter the deer relied mostly on "sugar beet tailings left in fields, waste hay and grain around riding stables, waste hay at a garbage dump and concentrated alfalfa pellets and powder near a processing plant". The greatest single mortality factor was car kills with an average of 27 deer being killed each year on city streets in Charleswood. Dogs, harassment by people, illegal shooting, parasites and diseases accounted for some mortality, but none had a significant influence on the base population. The researchers concluded that deer had "demonstrated its ability to quickly recover from the effects of severe winter conditions, to adjust to diminishing available habitat and to tolerate human pressure".

Studies on urban raccoon populations have been conducted by Schinner and Cauley (1973, 1974) in Clifton, Ohio (a suburb of Cincinnati), Cauley (1974) in Taylor, Michigan, and Hoffman and Gottschang (1977) in Glendale, Ohio (another suburb of Cincinnati). A significant difference in density of raccoons in urban and rural areas was apparent. Maximum densities in rural areas ranged from one raccoon per 11.7-16.2 acres, while Schinner and Cauley reported a range of 1/1.4-23 acres in Clifton and Hoffman and Gottschang reported 1/3.6 acres (1/1.46 ha) in Glendale. The great range in the Clifton population densities was due to an outbreak of canine distemper which reduced population estimates from 145 in 1968 to 51 in 1969. While this was the major population limiting factor during the study, dog and car kills and illegal hunting were also recorded as mortality sources.

Hoffman and Gottschang found that permanent water did not seem as important in the distribution of Glendale raccoons as the presence of supplemental foods, such as garbage and handouts by residents. Perhaps more important to the distribution of raccoons would be the presence of high density housing. Cauley reported no raccoon captures in densely housed areas in Taylor and attributed the lack of raccoons to the backyards being enclosed with a four foot chain-link fence, the presence of many dogs kept out-of-doors, little vegetative cover and a total lack of natural den sities.

The home ranges were found to be much smaller for urban raccoons (average of 20.6 acres in Clifton and 12.75 acres in Glendale) than reported for rural raccoon populations (a range of 27-500 acres). Schinner and Cauley noted that movements of urban raccoons were restricted to travel between den sites and feeding areas and did not show the random foraging characteristic of non-urban raccoons. Hoffman and Gottschang also observed extreme linearity of home range, averaging 5.5 times longer than wide in Glendale, and attributed it to the readily available food supply and the effect of the linear urban habitat. Not only did the raccoons adapt their travel routes to linear man-made structures such as fence lines, storm drains and street culverts, but they also used sewers, refuse dumps, attics, garages and chimneys as den sites. Cauley also reported the use of ground hog dens and outbuildings as den sites in Taylor.

Opossums were the only potential competitors of raccoons in urban areas to be reported (Hoffman and Gottschang).

These studies have indicated that the presence of supplemental feeding in the urban environment, whether intentional or accidentally provided as garbage or waste, can influence seasonal and/or daily activity and abundance of animals. The availability of food was probably the single most important factor affecting the spatial distribution, home ranges and population dynamics of urban wildlife. New mortality sources were introduced in the urban environment, while those of major importance in rural environments played a lesser role.

Squirrel studies within the urban environment have been conducted mostly in parks and cemeteries which were insulated from the influence of humans in nearby residential areas. These cemetery and park squirrel populations were actually in a habitat more closely related to rural environments and could not be expected to display all the characteristics of populations subjected to the full impact of human presence and activities in the urban environment.

Bakken (1952) studied the interrelationships of gray and fox squirrels in an 80 acre cemetery in Madison, Wisconsin, in which "the population was unfed, naturally occurring and relatively undisturbed." Robinson and Cowan (1954) studied a population of gray squirrels (mostly melanistic phase) which had been introduced into an isolated forest and park area of 1000 acres. The influence of human activity was minimal in their 60 acre study area and only about a third of the squirrels made some use of "hand-outs" from park visitors. Flyger's (1955, 1959, 1960, 1970, 1974) reports on gray squirrels have been referred to as being urban or suburban, but the squirrel populations studied were actually in two 10 acre woodlots relatively isolated from other woodlots. The woodlots were about one-third of a mile apart and were on the enclosed grounds of a hospital and were not disturbed by human activities. A portion of each woodlot had also been lightly grazed.

Hathaway (1973) studied gray squirrels in a 733 acre cemetery in a large unidentified midwest city. Selecting "a small portion in the middle of the oldest section of the cemetery in which to conduct the study," he noted that the squirrels were "not excited and endangered by the dogs, children, and high-speed cars that may plague squirrels in other sections of the city." Thompson (1977a, 1977b, 1978a, 1978b, 1980) studied a gray squirrel population in a 72 acre (28.7 ha) section of a cemetery in Toronto, Ontario. He noted that "although the squirrels in the cemetery were accustomed to the activity and presence of people, they were not as tame as those found in the surrounding residential areas... None of the squirrels sought or received 'handouts' from the cemetery visitors. Not one case was noted of artificial feeding of the squirrels by people visiting the cemetery," (1980:702).

The only squirrel study to be conducted in the residential ecotype was on fox squirrels by Cauley (1974) in Taylor, Michigan. He noted the abundance of food, a reduced home range (10.3 acres for juveniles and 5.3 acres for adults) and extensive use of the non-natural environment (travel along telephone cables and denning in chimneys and attics). This study was actually on four different species (cardinal, blue jay, raccoon and fox squirrel) within the urban environment and therefore supplied only limited information on squirrels.

While the cemetery and park studies on squirrels reported some of the differences observed in other species adapted to urban areas, no in-depth study has to date been conducted on squirrels in the urban environment. This East Lansing black and fox squirrel study is believed to be the first to do so.

METHODS AND PROCEDURES

Study Area

East Lansing is adjacent to the capital city of Michigan and is located in Ingham County in the south-central part of the state. It is mainly a residential community with a small downtown business district across from the Michigan State University campus. An aerial photograph taken on August 21, 1978 (Figure 1) and a street map of East Lansing (Figure 2) covering the same area show the residential nature of the town, degree of canopy cover and the location of the research area. The study site is in an older part of town where the trees have developed such large crowns that the streets are hidden from view in the aerial photograph. A different situation is obvious to the northeast of the research area where the streets of the newer subdivision are quite prominent.

The research area is bounded by Saginaw Street (M-78, Temporary I-69) on the north, Harrison Avenue on the west, Abbott Road on the east and Grand River Avenue (M-43) on the south. The area is gently rolling with elevations ranging between 840-870 feet. Covering a little more than 200 acres, the research area is 4% business district, 8% open park area (including a school building and playground) and 88% residential (20% occupied by paved streets and 68% being lots with

Figure 1. Aerial photograph of East Lansing and part of the Michigan State University campus showing the degree of tree canopy present in residential areas. The squirrel research area is outlined.

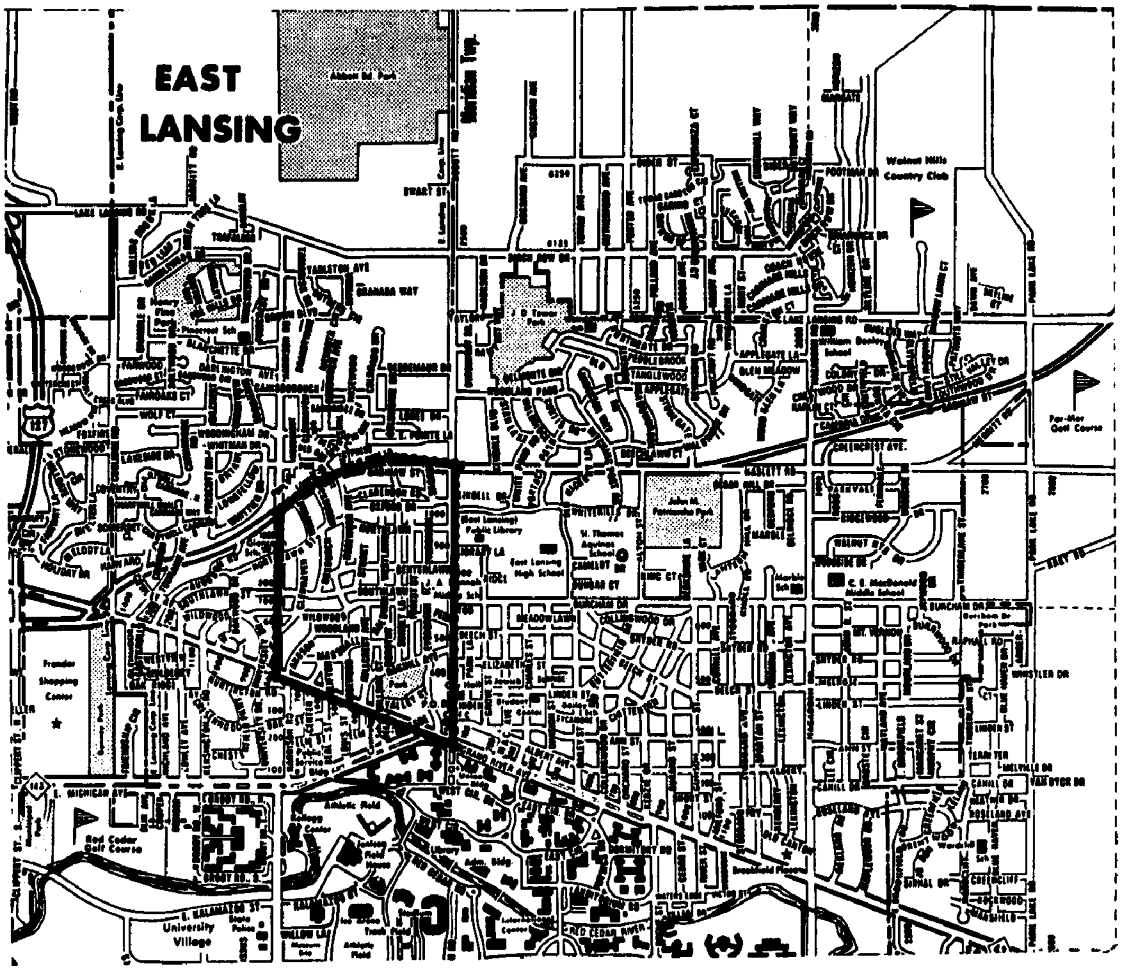


Figure 2. Street map of the same area of East Lansing and Michigan State University as shown in Figure 1.

houses). While the lots in some parts of the research area are about an acre in size, other parts of the area have houses very close together. A total of 598 houses are located in the residential area for an average density of about three houses per acre.

The planting of trees along city streets by city planners many years ago and the preservation of naturally occurring large trees by housing developers has had two important results: 1) the domination of some rather large areas by two or three species of the same genus, and 2) the presence of many large trees forming a moderately dense canopy covering the entire residential area in the research area. The dominant tree regions (Figure 3) are:

a. maple region (about 90 acres) composed of silver (*Acer saccharinum*), sugar (*A. saccharum*) and Norway (*A. platanoides*) maples - average d.b.h. = 22.5".

b. oak region (about 45 acres) composed of red, black and white oaks (*Quercus* spp) - average d.b.h. = 21.5".

c. elm region (about 45 acres) composed of american elm (*Ulmus americana*) - average d.b.h. = 22.76".

d. hickory region (about 5 acres) composed of shagbark hickory (*Carya ovata*) - average d.b.h. = 13.65".

Most of the residents within the research area are associated with Michigan State University either in a maintenance-clerical or administrative-professional capacity, or as students. Their cooperation was solicited by distributing a research explanation sheet (Appendix A) to as many of them as possible. Many hours were spent socializing with the residents and informing them of aspects of

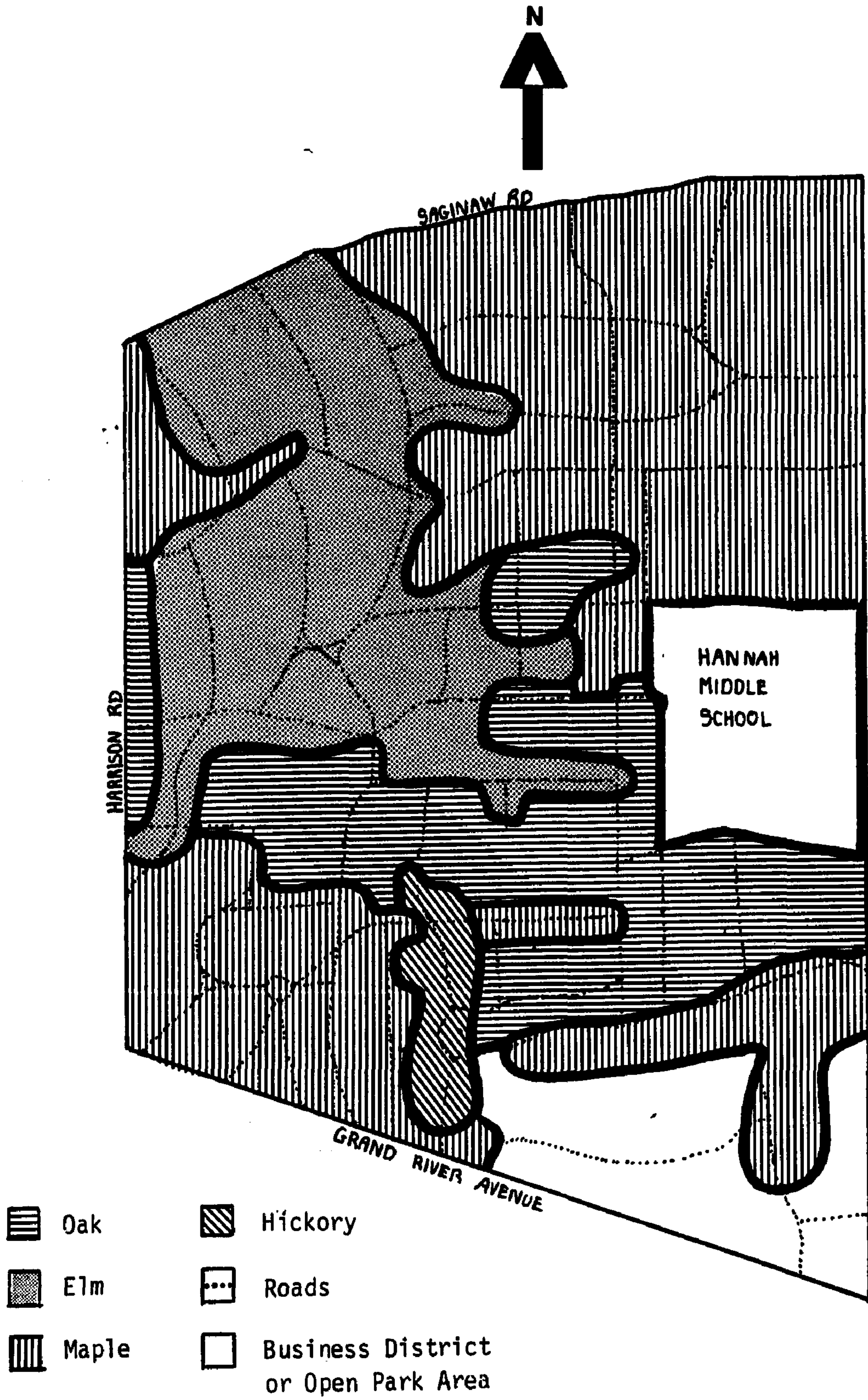


Figure 3. Dominant tree regions of the 200 acre squirrel research area in East Lansing, Michigan.

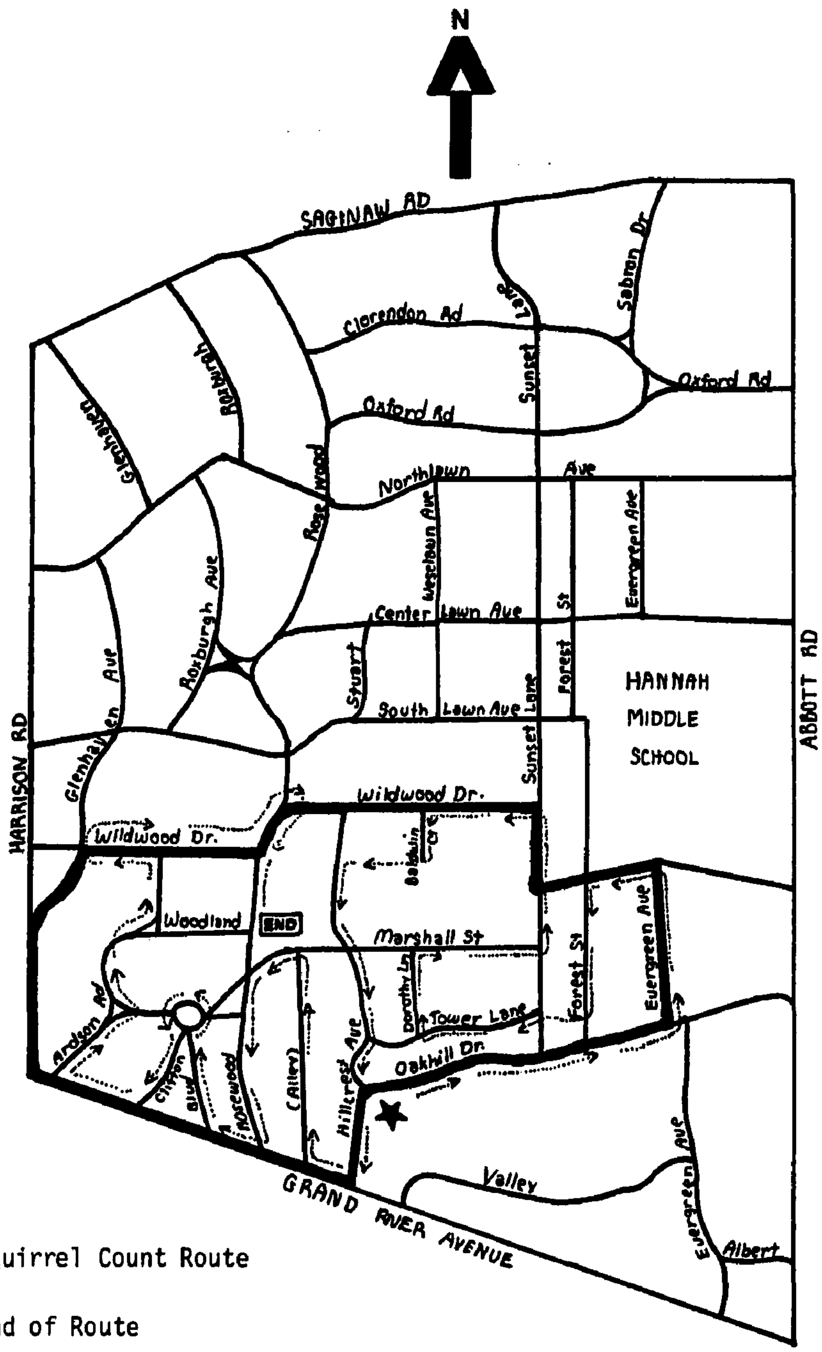
squirrel biology, and the importance of their assistance and goodwill to the success of the study cannot be overemphasized.

Trapping and Marking

To study the behavioral interactions and related biology of the black and fox squirrel populations, it was necessary to capture and mark them for individual recognition. A 50 acre area in the southern part of the research area (Figure 4) was selected as the trapping area. This area included parts of each of the dominant tree regions and was believed to be representative of the entire area.

Wooden box traps (Figure 5a) were used for capturing squirrels because they would provide a greater degree of insulation from the natural elements than would open wire cages. Fifteen traps were built after that described in Wildlife Management Techniques Manual, 4th Edition (Schemnitz, 1980:64). The traps were baited with cracked corn, sunflower seeds, and/or acorns and hickory nuts. To reduce the likelihood of mortalities in the traps, they were checked twice a day - at midday and shortly before sunset. Since squirrels molt over summer, trapping was confined mainly to fall and winter to mark again individuals captured the previous year and also to mark new juveniles and subadults.

To remove trapped squirrels from the box trap and restrain them for identification and marking, (Figures 5b and 5c), two handling devices (one for adult fox squirrels and the other for the smaller black squirrels and young fox squirrels) shaped like funnels were



Squirrel Count Route

End of Route

Beginning of Route

Trapping Area Boundary

Figure 4. Location of the 50 acre trapping area within the East Lansing, Michigan, squirrel research area. Route followed for squirrel population counts is indicated.

Figure 5. Equipment and procedure used in the East Lansing, Michigan, squirrel study (June 1977 - May 1980).

(a) Box traps, handling cones, weighing and tagging equipment, and field identification cards used during squirrel study.

(b) Locking trap door open so trapped squirrel can enter handling cone.

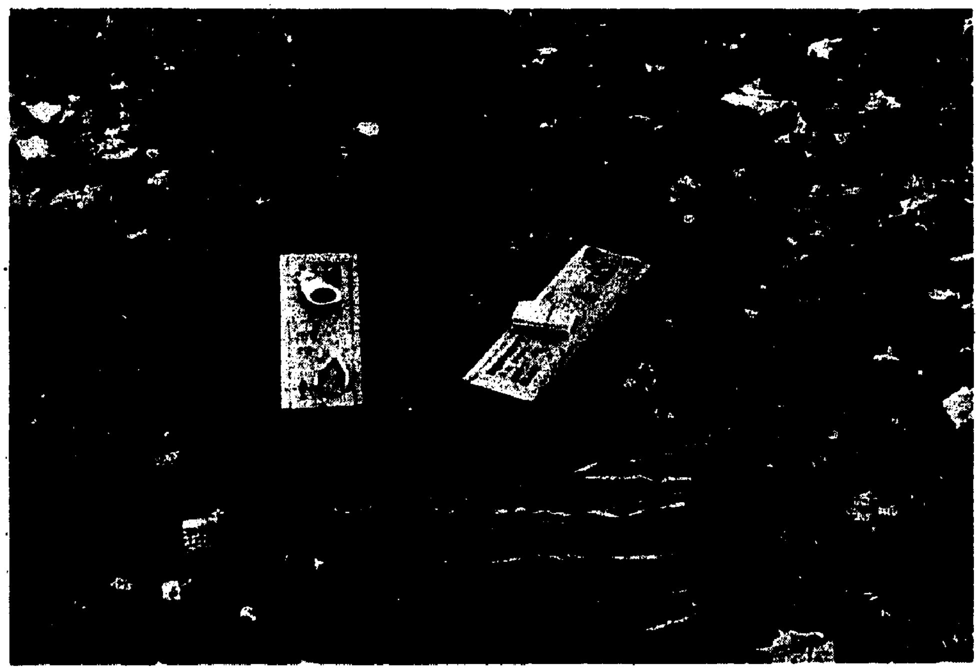


Figure 5 (a).

Figure 5 (b).

Figure 5 (cont'd.)

(c) Blowing in screened end of trap to encourage squirrel to leave trap.

(d) Nose of black squirrel is protected by foam padding at end of handling cone while being eat-tagged.

Figure 5 (c).

Figure 5 (d).

Figure 5 (cont'd.)

(e) Bleaching black squirrel with Q-tips and Helene Curtis "Ready-Set-Glow" bleaching solution.

(f) Release of fox squirrel marked on right side with Nyanzol-D.

Figure 5 (e).

Figure 5 (f).

Figure 5 (cont'd.)

(g) Black squirrel bleached on head and left side is easy to identify from a distance.

(h) Black squirrel calmly waiting in handling cone while bleach solution begins to take effect.

Figure 5 (g).

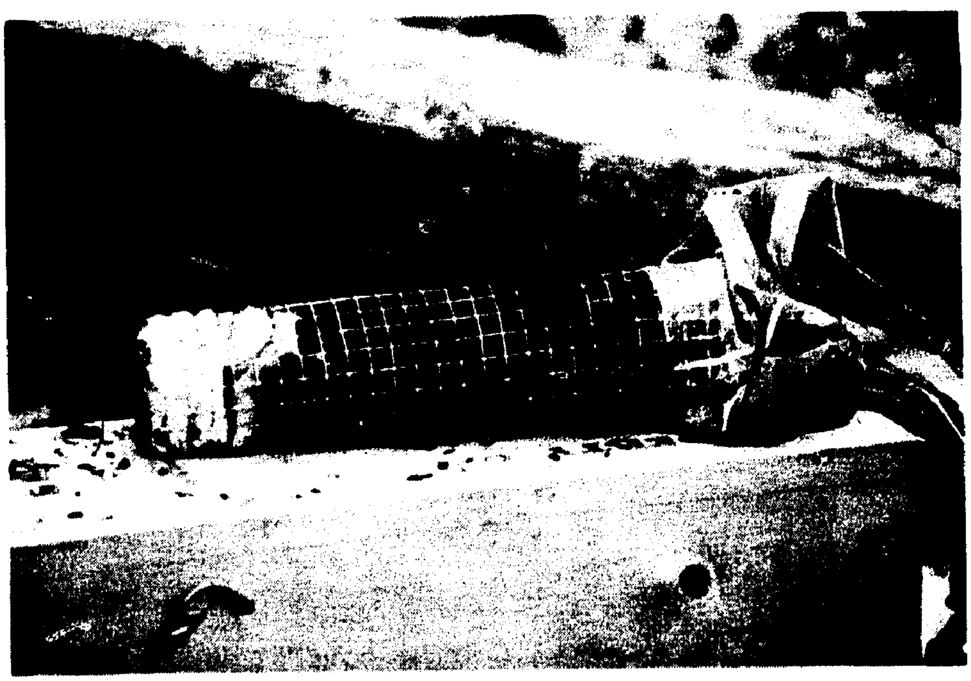


Figure 5 (h).

constructed. The wire cone end was made of one half inch mesh wire rolled to fit snuggly around a stuffed fox squirrel, and another made to fit around a stuffed black squirrel. The mesh wire of one end was cut and folded in, and all overlapping seams were sewn securely together with soft copper wire woven through the mesh wire. One to two inches of foam padding was stuffed inside against this end to protect the squirrel's nose from injury. A canvas funnel about 24 inches long was made with one end small enough to be hand sewn to the open end of the mesh wire cone. The other end, with an elastic band sewn in, was large enough to fit snuggly over the end of a box trap.

Two sets (one for each ear) of numbered monel metal size 1 ear tags and a pair of size 1 pliers were obtained from the National Band and Tag Company of Newport, Kentucky, and used to permanently identify captured squirrels (Figure 5d).

As a short term method for easier identification, fox and gray squirrels were dyed purple-black with Nyanzol-D (Figure 5f) obtained from J. Belmar Inc., North Andover, Massachusetts. Since Nyanzol-D would not show up on their fur, black squirrels were bleached orange-blonde with Helene Curtis "Ready-Set-Glow" hair frosting mixture (Figure 5 e-g). In place of the solution provided with the Helene Curtis kit, a solution of 240 ml of 15% hydrogen peroxide and 10 ml of concentrated ammonium hydroxide (58%) was added to the frosting powder to increase the speed of bleaching. (A 30% hydrogen peroxide solution was first tried, but resulted in too much skin irritation and subsequent shedding of fur by bleached squirrels.) After applying the bleach or dye with Q-tips, the canvas portion of the funnel was folded over the squirrel in the cone to reduce stressing the squirrel while it sat for about five minutes for the bleach or dye to take effect (Figure 5 h). (If released immediately after marking, the squirrels had the habit of licking off the solution before it could thoroughly affect the fur). When not being used in the field, the bleaching solution was stored in the refrigerator to extend the effective life of the hydrogen peroxide. This procedure was not needed for the Nyanzol-D.

A system for identifying individual squirrels by body markings was devised in which the squirrel body was divided into twelve distinct regions: right shoulder, left shoulder, head and neck, right side, left side, mid-back, right flank, left flank, rump, tail base, mid-tail and tail tip. By marking each squirrel with a combination of one, two or three body regions, hundreds of squirrels could easily be individually identified at a distance with binoculars. Since fox and black squirrels were marked different colors, the same body region combinations could be used twice, thereby doubling the number of squirrels that could be marked.

Edge-punched cards after that described in Wildlife Management Techniques Manual, 4th Edition (Schemnitz, 1980:46) were used as field identification cards, except that 3x5 index cards were used instead of keysort cards (Figure 6). Immediately after a squirrel had been captured and marked, the appropriate holes were notched for the species, sex and body regions marked. Ear tag number was noted and such things as changes in body markings due to loss or regrowth of fur,

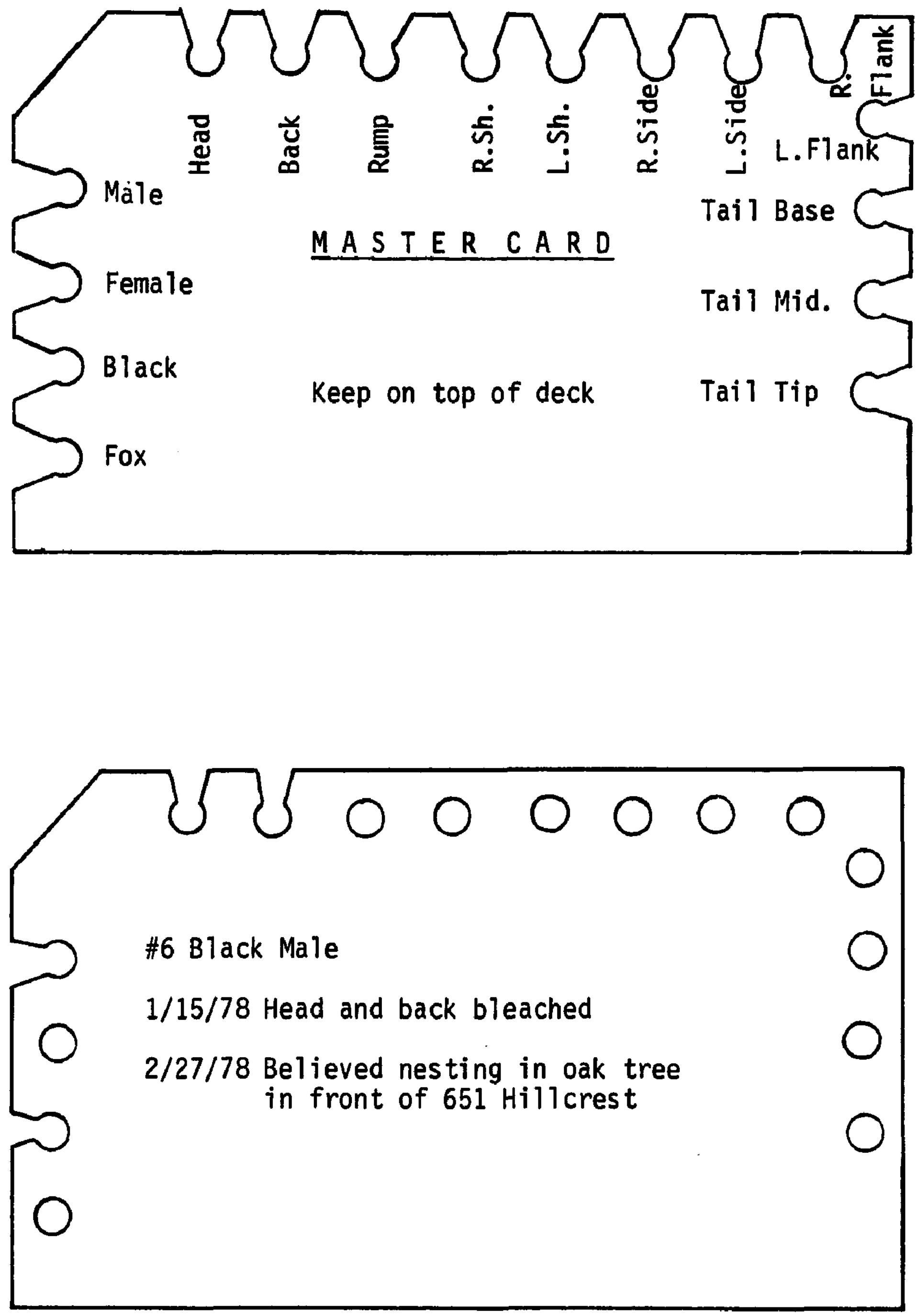


Figure 6. Edge-punched squirrel indentification cards used for East Lansing, Michigan, squirrel study.

pregnant or lactating condition, or information on nest locations were recorded under remarks. The pack of cards of all living marked squirrels (cards for recovered dead squirrels were removed) were always carried in the pocket while in the field, along with a short nail to serve as the card extractor.

Field Observations

All field observations were recorded on a portable cassette tape recorder and later transferred to 5x8 index cards. Tours through the research area by foot or bicycle were made under all weather conditions at least three times during each month for each two hour period of daylight. During the 36 months of the study, some observations of the squirrels were made almost every day. Over 4000 hours were spent gathering data, averaging about 30 hours/week.

During a tour of the research area, the identification number and/or species of observed squirrels were recorded along with the time, date, location and activity in which the squirrels were engaged. Incidental observations were also recorded while I was engaged in other research activities in the area. Such activities involved mapping dominant tree regions and the distribution of supplemental feeders or overwinter leafnests, checking traps and marking or weighing squirrels, conducting squirrel counts for population estimates, touring the area for spring litter counts or squirrel mortality recovery, gathering fall mast samples or observing feeding on natural food sources or at supplemental feeders, and determining the number of squirrels in a winter nesting aggregation.

Distribution of Black Squirrels

A preliminary survey conducted in the spring of 1977 revealed that most of the black squirrels were rather continuously distributed throughout the East Lansing area. However, a number of discontinuous clumps of black squirrels were located or reported in woodlots and neighborhoods a good distance from the East Lansing population of black squirrels. To determine the boundaries of the main body of the black squirrel population and also to locate isolated groups of black squirrels in the Greater Lansing area, a news release about the black squirrel study was prepared by the Michigan State University Office of Information Services (Appendix B). This newspaper release requested information from area residents about the presence of black squirrels in their neighborhoods. Publication of this article in local newspapers and an appearance on a local radio station (WKAR) talk show resulted in many letters and phone calls from interested individuals. Each lead was followed by a discussion with the resident to determine when the black squirrels first appeared in the neighborhood and approximately what portion of the present squirrel population was black. The presence of black squirrels in all reported neighborhoods was later verified by field observation. Reports of black squirrels being present on parts of the Michigan State University campus north of the Red Cedar River were investigated by periodic systematic tours through this area and also through the Sanford Natural Area on the south side of the river.

Population

Estimates

The composition of the squirrel population was measured each fall and winter. Squirrel counting walks (tagged and untagged, black and fox squirrels) were conducted through the trapping area following a predetermined course (Figure 3) that would minimize the likelihood of counting the same squirrel twice. The walks were taken during peak squirrel activity time in the morning on sunny and mild days to increase the probability of obtaining a count which accurately represented the true population compositon. Population estimates were made using Bailey's modified formula of the Petersen estimate (Begon, 1979:7):

$$\hat{N} = \frac{r(n+1)}{(m+1)}$$

where n is the total number of squirrels observed, r is the number of marked squirrels in the population, and m is the number of marked squirrels observed. The formula for the standard error of Bailey's estimate is:

$$SE_{\hat{N}} = \sqrt{\frac{r^2(n+1)(n-m)}{(m+1)^2(m+2)}}$$

Natality

Natality was measured by determining the size of the litters as they emerged from the nest during daily morning tours of the entire research area in April and May. Dates of nest-leaving were noted for marked females with litters the first day they were seen. Unmarked females with litters were also noted as to location and probable leafnest site. Any unmarked females with litters observed in the same general area on subsequent days were disregarded and considered as having been already recorded, unless the female and litter could definitely be identified by different body markings or coloration. To avoid double-counting, litters appearing during the summer and fall were recorded only when the identity of the female and litter was definite. Since fur was molted during this time, very few females could be definitely identified and thus few litters were recorded.

Mortality

Mortality was measured by making evening tours of research area roads to recover squirrels killed by cars. Information was also obtained from residents regarding any squirrel mortality by household pets they observed, or by any other predators known to be present in the area. Residents also assisted by recovering squirrel kills for the study. The presence of diseases in the squirrel population was limited to noting the occurrence of ectoparasite infestations on handled or observed individuals.

Movements

Daily Activity

Seasonal differences in the daily activity patterns of black and fox squirrels were determined in spring (March, April and May), summer (June, July and August), fall (September, October and November), and winter (December, January and February). At the end of the study, data from all three years were combined for each of the four seasons (i.e., daily activity patterns for each season was actually a total of nine months of observations). The daylight hours were divided into two hour time periods (before 7 AM, 7-9 AM, 9-11 AM, 11 AM-1 PM, 1-3 PM, 3-5 PM, and after 5 PM). Periods of time spent in the field making tours of the research area or conducting routine activities associated with the study were considered observation periods during which squirrels could potentially be observed. Observation periods varied in length and could include a number of daylight time periods. For example, observations made from 7:30 AM to 2:30 PM would count as observation periods in the time periods of 7-9 AM, 9-11 AM, 11 AM-1 PM and 1-3 PM, or a total of four observation periods). While the number of observation periods during each of the daylight time periods fluctuated each month, the total number of observation periods during each daylight time period were comparable, season to season, when totaled for the entire study. (The only exception was during winter when the early morning and late evening time periods were dark and had no observed squirrel activity). The average number of squirrels observed during each observation period of each daylight time period was used to plot the daily activity pattern for each season.

Home Range

To determine the minimum home ranges of black and fox squirrels, the locations of each marked squirrel observed while making tours of the research area or conducting routine activities associated with the study were plotted on scaled down maps of the research area. To obtain an accurate representation of the area utilized throughout the year, only those individuals captured and/or observed at least five times during each season were used.

Food Availability

Food available to the squirrels consisted of that naturally occurring on vegetation in the area and that supplied by residents at supplemental feeders. Observations were made on the squirrels' feeding habits to ascertain which foods were most heavily used during various times of the year. Since the mast crop is the major natural food source available to squirrels in the fall and through much of the winter, measurements of the mast abundance were made. Each fall, three 1 m^2 samples were gathered under the same randomly selected oak, hickory, maple and walnut trees. The distribution of supplemental feeders was mapped and observations made on their use by squirrels to determine the squirrels' use of them as a food source during winter.

Interspecific Aggressive Behavior

The aggressive interactions between black and fox squirrels were carefully recorded. The unit measuring aggressive interactions was the "encounter," defined as the approach of two individuals near enough to each other so as to produce a behavioral response. Encounters were classified into four types, based on the severity of the interaction:

1. Tolerance - each squirrel seemed aware of the other's proximity but did nothing to cause the other to move farther away
2. Mild Aggression - one squirrel chattered softly and/or flicked its tail, causing the second squirrel to move away

3. Moderate Aggression - one squirrel chattered and flicked its tail and/or made a short rushing charge (less than five feet) causing the second squirrel to move away

4. Severe Aggression - much chattering and/or tail flicking and a long chase (over five feet) by one squirrel causing the second squirrel to move away.

An index of aggression was computed using the following ratings:

tolerance = 0

mild aggression = 1

moderate aggression = 2

severe aggression = 3

Weather and Winter Weight Fluctuations

Weather data were obtained from the Lansing Weather Bureau for the months of November through March for the Winters of 1977-78, 1978-79, and 1979-80 to document the severity of winters during the study. Special attention was given to those factors which put physiological stress upon the squirrels, such as measurements on the severity of the cold, amounts of snowfall and quantity of snowcover on the ground.

From October 27, 1979 to February 22, 1980, intensive trapping and weighing of squirrels was conducted to measure the weight fluctuations experienced during this most stressful time of the year for the squirrels. Data obtained would be used as an indirect reflection of the physiological condition of the individuals handled.

Nests

With relatively few dens available to the squirrels (old trees with many hollow cavities were often considered safety hazards in the urban areas and therefore cut down), leafnests were the most common form of nesting. (A few squirrels nested in homes, but they were often quickly trapped out by the residents). Since winter is the easiest time to locate leaf nests and dens and also to differentiate between abandoned and maintained nests, the location of overwintering leaf nests and the species of trees they were in were mapped during the Winters of 1978-79 and 1979-80. The distribution of leaf nests was used to determine whether the squirrels preferred nesting in one species of tree or in one of the dominant tree regions.

The sizes of winter nest aggregations were determined based on the following observation. When nesting in groups during winter, a squirrel often hesitated at the nest entrance and exchanged some muted calls with any occupants of the nest (this calling has also been observed by Bakken, 1959:403). After entering the nest, this individual and the other occupants usually emerged and ran around the tree for a few minutes, then all would reenter the nest for the night. Squirrels entering a nest without hesitating to call and not reemerging later, were considered to be nesting alone. On January and February evenings (about 5-6 PM) during all three winters of the study, the last squirrel released from the traps was followed to its nest to determine how many individuals were nesting together. The data were compiled for each winter to determine whether there was a difference between black and fox squirrels in the average winter nesting aggregation size.

Interactions with People

Impromptu discussions with residents in the research area were often used to obtain their opinions on the introduction of black squirrels into East Lansing, how black squirrels' behavior compared with that of the fox squirrels, and also anecdotes concerning problems with and the behavior of squirrels. The opinions of residents outside the research area who responded to the newspaper articles or radio interview were also obtained when they were interviewed about the presence of black squirrels in their neighborhoods.

RESULTS

Distribution of Black Squirrels

The area occupied by black squirrels, as of fall 1981, included the major portion in East Lansing (Figure 7) and eleven isolated populations located throughout the Greater Lansing area (Figure 8).

Black squirrels were common throughout the older residential areas of East Lansing from Park Lake Road on the east to Frandor Shopping Center on the west. The presence of the Shopping Center and the superhighways (US 127 and I-496) appeared to have impeded further spreading to the west. While black squirrels were known to be present north of Saginaw Street between Coolidge and Abbott Roads, the extent of their penetration into the newer housing developments there was unknown. Not observed to the north of Towar Park, black squirrels were found as far northeast as Walnut Hills Country Club. Their presence in the new subdivisions between these points was not ascertained. Only in the last few years was there any movement of black squirrels to the south of town. They were common near Red Cedar School and some were seen along the Red Cedar River near University Village. Two black squirrels were reported near the Michigan State University baseball diamond in the trees lining the Red Cedar River. In the Fall of 1980, a lone black squirrel was nesting in the sugar maple west of Cowles

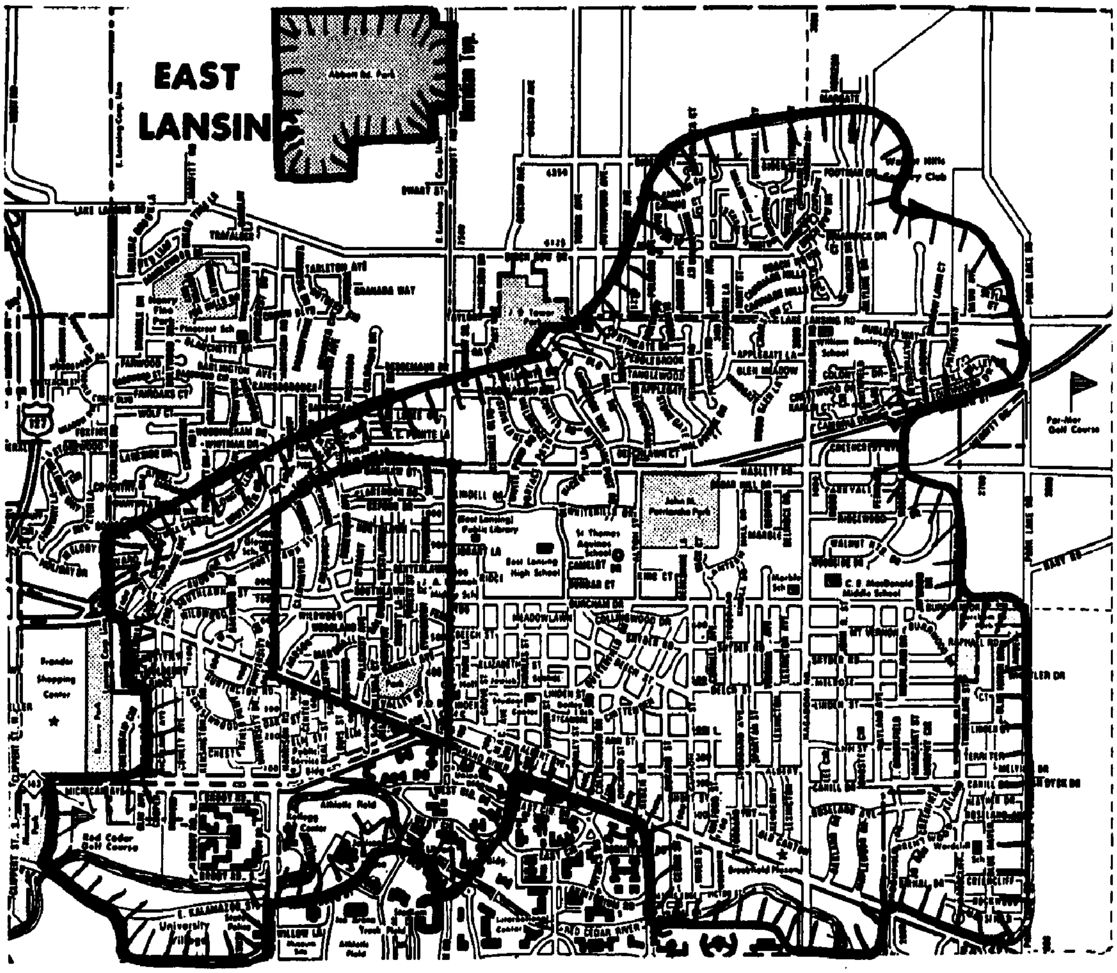


Figure 7. Distribution of black squirrels in the East Lansing, Michigan, area as of fall 1981. Isolated population of black squirrels in Abbott Road Park also indicated.

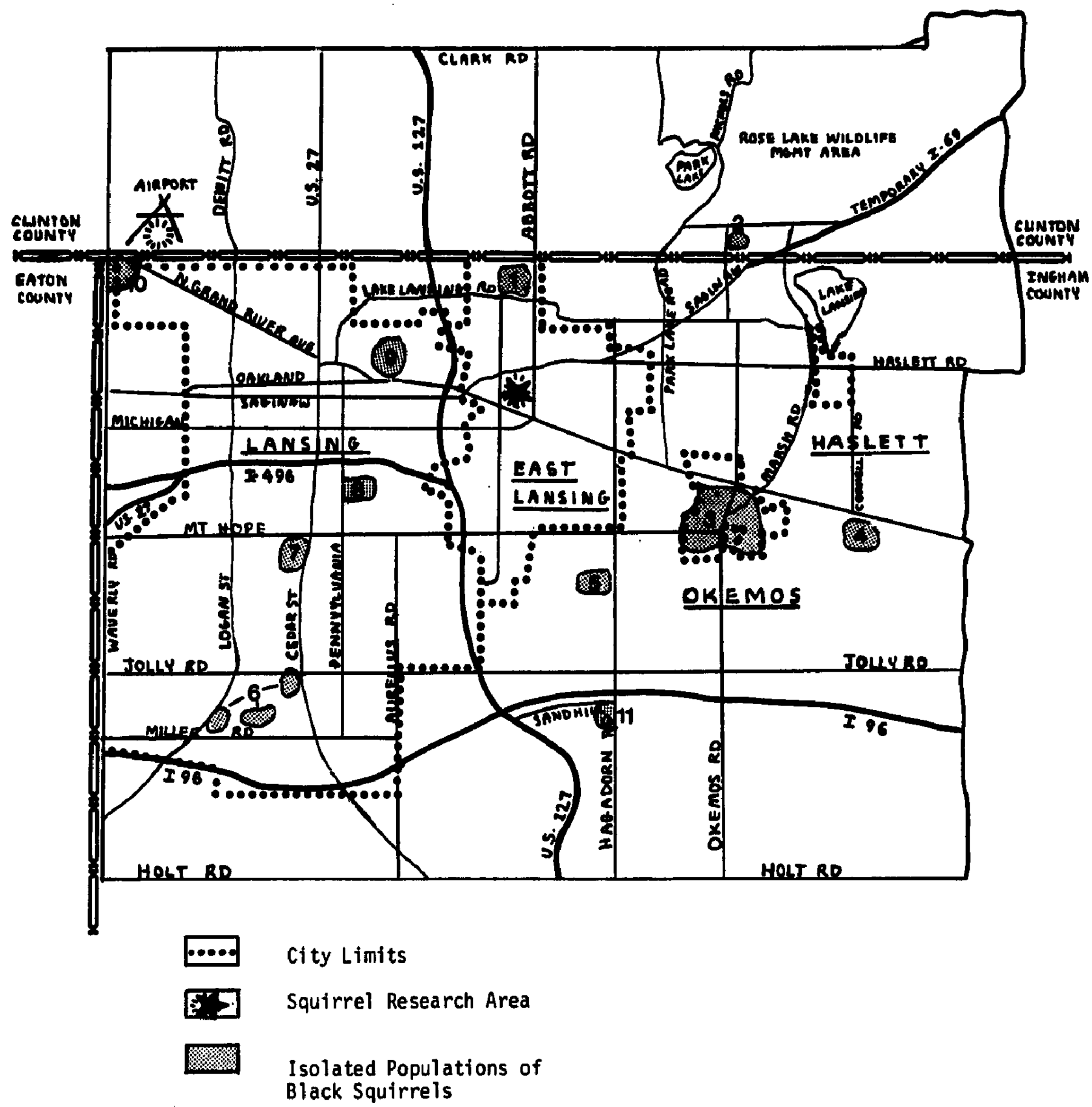


Figure 8. Locations of the eleven isolated populations of black squirrels discovered in the Greater Lansing, Michigan area, as of fall 1981.

House and was frequently observed near Beaumount Tower. By the Fall of 1981, three black squirrels were on the north campus and a fourth was later observed across the library bridge near the stadium. The first black squirrel in Sanford Natural Area was observed during the Fall of 1978 and by the Fall of 1981 at least five were in the preserve.

Below are the locations and descriptions of the eleven isolated populations of black squirrels discovered in this study:

1. Abbott Road Park - unknown number of black squirrels released by agents of the Ingham County Animal Control Department.
2. 16961 S. Nichols Road (1/2 mile north of the Clinton County line) - two black squirrels first appeared in late spring 1981 in the yard of Ted and Julie Wycoff.
3. City of Okemos - a large population established south of Grand River Avenue for at least five years.
4. Grand River Avenue and Cornell Road, south of Ethel Road - at least two black squirrels appeared regularly at the feeder of Mr. Roger Clark.
5. Toomey Woodlot, Michigan State University - population established in 1972-73 by release of about twenty individuals by East Lansing residents.
6. Cedar Street - Jolly Road - Logan Street - Miller Road block -- black female #69 tagged in East Lansing on December 11, 1978 captured by Lansing Vector Control on October 10, 1979 at Valencia and South Logan Street; a few black squirrels observed in a small woodlot on South Washington about 1/4 mile north of Miller Road; two black squirrels observed running

across Jolly Road just west of Cedar Street - all of these may be part of a small population scattered over a large area or the result of numerous separate introductions.

7. Walter French School area - many black squirrels reported by students to the south and west of school, but only a few actually observed in 1980.
8. Potter Park Zoo - many black squirrels released by Ingham County Animal Control Agents.
9. Groesbeck Golf Course - many black squirrels reported to west in Bancroft and Porter Parks, but only a few observed in 1979.
10. West of Airport (6800 Grand River Avenue about 1/2 mile east of I-96) - Mrs. Clark lived in house on 10 acres of land for 38 years and first black squirrel appeared at feeder in June, 1981.
11. Sandhill Road - two orphaned black squirrels tagged by Marti Schneiderman and released in a private woodlot in Fall of 1981.

Population

Estimates

Black and fox squirrel population estimates, based on counts made during three winters of the study, ranged for the most part between 30 and 70 individuals (Table 1; Figure 9). Due to the lack of marked fox squirrels during the Winter of 1977-78, only the population estimates of the black squirrel population could be calculated. However, the fox squirrel population was believed to have been about equal to the black

Table 1. Population estimates of black and fox squirrels in East Lansing, Michigan, using Bailey's modified formula of the Petersen estimate. Estimates were based on squirrel counts obtained by walking a predetermined course through a 50 acre trapping area in the research area.

B L A C K   S Q U I R R E L S

Dates of Squirrel Counts	Observed Marked (m)	Total Observed (n)	Marked in population (r)	Population Estimate	Standard Error
1977-78					
Dec 11	-	10	-	-	-
Dec 17	-	9	-	-	-
Dec 23	1	15	2	16	8.6
Jan 11	1	12	4	26	13.8
Jan 18	2	19	6	40	18.4
Jan 23	3	22	7	40	16.4
Feb 9	3	17	8	36	14.2
Feb 14	7	22	15	43	11.6
Feb 23	4	11	18	43	13.5
1978-79					
Oct 20	-	12	-	-	-
Oct 31	1	13	5	35	18.7
Nov 7	1	14	5	38	20.2
Nov 30	2	11	11	44	19.1
Dec 10	4	18	14	53	18.6
Dec 16	6	22	15	49	14.5
Dec 17	5	17	15	45	13.9
Jan 12	4	12	15	39	12.5
Jan 27	6	16	15	36	9.9
Feb 3	4	11	15	36	11.2
Feb 20	3	8	15	34	11.3
Feb 28	5	13	15	35	10.0
Apr 3	5	14	15	38	11.0
Apr 14	1	3	15	30	12.2
Apr 20	2	6	15	35	13.2
1979-80					
Oct 31	6	30	16	71	22.0
Nov 18	10	25	29	69	15.0
Dec 10	8	21	29	71	17.2
Dec 19	10	26	29	71	15.8
Jan 9	10	29	29	79	18.2
Jan 25	10	26	29	71	15.8
Feb 4	8	17	33	66	14.8
Feb 18	9	20	34	71	15.6
Apr 13	11	22	34	65	12.5
Apr 20	11	23	34	68	13.3

Table 1 (cont'd.)

FOX SQUIRRELS

Dates of Squirrel Counts	Observed Marked (m)	Total Observed (n)	Marked in population (r)	Population Estimate	Standard Error
1977-78					
Dec 11	-	13	-	-	-
Dec 17	-	8	-	-	-
Dec 23	-	12	-	-	-
Jan 11	-	10	-	-	-
Jan 18	-	9	-	-	-
Jan 23	-	15	-	-	-
Feb 9	1	13	2	14	7.5
Feb 14	1	15	3	24	13.0
Feb 23	1	13	3	21	11.2
1978-79					
Oct 20	1	11	1	6	3.2
Oct 31	1	14	2	15	8.1
Nov 7	1	14	2	15	8.1
Nov 30	1	12	5	33	17.3
Dec 10	2	21	6	44	20.4
Dec 16	2	16	7	40	18.0
Dec 17	2	17	7	42	19.2
Jan 12	3	19	7	35	14.0
Jan 27	3	20	7	37	14.8
Feb 3	2	14	7	35	15.7
Feb 20	2	12	7	30	13.3
Feb 28	1	7	7	28	14.0
Apr 3	3	16	7	30	11.6
Apr 14	1	5	7	21	9.9
Apr 20	1	6	7	25	12.0
1979-80					
Oct 31	2	18	4	25	11.6
Nov 18	4	16	12	41	14.0
Dec 10	4	13	17	48	15.6
Dec 19	7	21	17	47	12.4
Jan 9	9	23	20	48	11.1
Jan 25	9	20	21	44	9.6
Feb 4	7	12	24	39	8.1
Feb 18	8	15	26	46	9.7
Apr 13	11	21	26	48	8.9
Apr 20	8	16	26	49	10.7

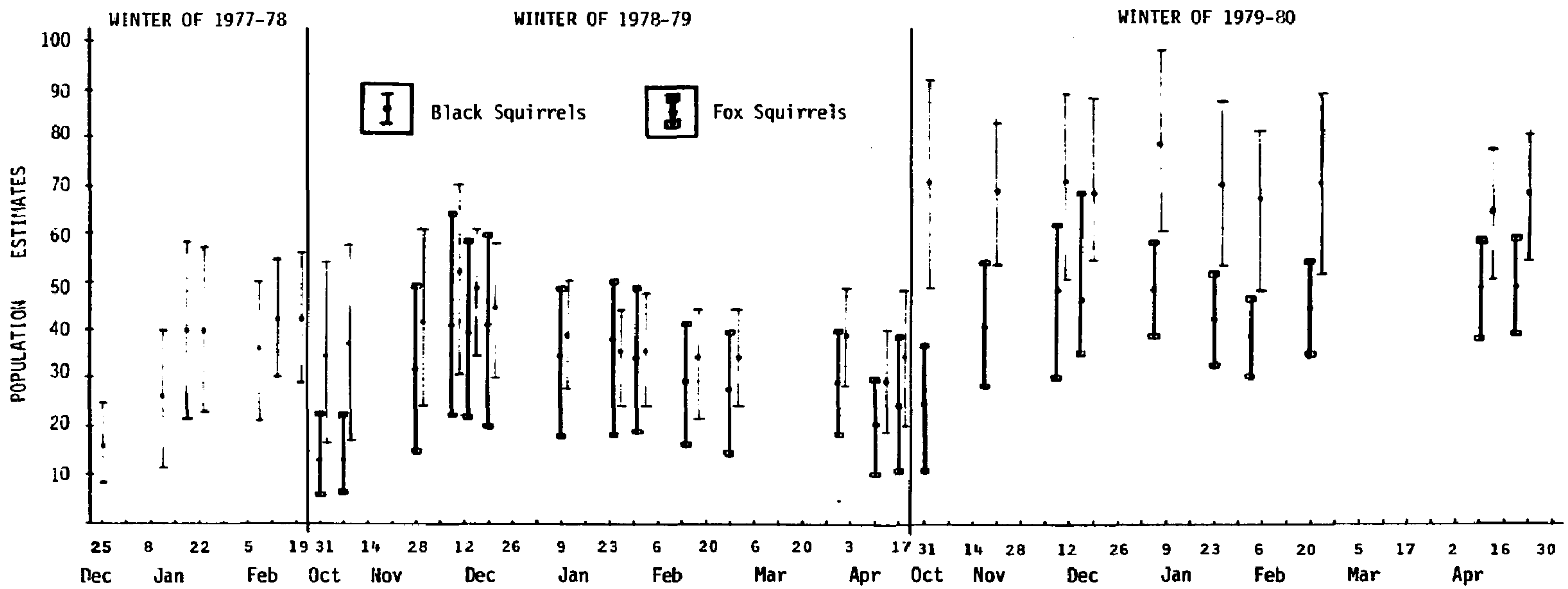


Figure 9. Estimates (± S E) of black and fox squirrel populations in a 50 acre trapping area in East Lansing, Michigan, for the Winters of 1977-78, 1978-79 and 1979-80. Due to a lack of marked fox squirrels, only black squirrel population estimates were calculated for 1977-78.

squirrels that winter, because they were observed in the squirrel counts about as often as the black squirrels. The black and fox squirrel populations appeared comparable for the Winters of 1977-78 and 1978-79, being near 40 individuals for each species within the 50 acre trapping area. This was a total squirrel density of 1.6/acre.

During the Winter of 1979-80, the fox squirrel population was near 50 individuals and the black squirrel population had increased to near 70 individuals. This was a total squirrel density of 2.4/acre.

Trap-retrap methods of population estimation were not used because the traps appeared to be biased, capturing more black squirrels than would reasonably be expected. Chi-square analysis (Table 2) comparing the trapping success (both first-time captures and subsequent recaptures) during the study with the expected success based on the proportions of black and fox squirrels observed in the population counts indicated that the probability of obtaining these results by chance was very low for recaptured animals during all three winters and for first-time captures during the Winters of 1977-78 and 1978-79. Only during the Winter of 1979-80 was the probability of obtaining the first-time captures very high, and it is suspected that the mildness of this winter (see Table 7) influenced these results. During most of the study, the black squirrels were trapped with a disproportionately greater frequency than the fox squirrels.

Table 2. Comparison of trapping success of squirrels in East Lansing, Michigan, with expected success based on black and fox squirrel proportions observed in the population on squirrel counts (data summarized from Table 1).

	Year	Total Number of Squirrels Observed	% of Total Observed	Number of Squirrels Captured		Number of Squirrels Expected to be captured		Probability of Obtaining these Results by Chance
				First Captures	Recaptures	First Captures	Recaptures	
Black	1977-	137	55.9	33	44	25	27	1st Captures
Fox	1978	108	44.1	11	4	19	21	.025>P>.01
Total		245	----	44	48	44	48	Recap. .005>P
Black	1978-	190	48.2	20	20	14	13.5	1st Captured
Fox	1979	204	51.8	9	8	15	14.5	.05>P>.025
Total		394	----	29	28	29	28	Recap. .025>P>.01
Black	1979-	239	57.7	40	63	40	51	1st Captures P>.95
Fox	1980	175	42.3	30	26	30	38	Recaptures
Total		414	----	70	89	70	89	.025>P>.01

Natality

Litter sizes for the black squirrels during the Springs of 1978, 1979, and 1980 appeared to be larger than that of fox squirrels, and for both species litter size for the Spring of 1979 appeared to be smaller than in 1978 or 1980 (Figure 10). T-tests on differences between the means, however, indicated that 1) average litter size for black squirrels showed no significant differences year to year, 2) the average fox squirrel litter for the Spring of 1979 was significantly (.001 level) smaller than in 1978 or 1980, 3) average black and fox squirrel litter sizes were not significantly different in the Springs of 1978 or 1980, but 4) in 1979, the average black squirrel litter was significantly (.001 level) larger than the average fox squirrel litter.

The first appearance of litters out of the nest occurred later in the Spring of 1979 than in 1978 or 1980 (Figure 11). Using April 20 as the first day litters appeared, t-tests on differences between the means indicated the average day of emergence during the Spring of 1979 was significantly (.001 level) later for both the black and fox squirrels than was true for the Springs of 1978 or 1980. There was no significant difference in the average day of emergence between black and fox squirrel litters in the Springs of 1978 or 1980, but the black squirrel litters in the Spring of 1979 emerged significantly (.001 level) earlier than the fox squirrel litters.

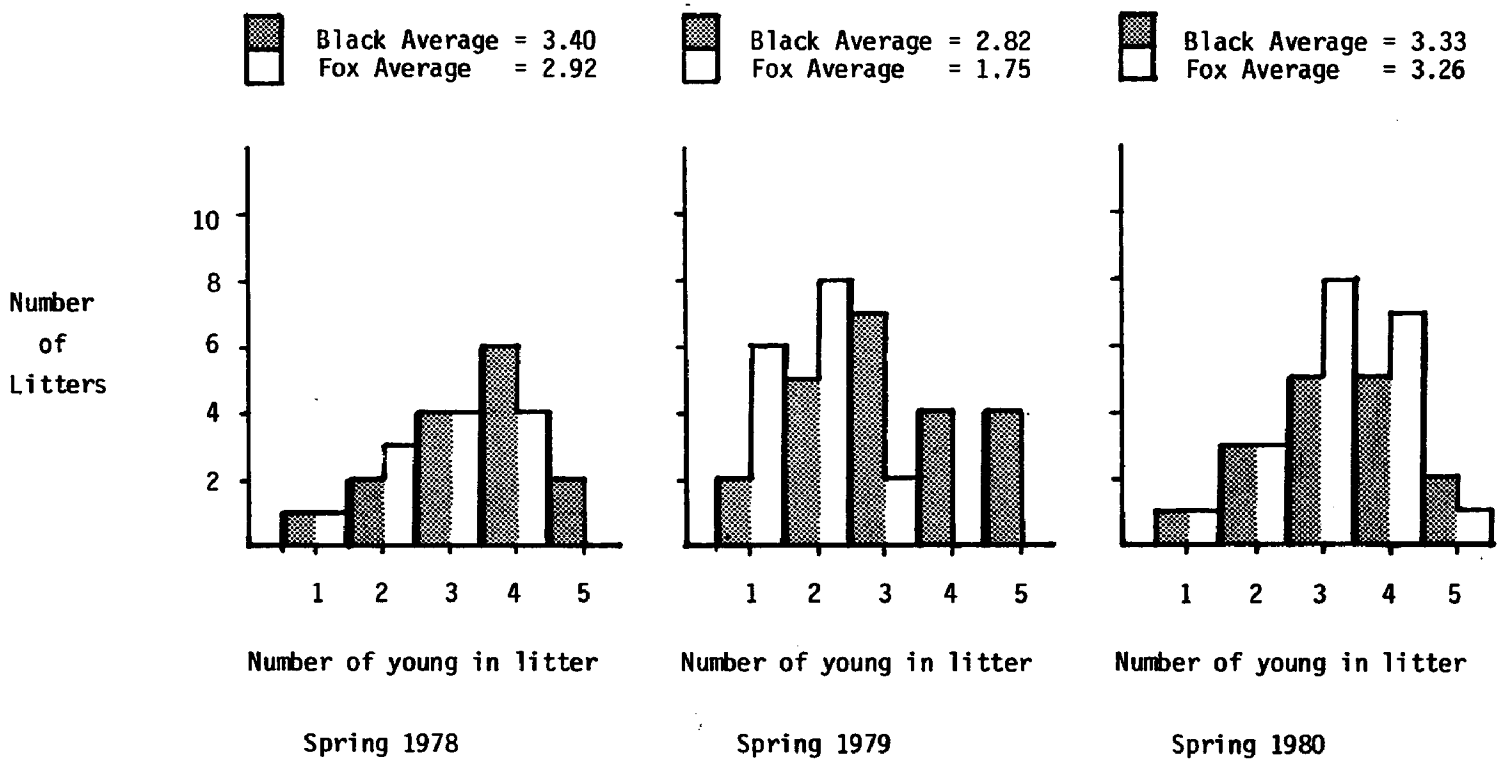


Figure 10. Spring litter sizes of black and fox squirrels in East Lansing, Michigan, for 1978, 1979 and 1980.

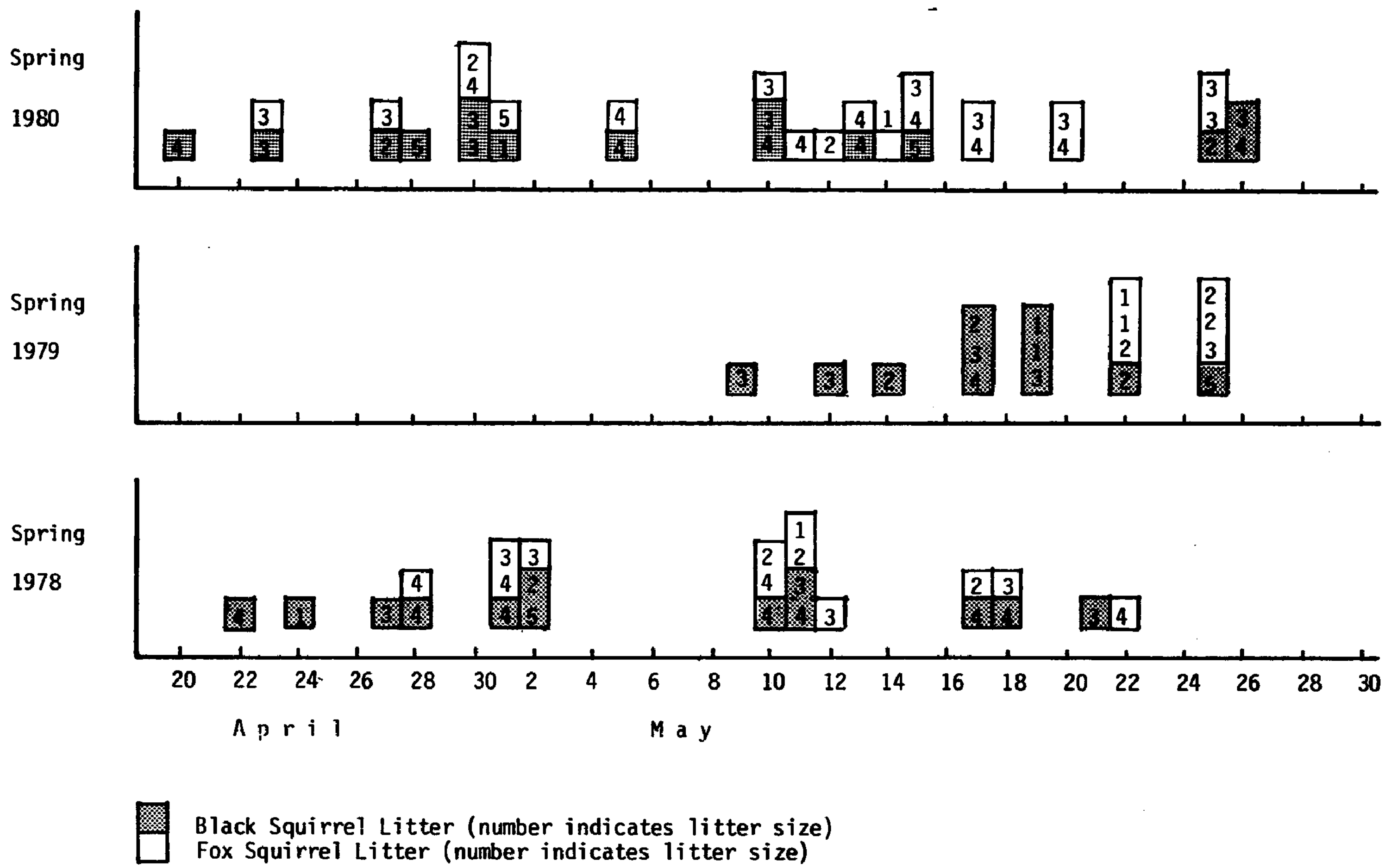


Figure 11. Dates on which black and fox squirrel litters in East Lansing, Michigan, were first observed out of the nest in April and May of 1978, 1979 and 1980.

Mortality

During the study, 29 dead squirrels were recovered in the research area: 12 black and 12 fox squirrels were killed by cars; 3 black squirrels were killed by cats; and 2 black squirrels were killed in accidents. The greatest part of the car mortality (17/24) occurred among juveniles recently out of the nest. Few car kills occurred when snow covered the ground.

Most of the squirrels handled during the study had fleas. These were most abundant on the squirrels during February and March. Examination of three leaf nests blown down from trees revealed large numbers of fleas (50-100) in each nest. Sarcoptic mange and bald areas on the body were common during late winter. Sometimes 50-80% of the body was bare with raw bleeding areas obvious.

Movements

Daily Activity

Throughout the year, black and fox squirrels were similar in the pattern of daily activity, showing high levels of activity from 9 AM - 5 PM (Table 3; Figure 12). While black squirrels showed a slightly greater level of activity in the morning and late afternoon than did the fox squirrels in spring, this difference was not statistically significant.

Home Range

During this study, four black squirrels and three fox squirrels were observed often enough over a long enough time span to plot their minimum home ranges (Figures 13, 14, and 15). The majority of marked

Table 3. Daily activity of black and fox squirrels in East Lansing, Michigan, during each season. Activity level is based upon the average number of squirrels sighted while making observations during each two hour daylight time period during entire study (June 1977-May 1980). Time corrected to Eastern Standard Time.

SPRING

Daylight Time Periods	BLACK SQUIRRELS Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period	FOX SQUIRRELS Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period
←7 am	26	29	.90	27	29	.93
7-9 am	166	35	4.74	142	35	4.06
9-11 am	731	32	22.84	554	32	17.31
11am-1 pm	541	29	18.66	509	29	17.55
1-3 pm	551	30	18.37	536	30	17.87
3-5 pm	744	36	20.67	447	36	12.42
5→ pm	177	33	5.36	139	33	4.21

Table 3 (cont'd.)

SUMMER

		BLACK SQUIRRELS			FOX SQUIRRELS		
		Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period	Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period
	←7 am	262	32	8.19	248	32	7.75
Daylight	7-9 am	1104	39	28.30	53	39	24.43
	9-11 am	1059	41	25.83	1192	41	29.07
Time	11am-1 pm	956	38	25.16	1040	38	27.37
	1-3 pm	902	34	26.53	827	34	24.32
Periods	3-5 pm	1007	37	27.22	834	37	22.54
	5→ pm	805	44	18.29	560	44	12.73

Table 3 (cont'd.)

FALL

	BLACK SQUIRRELS			FOX SQUIRRELS		
	Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period	Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period
←7 am	141	30	4.70	157	30	5.23
Daylight 7-9 am	636	31	20.52	587	31	18.94
9-11 am	1074	36	29.83	1092	36	30.33
Time 11am-1 pm	835	35	23.86	857	35	24.49
1-3 pm	712	32	22.25	698	32	21.81
Periods 3-5 pm	761	32	23.78	647	32	20.22
5→ pm	360	41	8.78	417	41	10.17

Table 3 (cont'd.)

WINTER

		BLACK SQUIRRELS			FOX SQUIRRELS		
		Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period	Total Number of Squirrels Observed	Total Number of Observation Periods	Average Number of Squirrels Observed Per Period
	←7 am	0	6	0	0	6	0
Daylight	7-9 am	92	17	5.41	77	17	4.53
	9-11 am	291	27	10.98	248	27	9.19
Time	11am-1 pm	574	29	19.79	591	29	20.38
	1-3 pm	543	30	18.10	496	30	16.53
Periods	3-5 pm	272	27	9.71	323	28	11.54
	5→ pm	0	14	0	0	14	0

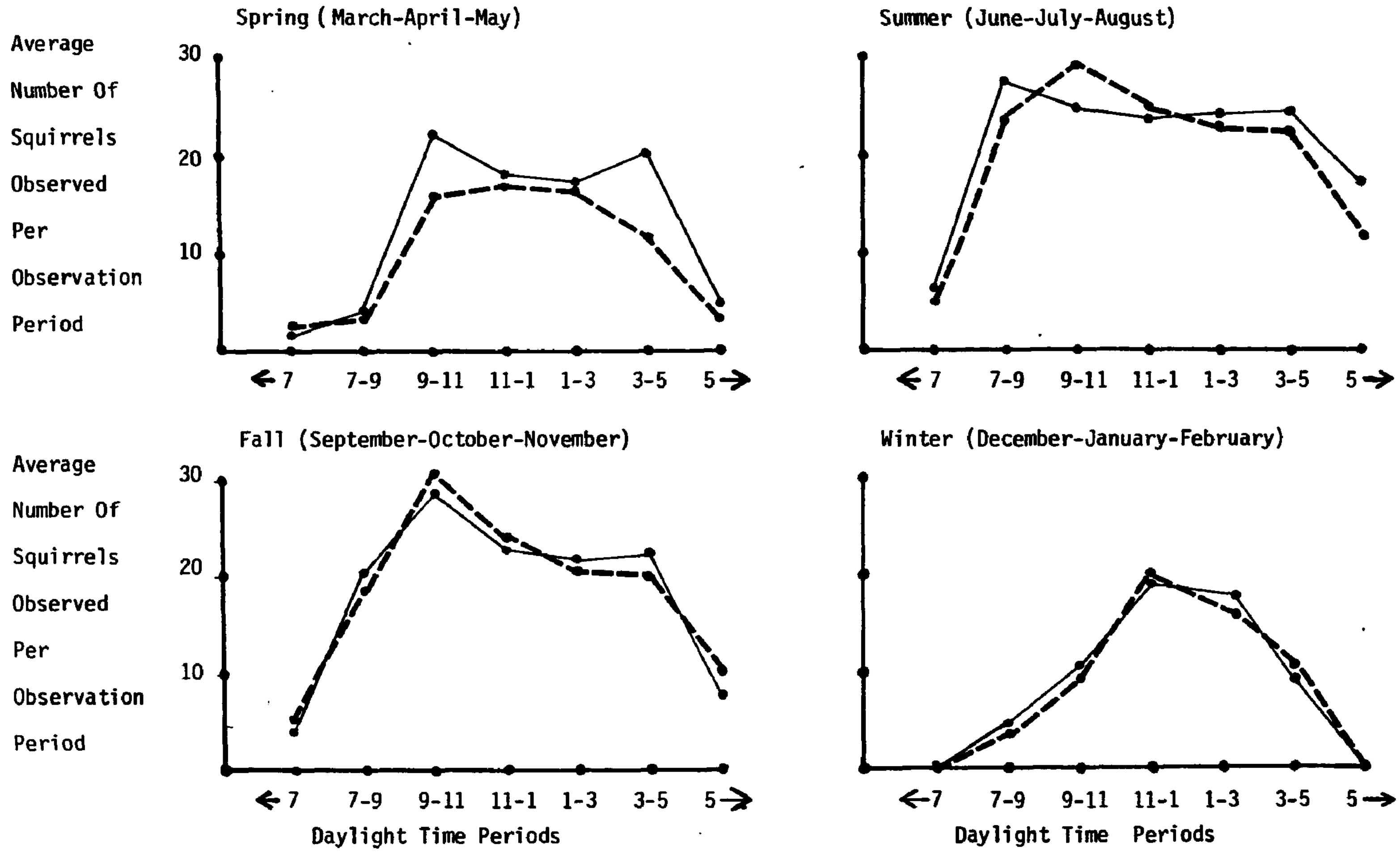


Figure 12. Daily activity patterns of black and fox squirrels during each season of the year in East Lansing, Michigan. Time is corrected to Eastern Standard Time. Black squirrels shown in solid line, fox squirrels in broken line.

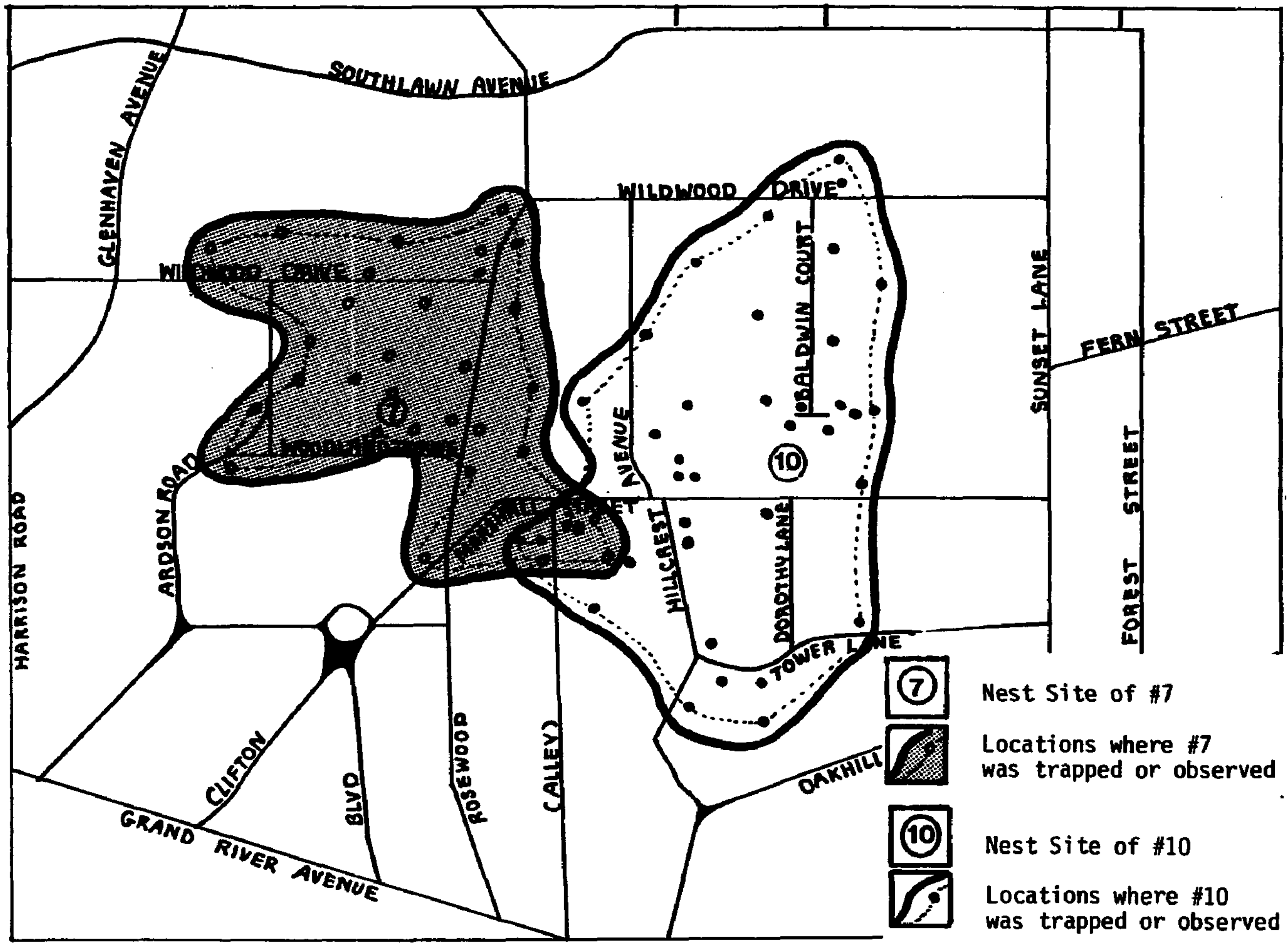


Figure 13. Home ranges of female black squirrels #7 (7.8 acres) and #10 (8.3 acres) in East Lansing, Michigan.

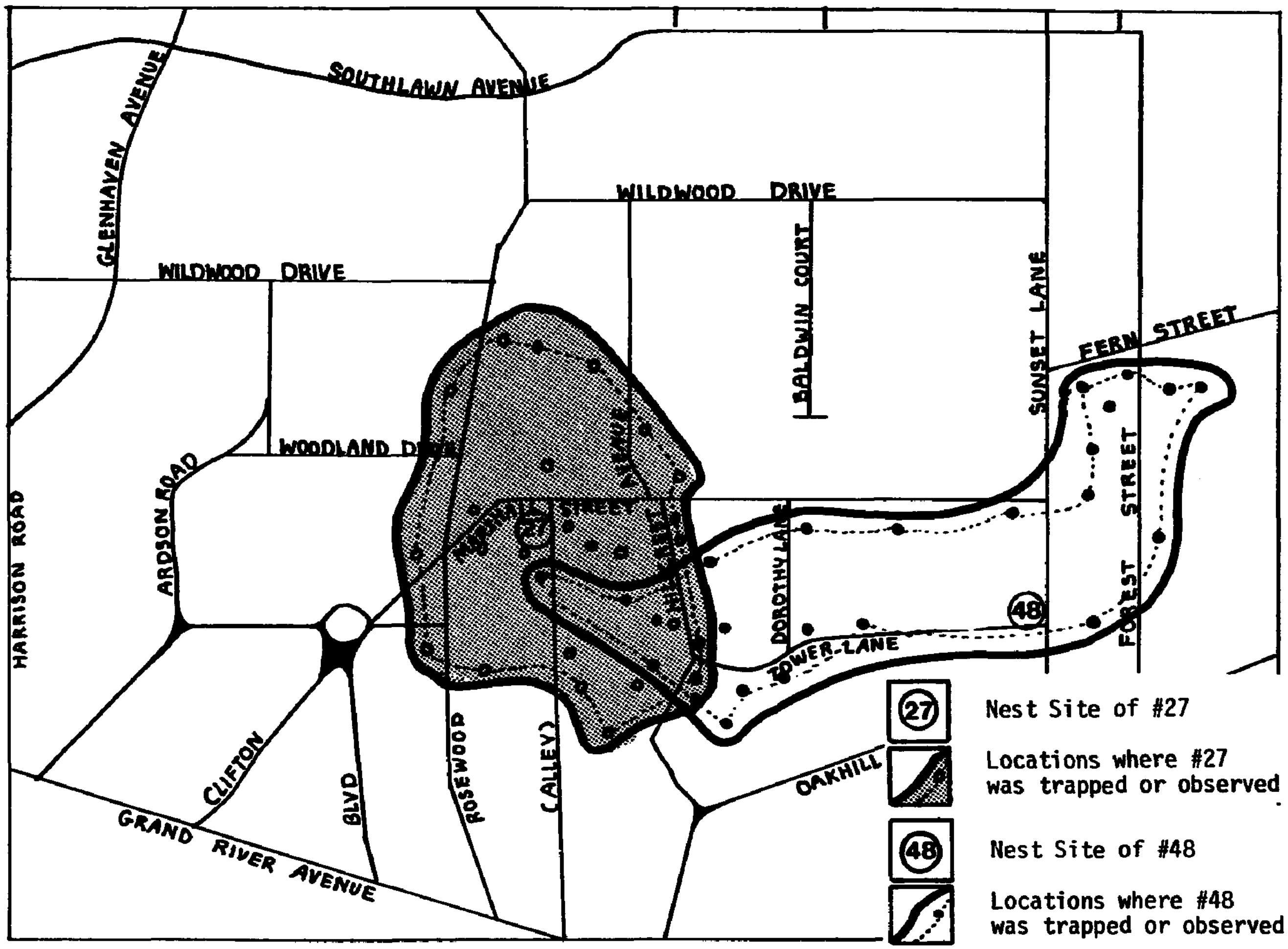


Figure 14. Home ranges of male black squirrels #27 (7.8 acres) and #48 (6.3 acres) in East Lansing, Michigan.

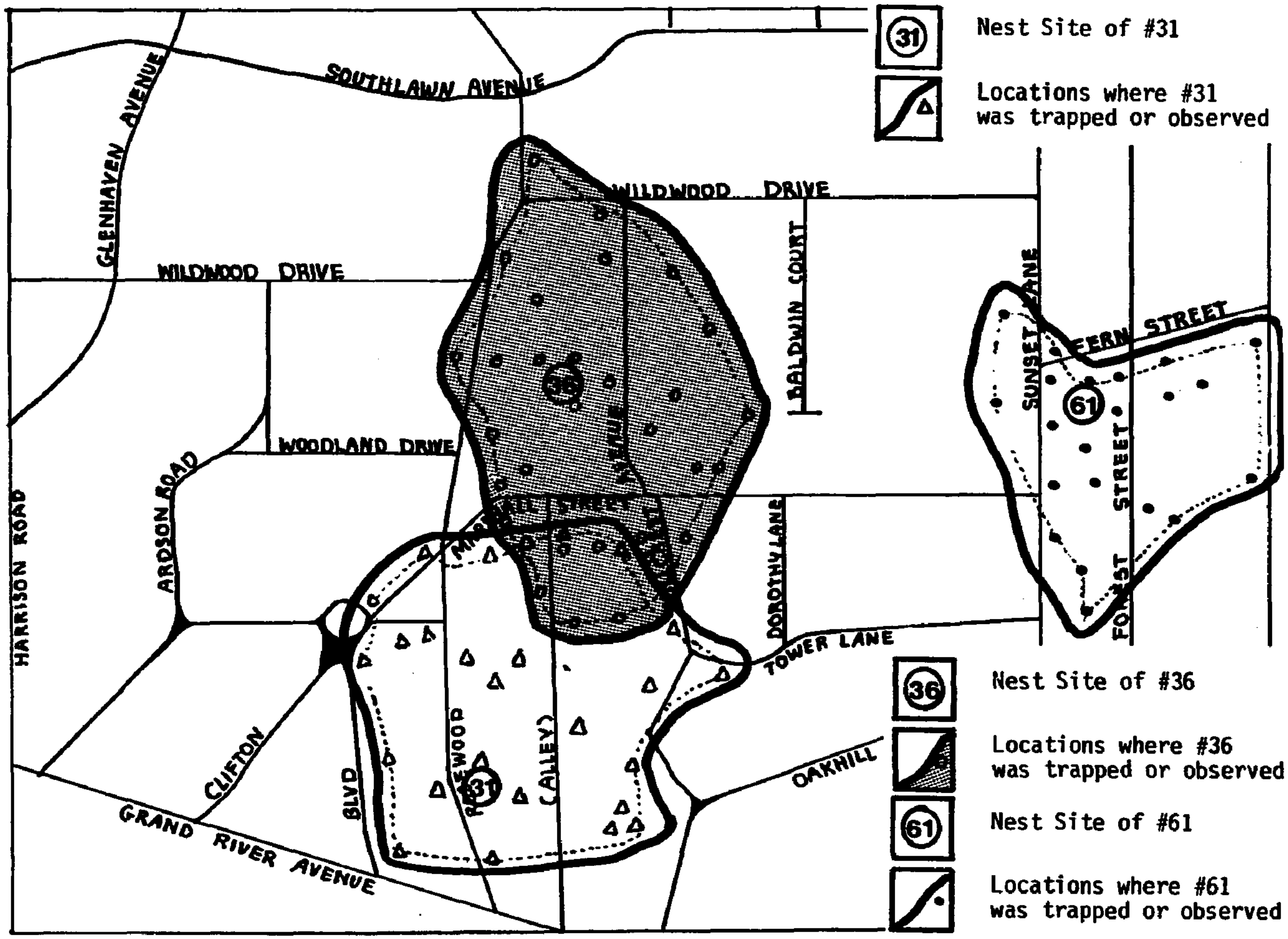


Figure 15. Home ranges of female fox squirrel #31 (9.1 acres) and male fox squirrels #36 (8.2 acres) and #61 (5.5 acres) in East Lansing, Michigan.

juvenile individuals was observed only until the "fall shuffle" and then never seen again. Only subadults and adults which established and maintained nests could be used for determining home ranges and most of these disappeared (most often during winter) before they had been followed for the required period.

While it was difficult to make any reliable comparisons with few data, it was interesting that the average home range of both types of squirrel was nearly identical (black squirrel = 7.55 acres; fox squirrel = 7.6 acres). This in itself may have been inaccurate, however, since fox male #61, with a home range of 5.5 acres, was suspected of using the trees along Evergreen Street, which locality was not as intensively patrolled as the trapping area to the west of it. The home range of #61, therefore, was probably larger. If so, this would have increased the average fox squirrel home range.

It should be noted that the home ranges of each of the other six squirrels included some of the hickory region. Some squirrels trapped in the fall in the hickory region were observed during the winter at feeding stations in the elm region far to the north. The movement of squirrels to the hickory region during the fall from another tree region was a common occurrence. Because of the clustering of trees throughout the research area, the squirrels appeared to move from one area to another as the fruit of each type of tree matured. For this reason, it was suspected that the home ranges of the squirrels studied might have been larger than measured.

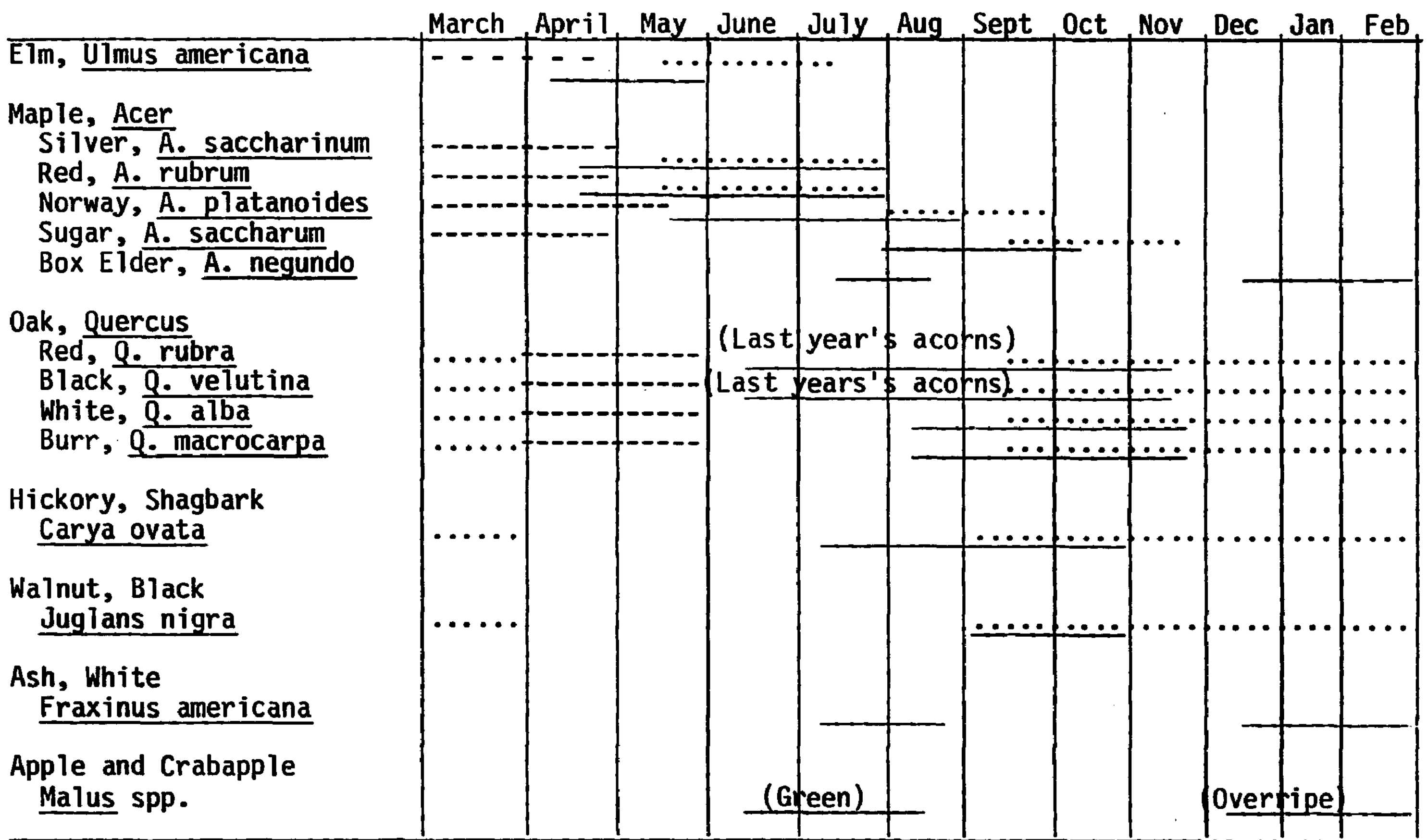
Another interesting difference regarding squirrel movements in urban areas was the use by both species of power and telephone lines as major traveling routes. The home range of black male #48 displayed a linearity in movement which connected distant areas of feeding and nesting. The majority of his needs were supplied by the oak trees along Sunset Lane and Forest Street and the hickory trees and supplemental feeders along Hillcrest Avenue. The power and telephone lines along Tower Lane and Marshall Street in the center of his home range, however, served as the main highways connecting his areas of activity. For the most part, power lines ran through the middle of residential blocks and this enabled squirrels to move through the quieter backyards rather than the frontyard along the streets.

Food Availability

Although both black and fox squirrels were known to raid residents' flower and vegetable gardens for bulbs, pumpkins, zucchini, etc., a number of tree species supplied the bulk of their natural food through much of the year (Table 4).

In late winter and early spring, when the snow was less than two inches deep, the squirrels were observed digging up nuts buried the previous fall. With snow depths greater than two inches, they relied on developing buds and flowers. The presence of a variety of maple species furnished a continuous supply of seeds from spring through fall, while a mixture of oaks provided acorns on the tree in summer and fall. Red and black oak acorns matured in the second year and were

Table 4. Major tree species used as natural food sources by black and fox squirrels at some time of the year in East Lansing, Michigan, study (June 1977-May 1980).



Parts of plant eaten:
---------- Buds and flowers
________ Fruit/seed/nut eaten on tree (ripe and/or unripe)
.... Fruit/seed/nut eaten on ground (on the surface or buried)

utilized by the squirrels mostly during the summer, while white oak acorns matured and were utilized in the fall of the first year.

Green apples were used by both black and fox squirrels during the summer, but fox squirrels were observed feeding on them more often. Interestingly, the squirrels went through great effort to gnaw away the fleshy part of the apple, but never ate the core or skin, which were discarded. During the winter months at times of deep snow, they were observed feeding on the brown overripe apples that remained on the tree. While they appeared to consume both the skin and fleshy parts then, they still discarded the core.

Spring litter juvenile black and fox squirrels were observed feeding on ash and box elder seeds during summer, but for the most part, the squirrels deferred use of these until the heavy snows of early winter covered the ground. Then, these seeds were often the only foods still hanging from the branches at this time.

The use of shagbark hickories by both black and fox squirrels was intriguing. In August and September, when the squirrels were "cutting nuts," individual trees appeared to ripen at different rates, some early, some later. This sequence of ripening hickory trees was the same each year and the squirrels would attack them in sequence. After converging on an early ripening tree, it was certain that they would appear at the next tree in the sequence a few days later. At times, the number of squirrels in a tree was so great and the activity so confusing, it was nearly impossible to record all the interactions. On August 20, 1978, nearly every squirrel in the hickory region had converged on one large shagbark. From early morning to near sunset, at least 25 black and fox squirrels were in that one tree at all times. Probably another 20-30 also moved in and out of the tree from neighboring hickories or nearby rooftops. While many of the nuts were eaten, it appeared much of the time was spent just gnawing away the green husks. A large part of the discarded nuts had the husk partly or entirely gnawed away while the nuts were left intact. Two 30-gallon plastic trash cans were filled with the discarded nuts and later offered to the squirrels during winter. In the cold season, nearly all were eaten.

The major natural food sources available to the squirrels during the fall seasons of 1977, 1978, and 1979 varied from year to year (Table 5). The food supply in the Fall of 1977 was abundant, but a dearth of acorns and walnuts occurred in the subsequent fall. Only hickories produced consistently large crops, and in the Fall of 1978 these were supplemented by a bumper crop of sugar maple seeds which helped make up for the lack of acorns and walnuts. About a hundred shagbark hickories were in the hickory region but they alone could not provide an autumn supply of nuts for the entire squirrel population. The squirrels relied heavily upon supplemental feeders from November through the entire winter.

Feeding stations in the research area varied in design from elaborately built platforms (often attempting to be squirrel proof), to others that were no more than piles of seeds dropped on the ground. While the majority of the feeding stations were meant primarily for birds, much seed was scattered to the ground by the birds, thereby making it available to ground foraging mammals. During the period of

Table 5. Availability of natural foods to East Lansing, Michigan, squirrels during fall seasons of 1977, 1978 and 1979.

	Species of tree sampled			
	Oak	Hickory	Maple	Walnut
Fall 1977				
Number of trees sampled	23	10	7	3
Average number of nuts (seeds) per m^2 under tree (± S E)	21.6 (±4.0)	13.1 (±1.3)	42.3 (±6.6)	5.2 (±0.5)
Fall 1978				
Number of trees sampled	23	10	7	3
Average number of nuts (seeds) per m^2 under tree (± S E)	2.3 (±1.1)	17.8 (±1.6)	217.4 (±9.8)	0.33 (±0.3)
Fall 1979				
Number of trees sampled	23	10	7	3
Average number of nuts (seeds) per m^2 under tree (± S E)	8.7 (±1.1)	16.7 (±1.5)	13.0 (±1.6)	1.1 (±0.2)

this study, a number of mammal species were observed feeding at these supplemental feeding stations during some time of the year. These included black squirrels (*Sciurus carolinensis*), fox squirrels (*S. niger*), red squirrels (*Tamiasciurus hudsonicus*), flying squirrels (*Glaucomys volans*), chipmunks (*Tamias striatus*), thirteen-lined ground squirrels (*Citellus tridecemlineatus*), rabbits (*Sylvilagus floridanus*), raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), skunks (*Mephitis mephitis*), woodchucks (*Marmota monax*), rats (*Rattus norvegicus*) and mice (*Peromyscus* spp.).

Of the 598 houses in the research area, 183 (30.6%) maintained a total of 250 feeding stations, an average of 1.25/acre (Figure 16). While there was some clumping of these feeders, there was no residential block devoid of them. The density of feeders in the dominant tree regions making up the majority of the research area ranged from about 1.0-1.5/acre. Only the small hickory region had a disproportionately higher density of 2.55/acre. It would be reasonable to expect, therefore, that almost every squirrel nesting overwinter in the research area would have had at least five feeders within its home range to supplement its natural food supply.

Interspecific Aggressive Behavior

Black and fox squirrels were tolerant of each other during late spring, summer, and early fall, but became increasingly aggressive during late fall and reached a peak in late winter (Table 6; Figure 17). During this time of year, the blacks were far more aggressive than the fox squirrels, the differences between indices being significant.

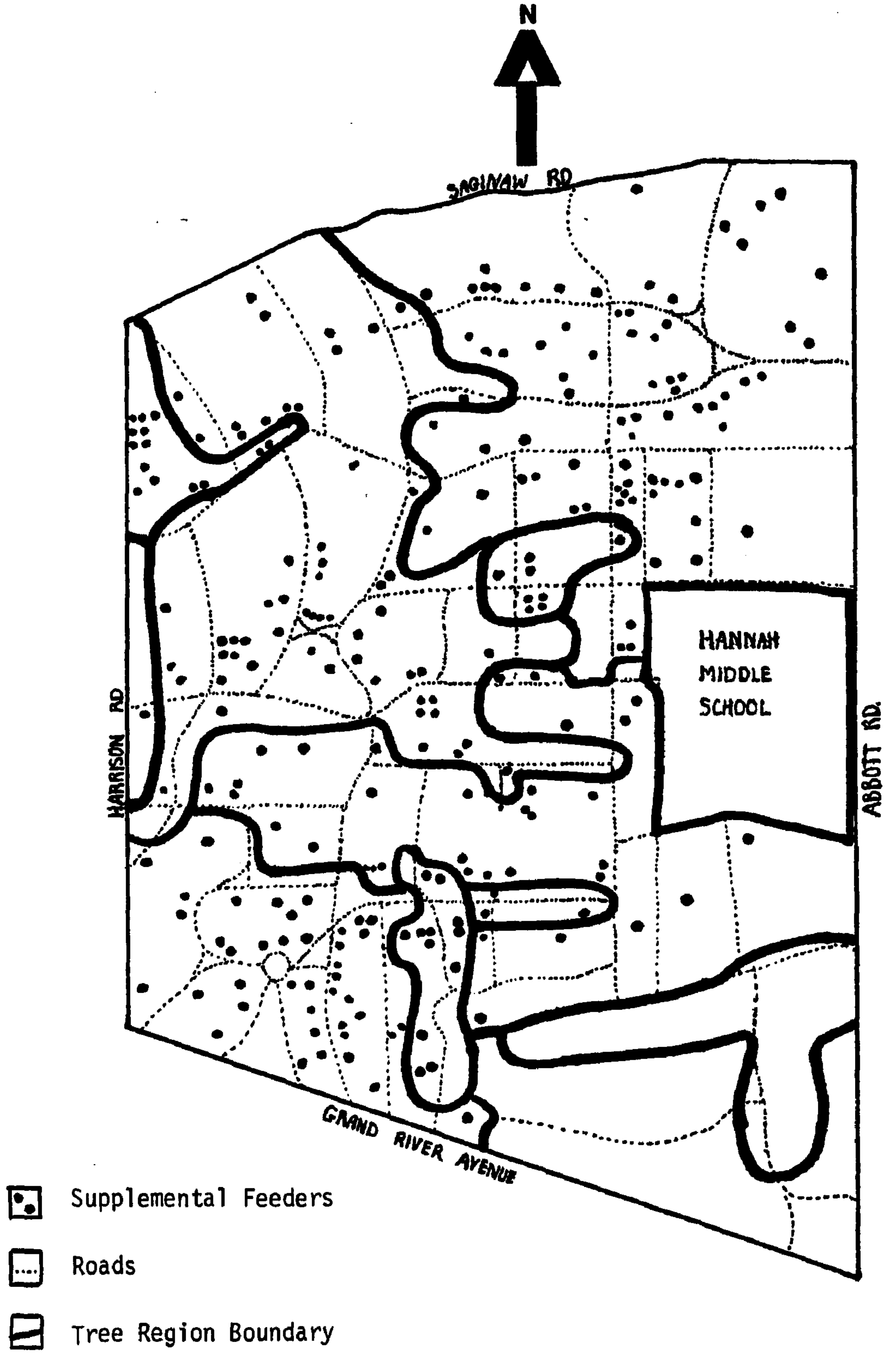


Figure 16. Distribution of supplemental feeders maintained by residents in East Lansing, Michigan, squirrel research area. Density of feeders in each tree region was: oak = 1.02/acre; elm = 1.34/acre; maple = 1.55/acre; hickory = 2.55/acre.

Table 6. Monthly indices of aggression based on encounters between black and fox squirrels in East Lansing, Michigan. Encounters rated at 3 = severe aggression, 2 = moderate aggression, 1 = mild aggression, 0 = tolerance or submissive behavior (moving away). Difference between black and fox squirrel indices tested with t-tests.

YEAR	Month	Total Number of Encounters	BLACK SQUIRRELS TOL. (0)	MILD (1)	MOD. (2)	SEV. (3)	Index Value	Standard Error	FOX SQUIRRELS TOL. (0)	MILD (1)	MOD. (2)	SEV. (3)	Index Value	Standard Error	Difference Between Indices
1	June	38	34	4	0	0	0.105	0.050	33	5	0	0	0.132	0.055	n.s.
	July	81	75	5	1	0	0.086	0.036	74	7	0	0	0.086	0.031	n.s.
9	August	64	57	3	4	0	0.172	0.065	58	5	1	0	0.109	0.045	n.s
	Sept.	78	69	7	2	0	0.141	0.047	68	9	1	0	0.141	0.043	n.s.
7	Oct.	91	74	12	5	0	0.242	0.057	78	10	3	0	0.176	0.048	n.s.
	Nov.	71	56	11	4	0	0.268	0.066	60	8	3	0	0.197	0.058	n.s.
7	Dec.	59	51	6	2	0	0.169	0.059	51	5	3	0	0.186	0.066	n.s.
1	Jan.	91	49	18	15	9	0.824	0.108	75	6	6	4	0.330	0.082	* * *
	Feb.	125	64	20	30	11	0.904	0.094	103	9	7	6	0.328	0.070	* * *
9	March	91	56	8	9	18	0.879	0.128	81	5	3	2	0.187	0.062	* * *
	April	34	31	1	1	1	0.176	0.106	32	1	1	0	0.088	0.064	n.s.
7	May	59	47	7	4	1	0.305	0.087	49	6	2	2	0.271	0.089	n.s.
	June	75	63	9	3	0	0.200	0.057	64	9	1	1	0.187	0.059	n.s.
8	July	111	100	10	1	0	0.108	0.032	95	13	3	0	0.171	0.042	n.s.
	Aug.	151	121	20	1	9	0.325	0.063	132	11	8	0	0.179	0.041	n.s.
	Sept.	145	102	26	13	4	0.441	0.064	124	10	8	3	0.241	0.054	*
	Oct.	105	63	17	16	9	0.724	0.099	83	10	8	4	0.362	0.076	* *
	Nov.	106	52	18	21	15	0.991	0.109	81	7	11	7	0.472	0.090	* * *
	Dec.	105	41	22	28	14	1.143	0.106	85	8	8	4	0.343	0.076	* * *

Table 6 (cont'd.)

YEAR	Month	Total Number of Encounters	BLACK SQUIRRELS TOL. (0)	MILD (1)	MOD. (2)	SEV. (3)	Index Value	Standard Error	FOX SQUIRRELS TOL. (0)	MILD (1)	MOD. (2)	SEV. (3)	Index Value	Standard Error	Difference Between Indices
1	Jan.	106	38	12	31	25	1.406	0.116	81	10	9	6	0.434	0.084	* * *
	Feb.	111	34	19	28	30	1.486	0.112	88	10	8	5	0.369	0.076	* * *
9	March	72	35	11	15	11	1.028	0.135	52	10	8	2	0.444	0.094	* * *
	April	60	41	13	6	0	0.417	0.086	44	10	5	1	0.383	0.092	n.s.
7	May	67	56	8	2	1	0.224	0.069	52	10	4	1	0.313	0.080	n.s.
	June	73	67	6	0	0	0.082	0.032	67	6	0	0	0.082	0.032	n.s.
9	July	81	75	5	0	1	0.099	0.045	69	8	2	2	0.222	0.068	n.s.
	Aug.	87	68	12	2	5	0.356	0.084	71	8	4	4	0.322	0.082	n.s.
	Sept.	129	92	21	10	6	0.457	0.073	103	14	7	5	0.333	0.066	n.s.
	Oct.	119	74	21	16	8	0.647	0.087	98	9	7	5	0.319	0.070	* *
	Nov.	89	57	12	12	8	0.674	0.108	71	7	8	3	0.360	0.083	*
	Dec.	116	65	21	17	13	0.810	0.098	98	11	3	4	0.250	0.062	* * *
1	Jan.	135	70	27	25	13	0.859	0.089	117	9	6	3	0.222	0.054	* * *
	Feb.	138	76	21	23	18	0.877	0.094	120	8	7	3	0.225	0.054	* * *
9	March	151	91	34	19	7	0.616	0.071	129	13	7	2	0.219	0.048	* * *
	April	136	96	28	8	4	0.412	0.063	113	16	5	2	0.235	0.050	*
8	May	165	114	39	8	4	0.406	0.054	132	23	7	3	0.279	0.049	n.s.
0															

Levels of significance: * = .05 ** = .01 *** = .001

$$\text{Index Value} = \frac{\Sigma(\text{Encounters X Rating})}{\text{Total Encounters}}$$

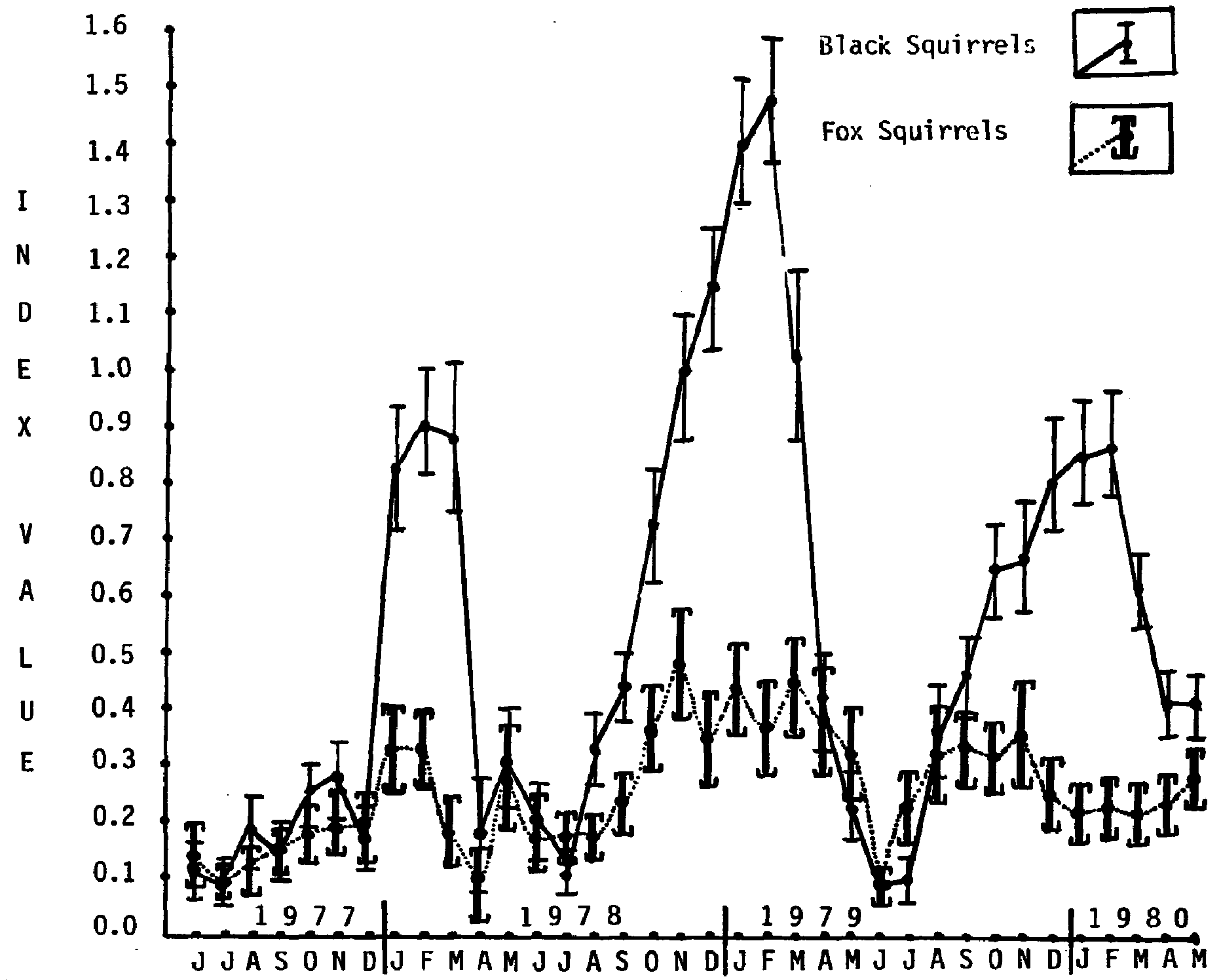


Figure 17. Indices of aggression (± S E) for black and fox squirrels during 36 month study in East Lansing, Michigan.

Most of the interactions between species during late spring, summer and early fall were observed to be distributed rather uniformly throughout the research area. During the warmer months, both species were feeding on naturally occurring food sources which tended to be dispersed over large areas (thousands of square feet). They often fed tolerantly in mixed groups, sometimes 10-15 individuals spread over two house lots. Displays of aggressive behavior were observed only where a person had put out some food in a small area (one or two feet in diameter) which could be easily dominated by one individual. For the most part, aggressive behavior during this time of the year was displayed only by females near their nests or with recently emerged litters of juveniles.

Once snow had accumulated to a depth of two inches or more, the squirrels seldom dug the nuts they had buried. Instead they relied on the more easily obtainable supplemental foods put out at feeding stations by residents. During winter, these places were where the vast majority of behavioral interactions took place. With most feeding stations consisting of a single bird feeder, a lone squirrel could easily dominate the concentrated food source while other less aggressive individuals were chased away and had to wait their turns.

Black squirrels excelled at dominating a feeder when they wanted to feed there. They would drive away or warn off fox squirrels two or three times as often as they were driven away or warned off by fox squirrels. During the winter, tolerance was observed mostly when a black and fox squirrel happened to be sunning themselves in the same tree or where a supplemental feeding station had a number of feeders or food scattered widely about.

During the Winter of 1977-78, heavy snow did not arrive until the end of December and the squirrels fed until then on bumper crops of acorns, hickory nuts and walnuts. A twenty inch snowfall in January remained on the ground well into March and this was reflected in the high level of black squirrel aggression at the feeding stations throughout that period.

The failure of oaks to produce acorns in the Fall of 1978 forced squirrels to rely more heavily on hickory nuts and the bumper crop of sugar maple seeds in late summer and early fall. As these natural sources of food diminished, aggression at feeding stations appeared much earlier than the previous year and at higher levels for both black and fox squirrels. The black squirrel aggression level for the five months from November 1978 - March 1979 was continuously higher than the peak aggression levels of the preceding and succeeding years.

With only a slight crop of acorns, walnuts and sugar maple seeds in the Fall of 1979, the squirrels again turned early to the hickory nuts as the major natural food source. Again the aggression at the feeding stations appeared in fall, but moderated somewhat as the winter turned out to be exceedingly mild. With little snow on the ground, the squirrels foraged throughout the winter and did not rely totally on the feeding stations. Possibly the milder temperatures also allowed the squirrels to remain out of the nest longer with reduced body heat loss. Both of these factors evidently had the effect of reducing the severity of encounters and increasing the number of tolerant interactions through the winter.

Weather and Winter Weight Fluctuations

The climatological data for Lansing, Michigan, during the Winters of 1977-78, 1978-79, and 1979-80 (Table 7) showed that the first two were more severe in terms of both cold and snowfall. Perhaps one of the most important climatological factors was the number of days with two or more inches of snow on the ground, since this influenced the squirrels' dependence on the supplemental feeders. The trapping and weighing of black and fox squirrels from October 27, 1979 to February 22, 1980 happened to take place during a very mild winter having relatively few days of deep (2+") snow cover.

During this trapping period, changes in the weights of 24 black and 12 fox squirrels captured and weighed more than once were recorded (Table 8). While six adult black squirrels were captured and weighed once, they were never subsequently recaptured and, therefore, no data were obtained for this age group. However, six adult fox squirrels were each captured and weighed a number of times. Of these, one gained 45 g, another showed no gain and four others lost a total of 455 g. Three of these adults were females which should have been mating and becoming pregnant during the January-February period they were observed. Only one gained weight, however, while another managed to maintain its weight over a 24 day period. The third lost 205 g during a 43 day period.

The subadults appeared to have gained weight better than the adults. Of the 14 black subadults that were weighed a number of times, six were followed through fall and winter and gained a total of 245 g.

Table 7. Climatological data for Lansing, Michigan, during the Winters of 1977-78, 1978-79 and 1979-80.

	Days with Minimum Temperature Below 0^{o} F	Days with Average Daily Temperature Below 32^{o} F	Degree Days Below 32^{o} F	Monthly Ave. Temperature Departure From Normal	Snowfall Per Month (Inches)	Days with Snow on Ground Over 2 inches
1977-78						
Nov	0	9	74	+ 1.1	8.1	5
Dec	3	19	254	- 1.8	13.3	9
Jan	6	30	441	- 5.0	34.0	31
Feb	14	28	564	-12.7	6.7	28
March	7	20	249	- 7.3	4.6	28
Total	30	106	1582	-25.7	66.7	101
1978-79						
Nov	0	7	28	+ 1.4	7.0	3
Dec	0	20	176	- 0.3	14.7	17
Jan	10	31	486	- 6.5	27.1	29
Feb	13	26	536	-11.0	4.1	28
Mar	0	9	71	+ 4.9	4.2	4
Total	23	93	1297	-11.5	57.1	81
1979-80						
Nov	0	10	33	0.0	7.2	3
Dec	1	17	127	+3.5	3.2	4
Jan	4	26	320	-0.4	6.7	1
Feb	6	23	366	-4.4	5.5	6
March	2	14	149	-3.0	8.8	3
Total	13	90	995	-4.3	31.4	17

Table 8. Changes in the weights of East Lansing, Michigan, squirrels captured more than once during the October 27, 1979 to February 22, 1980 trapping period. Weights in grams.

	I.D. Number		Sex	Age Group	First Capture Weight	Last Capture Weight	Weight Gain/ /Loss	Number of Days Between First and Last Captures	Comments
B	1	70	M	JUV	305	305	0	6	
L	2	73	M	SUB AD	465	500	+ 35	99	
A	3	74	F	SUB AD	495	555	+ 60	117	
C	4	76	M	SUB AD	515	520	+ 5	2	
K	5	77	F	SUB AD	460	480	+ 20	4	
	6	78	M	SUB AD	475	540	+ 65	94	
S	7	79	F	SUB AD	510	555	+ 45	9	
Q	8	81	M	SUB AD	505	490	- 15	91	
U	9	83	F	SUB AD	440	450	+ 10	4	
I	10	84	F	JUV	360	380	+ 20	2	
R	11	85	M	SUB AD	450	440	- 10	21	
R	12	86	M	JUV	330	345	+ 15	15	
E	13	87	F	JUV	310	315	+ 5	2	
L	14	89	M	SUB AD	500	485	- 15	19	
S	15	94	M	SUB AD	470	480	+ 10	95	
	16	97	F	JUV	320	435	+115	65	
	17	98	F	JUV	330	380	+ 50	2	
	18	99	M	SUB AD	450	540	+ 90	105	Lost weight to 385 before gaining to 540
	19	101	M	JUV	385	430	+ 45	7	
	20	105	M	JUV	395	510	+115	99	
	21	106	M	JUV	365	490	+125	99	
	22	107	F	JUV	370	435	+ 65	79	
	23	121	F	SUB AD	525	530	+ 5	17	
	24	124	F	SUB AD	505	465	- 40	19	

Table 8 (cont'd.)

	I.D Number		Sex	Age Group	First Capture Weight	Last Capture Weight	Weight Gain/ /Loss	Number of Days Between First and Last Captures	Comments
F	1	36	M	AD	800	690	-110	80	
O	2	82	F	SUB AD	660	750	+ 90	107	
X	3	88	F	JUV	335	380	+ 45	6	
	4	90	M	JUV	445	440	- 5	19	Lost weight to 385 before gaining to 440
S	5	100	M	SUB AD	605	640	+ 35	57	
Q	6	110	F	SUB AD	600	560	- 40	89	Gained weight to 675 before losing to 560
U	7	111	M	AD	825	715	-110	84	
I	8	114	F	SUB AD	610	620	+ 10	88	
R	9	115	F	AD	935	980	+ 45	69	
R	10	117	F	AD	825	620	-205	43	
E	11	118	M	AD	765	735	- 30	25	
L	12	122	F	AD	770	770	0	24	
S									

Four subadult fox squirrels were also followed through most of fall and winter but managed to gain only a total of 95 g.

Perhaps the most spectacular weight changes were recorded for black juveniles. The summer litters in 1979 were well behind schedule, the juveniles first emerging from the nest in late October and early November and weighing slightly more than 300 g. Had they been subjected to the typical late fall/early winter weather of Michigan, they would have had little chance of survival. However, the very mild weather that occurred allowed them to achieve subadult weight (450+ g) by the time the first snows and cold weather arrived in January. Ten black juveniles gained a total of 565 g, of which four individuals were followed through fall and winter and accounted for a total of 430 g gained.

Only two fox juveniles were captured during the fall, but neigther was captured or observed during winter. One individual gained 45 g in a week, while the other lost 60 g before regaining 55 g within a three week period.

Since the ten black squirrel juveniles contributed significantly to the total black squirrel weight gain, but the two fox squirrel juveniles made only a slight contribution to the total fox squirrel weight gain, statistical comparisons were made only between the adult and subadult black and fox squirrels (Table 9). While the total weight gain/loss of the 14 subadult black squirrels handled throughout the entire trapping period (regardless of how long they were followed) was +265 g, and that of the 10 adult and subadult fox squirrels was -315 g, the difference between the means of these groups was not significant at

Table 9. Comparison of adult and subadult black and fox squirrel weight changes (in grams) captured in East Lansing, Michigan, from October 27, 1979 to February 22, 1980. Differences between means tested with t-test.

	Number of Individuals	Identification Numbers *	Total Weight Gain/Loss	Average Weight Gain/Loss	Comments
Black squirrels caught more than once	14	73 - 74 - 76 - 77 - 78 - 79 - 81 - 83 - 85 - 89 - 94 - 99 - 121 - 124	+ 265	+ 18.93	Average weight gain/loss of these groups not significantly different at .05 level, but significantly different at 0.1 level
Fox squirrels caught more than once	10	36 - 82 - 100 - 110 - 111 - 114 - 115 - 117 - 118 - 122	- 315	- 31.5	
Only individuals followed through entire trapping period.	6 black	73 - 74 - 78 - 81 - 94 - 99	+ 245	+ 40.83	Not significantly different at .05 level, but significant at 0.2 level.
	7 fox	36 - 82 - 100 - 110 - 111 - 114 - 115	- 80	- 11.43	
Only individuals followed through winter weather period (1/5-2/22/80)	6 black	73 - 74 - 78 - 81 - 94 - 99 -	+ 235	+ 39.17	Significantly different at .05 level.
	9 fox	36 - 82 - 110 - 111 - 114 - 115 - 117 - 118 - 122	- 315	- 35.00	

*See Table 8.

the .05 level, but was significant at the 0.1 level. Also, while the total weight gain/loss of the 6 subadult black squirrels followed through the fall and winter was +245 g, and that of the 7 adult and subadult fox squirrels was -80 g, the difference between the means of these groups was not significant at the .05 level, but was significant at the 0.2 level. The groups of individuals involved in these comparisons showed weight fluctuations occurring during fall and winter. When comparing the weight changes occurring in individuals followed only during the winter weather period (1/5 - 2/22/80), however, the 6 subadult black squirrels gained a total of 235 g and the 9 adult and subadult fox squirrels lost a total of 315 g and the difference between the means was significant at the .05 level. Apparently the fox squirrels did fine during the mild fall and early winter weather, but had difficulty maintaining weight when the winter weather finally arrived. This was so in spite of the fact that this weather was not as severe as that occurring in the previous winters.

Nests

Overwinter Leaf Nest Sites

The number of winter leaf nests maintained in the various tree species by black and fox squirrels changed appreciably from the Winter of 1978-79 to the Winter of 1979-80 (Table 10). The nearly 50% increase in total leaf nests in the Winter of 1979-80 may have been due to the milder weather that winter and/or an increased squirrel population (see population estimates). While oak trees contained the largest number of leaf nests during both winters, there was only a

Table 10. Comparison of tree utilization as winter leafnest sites in dominant tree regions by squirrels in East Lansing, Michigan.

		Number of leaf nests maintained in each tree species									
		Oak	Elm	Maple	Hickory	Apple	Willow	Ash	Others	Total Nests In Region	Percent Increase
Winter of 1978-1979	Oak Region	96	2	2	2	--	--	1	--	103 50.7%	
	Elm Region	2	33	2	--	--	--	--	5	48 23.6%	
	Maple Region	9	6	27	--	2	4	--	--	42 20.7%	
	Hickory Region	1	1	3	5	--	--	--	--	10 5.0%	
	Total nests in species	108 53%	42 20%	34 17%	7	2	4	1	5	203	
Winter of 1979-1980	Oak Region	100	3	14	1	--	1	4	4	127 41.9%	23.3
	Elm Region	2	38	15	--	1	--	--	2	58 19.1%	20.8
	Maple Region	12	25	50	--	7	6	--	7	107 35.3%	154.8
	Hickory Region	2	1	2	4	1	--	--	1	11 3.7%	10
	Total nests in species	116 38%	67 22%	81 27%	5	9	7	4	14	303	49.3
Percentage Increase		7.4	59.5	138.2							

slight increase in the second winter. The largest part of the increase in leaf nest number was among the trees in the maple region. The use of maple trees as leaf nest sites also increased throughout the research area.

Winter Nest Aggregations

A major factor influencing the numbers of black and fox squirrels occupying nests over winter (Table 11) was the mating of many females during January and February. Upon becoming pregnant, they either drove out the other nest members or moved out themselves to alternate nests. This resulted in a larger number of single-occupant nests. With the squirrel population in the research area composed of approximately equal numbers of black and fox squirrels, an approximately equal number of single-occupant nests could be attributed to pregnant females for each species. During each winter, however, twice as many single-occupant nests were observed for fox squirrels.

Winter nest aggregations of black squirrels consistently averaged 40-45% larger than average fox squirrel nest aggregations. The differences between these means were statistically significant at the .01 level.

Interactions with People

Of 178 residents interviewed, 51 (28.7%) preferred fox squirrels to black squirrels, 73 (41.0%) had positive opinions in preference for the black squirrels and 54 (30.3%) expressed no preference, enjoying them both equally. None of those interviewed expressed a dislike for squirrels. Only two residents of the research area were known to spend much time "discouraging squirrels from entering their yards."

Table 11. Comparisons between differences in means of black and fox squirrel winter nest aggregations in East Lansing, Michigan.

Year	Black Squirrels Per Nest					Fox Squirrels Per Nest					Differences Between means
	1	2	3	4	Total	1	2	3	4	Total	
1977-78											
Number of Nests	7	14	9	2	32	16	8	3	0	27	Significant
Number of Squirrels	7	28	27	8	70	16	16	9	0	41	at .01 level
				$\bar{x}$ = 2.2					$\bar{x}$ = 1.5		
1978-79											
Number of Nests	6	13	10	5	34	14	10	6	0	30	Significant
Number of Squirrels	6	26	30	20	82	14	20	18	0	52	at .01 level
				$\bar{x}$ = 2.4					$\bar{x}$ = 1.7		
1979-80											
Number of Nests	9	14	7	1	31	20	8	2	0	30	Significant
Number of Squirrels	9	28	21	4	62	20	16	6	0	42	at .01 level
				$\bar{x}$ = 2.0					$\bar{x}$ = 1.4		

Most of the time people considered the black and fox squirrels as a source of pleasure and amusement, sometimes a source of problems and only rarely a source of a quarrel with a neighbor. Most people thought the fox squirrels were friendlier than the black squirrels and could more easily be enticed to take food from the hand or even enter the house. One resident of the research area operated an orphaned animal rehabilitation center in her house and many residents assisted in recovering young from blown-down nests or raising the young until big enough to be released in the neighborhood.

One retired resident derived pleasure from watching a female black squirrel, which nested in the attic, as she crossed the street on the telephone wire. This female, tagged #10 had the habit of traversing the wire upside down, sloth-style.

Squirrels nesting in attics caused problems for some residents. These nuisance animals were easily removed with livetraps obtained from the Ingham County Animal Control Department and the entrances into the attic were then sealed. While most of the residents felt it was their responsibility to make their houses squirrel-proof, one resident did not want any squirrels to come near the house and enforced this preference with a BB-gun and slingshot. This attitude resulted in a perpetual quarrel with the neighbor, who had three feeding stations in the backyard.

Two individuals, residing outside the research area, so disliked squirrels that they each had three live traps operating continuously in their backyards in an attempt to get rid of all the squirrels in the neighborhood. The animal control agent would check the traps daily to remove captured squirrels. Captured individuals would be released about a block away in sympathy with those residents who enjoyed having squirrels in the neighborhood.

DISCUSSION

Distribution of Black Squirrels

Disregarding isolated populations outside East Lansing, twenty years after its introduction into East Lansing the black squirrel population occupied an area of about five square miles (3200 acres). While much of the dispersal may have been natural, a significant portion must be attributed to human activity. A number of independent reports from long-time residents of the research area claimed that a resident, Dr. Musselman, living on Sunset Lane introduced a number of black squirrels to the neighborhood shortly after they had been introduced on the Michigan State University campus. Attempts to verify this failed since the family moved away after the deaths of Dr. Musselman and his wife. Other residents claimed to have moved some black squirrels to Whitehills Estates and near Park Lake Road in the East Lansing area, and even to locations outside the county. The Ingham County Animal Control Department most certainly contributed to the spread of black squirrels through the indiscriminate release of captured nuisance animals.

While the black squirrel population had managed to increase its distribution, it had not exclusively taken over any neighborhoods. Fox squirrels were still found throughout East Lansing and the proportion of black squirrels varied from 25% - 90% of any neighborhood squirrel population. The question is whether the black squirrel will eventually replace the fox squirrel, as they did in Marshall, Michigan.

Perhaps the most interesting question raised by the black squirrel presence in East Lansing was why it had not fared well on the Michigan State University campus. Individual black squirrels were often observed foraging along the edges of the campus and some had spent the entire fall season feeding on campus hickory nuts and acorns. To date, however, none has established a permanent residence. One factor possibly affecting the black squirrels was the presence of large numbers of students whose diurnal activity coincided with that of the squirrels. Compared to the quiet of a residential neighborhood during the daytime, black squirrels might have found a campus of thousands of students and bicycles harassing. The fox squirrels, on the other hand, had adjusted well to that activity and often approached students for "handouts". Perhaps there is a difference between black and fox squirrels in their tolerance of human activity.

Another factor that may have influenced the black squirrels on campus was the presence of many red squirrels (Tamiasciurus hudsonicus) there. Robinson and Cowan (1954) mentioned interactions between introduced eastern gray squirrels and the chickaree (T. douglasii), a close relative of the red squirrel, in British Columbia. Like the red squirrel, the chickaree is territorial and showed a preference for coniferous habitat. The chickaree was dominant in all conflicts with the much larger gray squirrel, but the gray squirrel never hesitated to trespass repeatedly. Conflicts between black and red squirrels on the Michigan State University campus may have affected the black squirrels' success there. At the start of the black and fox squirrel study in 1977, red squirrels were common on campus, but rarely observed in the residential neighborhoods. By the end of the study, however, red squirrels were sighted often in East Lansing and occasionally captured. In 1981, a number of residents reported conflicts involving red squirrels with black or fox squirrels at the supplemental feeders. Another conflict between a red squirrel and a black squirrel concerned the use of a den site. The dispute continued for over two weeks before the black squirrel managed to secure the den for its own use. The role of the red squirrel in the urban squirrel population awaits investigation.

Population

Estimates

Squirrel densities in rural environments vary with the vicissitudes of the natural food supply and may be expected to be less than those of urban squirrel populations which have a more constant food supply. D. Allen (1943) felt that a fall population of three fox squirrels per wooded acre was rarely exceeded and two per wooded acre was considered high. The squirrels studied by Bakken (1952) varied between .04 and 1.9/acre for fox and between 1.0 and 1.3/acre for grays. Brown and Yeager (1945) found fox squirrel densities in Illinois woodlots and wildlife areas to be between .02 and 2.23/acre and gray squirrels to be 1.49/acre. Uhlig (1956) reported gray squirrel populations in four West Virginia state forests varied between

.21 and 1.41/acre, during 1949 to 1954. Thompson (1978b) noted a gray squirrel population density of 1.73/acre in a Toronto cemetery.

The East Lansing squirrel population estimates were made during winter and therefore would have been less than were found the preceding fall. Robinson and Cowan (1954) reported a 21.6% decline in a gray squirrel population from autumn (.88/acre) to spring (.69/acre). A gray squirrel population studied by Longley (1963) experienced a 35% decline from fall (1.0/acre) to winter (.65/acre). Based on the population reductions recorded by these investigators, it is possible to approximate the East Lansing fall squirrel densities.

A squirrel density of 2.4/acre during the Winter of 1979-80 in East Lansing would have been the remnants of a 3.06 - 3.69/acre density in the previous fall, and a density of 1.6/acre during the Winters of 1977-78 and 1978-79 would have survived from a 2.04 - 2.46/acre density in the previous fall. It therefore would be reasonable to expect the East Lansing early fall squirrel population densities during this study to have been between 2.0 - 4.0/acre. This was generally higher than those normally found in rural populations.

Flyger (1970) reported that two "suburban Baltimore woodlots" had squirrel population densities shifting between 1.0 and 5.0/acre. The East Lansing squirrel population, even while living through two severe winters, fluctuated less than this and did not reach as low a level as the Baltimore woodlots. This was attributed to a more constant food supply in the residential ecotype.

Natality

Uhlig (1956) compared the average litter sizes of gray squirrels reported in studies from ten states and England for the years 1934-1955. He found that average litter sizes ranged between 2.1 and 3.43 with the average of all averages being 2.72. The gray squirrel population in a Toronto cemetery reported by Thompson (1978b) averaged 3.1± 0.4/litter. The average number of juveniles for all 48 East Lansing black squirrel spring litters was 3.16± .16. This was much higher than the average reported by Uhlig for rural gray squirrel populations and was comparable to that reported by Thompson. This was true despite the fact that this average included litters influenced by two winters of severe weather and a fall mast crop failure.

D. Allen (1942) reported that 38 fox squirrel litters had an average of 2.92± 0.1 young/litter, Brown and Yeager (1945) noted 85 litters with an average of 2.51/litter, and Packard (1956) found an average of 2.8/litter for 14 fox squirrel nests.

The average of all these 137 litters was 2.65/litter and the average of the 49 East Lansing fox squirrel spring litters was 2.65 ± .16 litter. In compiling this average, the East Lansing fox squirrel population had two years of spring litter averages which would have been among the highest of those reported for rural fox squirrel populations. The one year of poor reproduction (1979), however, lowered the average East Lansing fox squirrel spring litter size so as merely to equal to that reported for rural fox squirrel populations.

Though fox and gray squirrels can have two litters a year, Bakken (1955:55) noted that "the highest percentage of gray squirrel young appeared in June, while the highest percentage of fox squirrel young appeared in July. A smaller, secondary peak occurred in October indicating a second breeding season for the gray squirrel. This was not noted for the fox squirrel." After the peak of spring reproduction, both black and fox squirrel litters in East Lansing emerged from the nest throughout the summer with only a slight second peak occurring in early fall. The number and size of litters for both species appeared to be about equal, except during the Fall of 1979. In late October and early November, a group of eight black squirrel litters averaged 2.5/litter and only one fox squirrel litter of two young appeared. These must have been the second litters of females which produced delayed spring litters. This was the only time there appeared to be any differences between either numbers or size of black and fox squirrel summer litters.

Brown and Yeager (1945) found a considerable overlap in the two breeding and young-rearing seasons of both gray and fox squirrels. Bakken (1952) observed gray and fox squirrel mating-chases from January to June, but neither mentioned ever observing a mixed mating chase. The only report found in the literature concerning a mixed mating chase (Moore, 1968) was that of a fully adult fox squirrel involved in a gray squirrel chase. Black and fox squirrels in the East Lansing area were observed in mating chases from January through July and on only one occasion was a mixed mating chase observed. On that occasion, a queue of four male black squirrels was pursuing a female black squirrel when a fox squirrel joined in at the end of the line. Following the black squirrels through the trees for a distance of about 100 yards, the fox squirrel took up a position in the same tree that the black squirrels did upon stopping. About 15 minutes later, the chase resumed down the tree and across the lawn and the string of squirrels stretched out for about 60 feet with the fox squirrel at the end. Some quick moves by the female lost the last two blacks and the fox squirrel. One of the black squirrels eventually rejoined the chase, but the other black and the fox squirrel wandered off in another direction. The mating chase observed in the East Lansing study area involved a possibly mature, but probably inexperienced one year old fox squirrel. Such behavior is certainly rare and no matings or mixed offspring were observed during this study. No reports of cross-matings between fox and gray squirrels were found in the literature.

The reproduction achieved by black and fox squirrels in the East Lansing area appeared to have been similar for both species in 1978. This resulted in population estimates for the Winter of 1978-79 at about the same levels estimated for that of 1977-78. Reproduction in the Spring of 1979 was delayed to such an extent that most fox squirrels produced only one litter that year. The black squirrel spring litters, though later than usual, were earlier than the fox squirrels' litters. This seemed to allow sufficient time for a number of the black females to have second litters. These litters, emerging from the nests in late fall, managed to survive due to a fortuitously mild late fall and early winter (see Table 7). This resulted in a higher proportion of black squirrels in the trapping area during the Winter of 1979-80. This indicated that changes in East Lansing squirrel population compositions do not occur evenly each year. Rather it seems that small changes would occur following especially stressful winters.

Mortality

With the exception of hunting, the recorded known sources of mortality in rural squirrel populations are few. In an average year, Uhlig (1956:53) reported that 62% of the fall population were young of the year. For the population to remain stable, 62% mortality must occur and, on the average, he found hunting accounted for only 13% of the fall population. He noted that practically every report on gray squirrels concluded the effects of predation were usually not serious. Progulske (1955), however, found that in Virginia gray squirrels were second to rabbits in the diet of bobcats. Packard (1956:50) also noted that while previous investigations of predation on squirrels had yielded an imposing list of vertebrate predators, in most cases predation had been considered relatively unimportant to squirrel populations. During a study of a cemetery population of squirrels, Bakken (1952) reported only nine road kills and Robinson and Cowan (1954) discovered only two squirrels killed by cars and two by predators in an urban park squirrel population, suggesting neither was a major source of mortality.

Clark (1959) noted that the gray squirrel had fewer parasites than most other small and medium sized mammals native to the U.S. and supplied an incomplete list of 48 species of ectoparasites and 30 species of endoparasites. While citing predators and highway kills as contributing to mortality, D. Allen (1942:377) felt the most serious single factor in natural mortality was parasite infestation, specifically mange linked with poor mast crops. Brown and Yeager (1945), however, failed to support this contention. Based on two years of sampling, they found mange in only 0.03% of the 722 fox squirrels and 0.06% of the 353 gray squirrels examined. They concluded that the degree of infestation was negligible in most woodland populations, but that a heavier rate prevailed in some urban populations of both species of squirrel. Ingles (1947), however, reported that a great epidemic of scabies in Bidwell Park, California, in 1913 eliminated all the squirrels inside the 2400 acre park. The disease greatly reduced the squirrel population throughout its range in that state between 1913 - 1921. Uhlig (1956:35) also mentioned that the sudden crash of a population might well be attributed to coccidiosis (a protozoan-caused diarrhea in young squirrels) or malnutrition and mange, with the squirrels dying in their nests. J. Allen (1952:102) found sarcoptic mange at all times of the year, but the incidence was much higher during winter when food was short. Since weight loss accompanied those with mange, he believed mange to be a secondary ailment following dietary deficiency. This work indicated that the study by Brown and Yeager, which found a low incidence of mange, may have been conducted during times of abundant food.

The only other squirrel ectoparasites of any importance were fleas, which Fitzwater and Frank (1944) found in 60% of the active nests examined. Kilham (1959:374) suspected that mosquitoes were important vectors of squirrel fibromas (benign tumors consisting mostly of fibrous tissue). While adult squirrels were resistent, suckling juveniles were very susceptible to the tumor virus.

In the East Lansing squirrel population, the degree of mortality due to malnutrition and accompanying ectoparasite infestations was undetermined. It was believed to be appreciable, however, especially at the end of the severe Winter of 1978-79. The mast crop failure of the preceding fall probably contributed greatly to the poor health of those infested squirrels commonly observed during February and March, 1979. The black squirrels then mostly had only bare patches on the head, while the most seriously mange-affected individuals were fox squirrels. One fox squirrel, observed sunning itself on the edge of a driveway and using a tree trunk as protection against the wind, was bare over 75% of its body and allowed me to approach to within 10 feet before slowly scrambling up the nearby tree. Another fox squirrel observed sunning itself on the low branches of a small tree, had fur only on its legs and parts of its tail. Raw bleeding areas at the base of its tail and in the shoulder region were obvious. This individual allowed me to approach and touch its body with a pencil. While no mangy dead squirrels were recovered, squirrels displaying new growth of fur over large parts of their bodies were never observed in late March, indicating those individuals with severe mange had probably died in their nests.

As was found in the East Lansing study, cars probably account for a large part of squirrel mortality in all urban areas, even when drivers make a concerted effort to avoid hitting them, as has been observed frequently in the research area. Early in the study it was suspected that fox squirrels were more susceptible to being hit by cars because black squirrels showed a greater preference for crossing streets by moving through the trees than fox squirrels did. During the summer and fall of 1977, only one black squirrel was recovered as a car kill, while seven fox squirrels were run over. This appeared to support the idea of greater fox squirrel susceptibility to car mortality. As the study progressed, however, the number of recovered black squirrel car kills increased. This increase could possibly be attributed to the increasing proportion of black squirrels in the research area.

While moving through trees and along wires, squirrels were observed often to make mistakes. Falls to the ground were witnessed on a number of occasions, but only one fatality was recorded. This individual, a juvenile black, fell from a tree to the street below and landed on its head. The only other accidental squirrel fatality was one which attempted to escape from a box trap and managed to work itself halfway out of the mesh wire end of the trap. Caught by its waist and unable to move forward or backward, the individual froze in the snow.

While two orphaned fox squirrels, raised in captivity and released outside the research area, were later killed by dogs, no mortality due to dogs was observed in the research area or reported by residents. Cats, though, were suspected of being the major predator upon squirrels in urban areas. Although only black squirrel cat kills were recovered, three residents in the research area observed that their cats also killed fox squirrels. One woman's cat was reported to catch at least one squirrel a week during summer and fall, most often juveniles. On three occasions, one man attempted unsuccessfully to retrieve squirrels that his cat had killed, but the cat eluded him behind garages and through brush barriers.

Not all cats were killers and the squirrels soon learned to differentiate the "sissies" from the killers. One one occasion, squirrels feeding on a pile of peanuts were observed to pass within two feet of a cat curled up by the door of a house. Moments later, another cat came around the corner of the house and all the squirrels scattered for the trees, chattering loudly.

After observing many cats stalking squirrels, it appeared that the only chance a cat had of killing a squirrel was to approach unseen to within ten feet and catch the squirrel by the back of the neck and head in a quick rush. The three retrieved squirrels killed by cats all had puncture wounds in the skull, neck and shoulder area. Once a squirrel noticed a cat stalking it, the cat had virtually no chance of catching it. One black squirrel, observed feeding at a trap, was chased up a tree by a cat. After chattering at the cat from about six feet up the tree trunk, the squirrel descended and proceded toward the cat, which was between it and the trap where it had been feeding. When within three feet of the cat, the squirrel made a quick lunge at the cat, causing the cat to run about ten feet away. The squirrel fed at the trap for a few more minutes, then moved away. The cat made no further attempt to disturb the squirrel.

A goshawk was known to have spent a winter in the research area, redtail hawks had been sighted circling overhead on a number of occasions and a great horned owl was known to have been present in the research area throughout the study. These predators, however, were felt to have been too few to have accounted for much squirrel mortality.

Road kills and cat predation were believed to have been the major sources of mortality during the study. A combination of malnutrition and disease also were suspected of taking an appreciable portion during winters following food shortages.

Movements

Daily Activity

Rhythms in daily squirrel activity during the year have been reported to follow various patterns in different localities and environments. Studies conducted on gray squirrel and fox squirrel populations in rural woodlots and wilderness areas led Brown and Yeager (1945) and J. Allen (1952) to identical conclusions on their daily activity patterns in Illinois and Indiana, respectively. The gray squirrels displayed a bimodal activity pattern, they found, being most active in the early morning and late afternoon. The fox squirrels, though, had a unimodal activity pattern, being most active from late morning on through midday. Hicks (1949), however, presented data indicating a trimodal daily activity pattern throughout the year for fox squirrels in Iowa.

Horwich (1972) also observed a trimodal summer rhythm for gray squirrels in Maryland, and referred to a general trimodal curve reported for gray squirrels in Great Britain by Shorten and Courtier (1955). Thompson (1977b) also referred to Shorten and Courtier (1955) as reporting three peaks in summer diurnal activity. The 1955 article, however, made no statement and offered no data concerning daily activity patterns. A check of the available literature for articles written by Shorten (1945, 1946, 1951, 1953, 1954, 1955, 1956, 1957a, 1957b, 1959a. 1959b, 1964 and Taylor, Shorten et al., 1971), however, revealed only one statement concerning gray squirrel daily activity patterns, to which the authors must be referring: "The basic rhythm of activity shows three peak periods, the first and most important occurring between seven and ten a.m., the second for a short time around midday, and the last for about an hour before dusk" (Shorten, 1954:111). This statement by Shorten was not supported by data and actually conflicted with a statement made earlier in the book: "Early morning and late afternoon are the chief feeding-times, but when food is abundant and the weather fine, desultory feeding goes on all day," (1954:2). The argument for a trimodal activity pattern for gray squirrels is also weakened by the fact that the data offered by Horwich (1972) concerned the movements of a captive spring litter as the juveniles ventured progressively further from the nest during summer. No evidence could be located which supported the existence of a trimodal daily activity pattern during any season of the year for adult gray squirrels.

Bakken (1952) studied gray and fox squirrel populations sharing the same cemetery near Madison, Wisconsin. He found the gray squirrel daily pattern for spring to have early morning and late afternoon peaks, while the summer and fall activities were irregular with intermittent surges. The winter was more regular than any other season and showed a definite unimodal activity pattern centered around the midday hours. Unfortunately, the cemetery fox squirrel population and the number of observations made on daily activity were too few to make comparisons with the gray squirrel.

Another cemetery population of gray squirrels was studied by Thompson (1977b) in midtown Toronto, Ontario. That study indicated the gray squirrels held basically to a bimodal activity pattern which was most pronounced in summer. Through fall, the peaks were increasingly displaced toward midday until a unimodal winter activity pattern was achieved. The reverse occurred during spring leading to the summer bimodal pattern. Thompson suggested the bimodal activity pattern of summer could have resulted from squirrels avoiding the hottest part of the day, while the squirrels may have selected the warmest part of the day for activity during the winter.

The East Lansing black squirrel daily activity patterns for spring, summer and fall resembled the Toronto gray squirrel activity patterns for spring and fall, having high levels of activity throughout the day. The absence of a midday lull in the black squirrel's summer activity was the most striking difference between these two squirrel populations. The winter activities of both populations showed a similar unimodal pattern, except that the Toronto squirrel population appeared to be active earlier in the morning.

The earlier morning activity of the Toronto gray squirrels was apparent throughout the year. While part of this may have been due to Toronto being east of East Lansing and experiencing sunrise earlier in the same time zone, it probably was more a reflection of the way the data were collected. Thompson recorded observations only during good weather (defined as less than 40% cloud cover, winds of less than 10 mph and temperatures approaching averages) to reduce the effect of weather (1977:1186) and this would tend to increase the level of measured activity in the mornings. Observations on the East Lansing black squirrels were made regardless of the weather conditions, and the inclusion of many cold and inclement mornings would tend to reduce the average measured activity levels.

The East Lansing fox squirrels definitely showed a unimodal daily activity pattern throughout the year, as suggested by J. Allen (1952) and Brown and Yeager (1945). Their day began earlier in the morning, however, and extended throughout the entire day. There was no evidence of a trimodal pattern as indicated in the Iowa squirrel study by Hicks (1949).

Reports for either rural or urban environments could not be found which compared the daily activity patterns of sympatric black (gray) and fox squirrel populations of comparable proportions. The East Lansing black and fox squirrel populations were nearly equal, however, and the observed levels of activity were also nearly equal.

The differences between rural and urban squirrel populations, as indicated by the urban black and fox squirrels having nearly identical daily activity patterns throughout the year, the absence of the midday lull in black squirrel activity and the extension of fox squirrel activity into early morning and after midday, might have been accomodations of a high density urban squirrel population to an abundant food supply. Were all the individuals to feed at the "prime times" typical of rural squirrel populations, an increase in confrontations might result. A lengthening of the typical activity periods by some individuals feeding at other than prime times would avoid or reduce confrontations and all the individuals would obtain their food requirements.

Observations of squirrel behavior during late spring, summer and early fall suggested that aggressive interactions then tended more often to be intraspecific in nature. Interspecific behavior was most often tolerant (see Figure 17). The relationship of squirrel activity periods to intra-and interspecific social status warrents investigation.

Home Range

Home range could be defined as the area an animal traversed in the normal activities of food gathering, mating, caring for young, nest and shelter construction, and obtaining any other requirements for a successful livelihood. This definition necessarily restricts the term to established individuals and would not include young of the year as they moved away from the nest before they finally established themselves somewhere. Packard (1956:26) suggested that home ranges of individual squirrels might be larger in less favorable habitat than in favorable sites. Flyger (1960:365) felt the suitability of the habitat may determine the extent of space required to supply necessities and the degree to which the animals must move about in search of their requirements.

Studies in rural woodlots and forests or city parks and cemeteries indicated that the home ranges in those areas were mostly larger than those observed for the East Lansing residential black and fox squirrel population (5-10 acres). D. Allen (1943) thought fox squirrels moved over 10 acres in a season and perhaps 40 acres throughout the year. Both D. Allen (1943) and Baumgartner (1943) suggested that fox squirrel males moved more and farther than females. Packard (1956) indicated that this applied for both gray and fox squirrels in Kansas. Longley (1963) believed the gray squirrels in the woodlot he studied in Minnesota probably covered most of the 40 acre study area. In a cemetery at Madison, Wisconsin, Bakken (1952) observed that gray squirrel males covered about 24 acres and gray females approximately 10 acres. Fox squirrel females, he said, moved over 13 acres but gave no data for fox squirrel males. Based on measurements of distances gray squirrel males and females moved from their den trees, Robinson and Cowan (1954) estimated that Vancouver city park gray squirrel males moved over the entire study area of 50-55 acres through the year, but that females only moved over an area of 5-15 acres.

Only Flyger's (1960) study of gray squirrels in two 10 acre rural Maryland woodlots and Thompson's (1978a) study of gray squirrels in a Toronto cemetery reported home ranges comparable to or less than those of the East Lansing black and fox squirrel populations. Home ranges of the Maryland woodlot gray squirrels varied from 0.2-7.2 acres with an average of 1.4 acres. The Toronto cemetery female gray squirrels covered 4-5 acres and males about 5-10 acres most of the year. Longley (1963) felt the limited movements reported by Flyger were not typical. He speculated that the condition might be related to the high density of squirrels (6/acre) in the Flyger study. A condition which, he believed, indicated that the squirrels must have had a constant and adequate food supply. Flyger's woodlots probably did supply adequate and varied foods since they consisted mainly of mature stands of large mast producing trees, some of which were up to four feet in d.b.h. That factor was held in common with East Lansing and many other urban areas. Flyger (1970) emphasized the top quality squirrel habitat that is offered in many communities having mature uncrowded trees with large canopies providing excellent squirrel food and shelter. Besides the presence of many large canopied trees up to 52 inches d.b.h. in the East Lansing area, the existence of supplemental feeders provided a generous food supply overwinter.

Concerning behaviors associated with feeding, social group and agonistic interactions, Thompson (1978a) observed no seasonal differences at Toronto in the use of space within the home range. Some East Lansing squirrels, however, appeared seasonally to feed in different parts of the home range. This may have been due primarily to the clumped distribution of trees there (see Figure 3). For example, squirrels with both elm and hickory regions within their home ranges, spent spring and early summer in the elm region and most of the fall in the hickory region. The result was that, during any month or season, the area utilized to obtain living requirements was only a portion of the entire home range as calculated on an annual basis.

Thompson (1978a) also reported a difference between the sexes in the sizes of home ranges during the winter and summer mating periods. The females' ranges remained about 4-5 acres, while the males' increased to 15-30 acres. Flyger's (1960) study revealed no significant difference between the home range of the adult male and female gray squirrel, and no difference appeared to exist between sexes in either the black or fox squirrels of East Lansing.

The larger home ranges for Thompson's Toronto male gray squirrels during mating season possibly may have been due to the sparseness of trees on the cemetery (about 3/acre 13+ inches d.b.h. supplying about 45% canopy cover). These supported a less dense squirrel population (about 1.75/acre) and may have caused the males to move further when mating in order to find females in estrous. Mature woodlots with high squirrel densities (6/acre) or portions of urban areas, as in East Lansing, with parts having 60+% canopy cover and 3+ squirrels per acre, on the other hand, might offer enough females close by.

In summary, the home ranges of East Lansing black and fox squirrels were smaller than those reported for rural squirrel populations.

Probably this was because the urban environment provided a more constant food supply throughout the year. There was a greater concentration of uncrowded trees with large canopies, but also supplemental feeders maintained by residents certainly played a role.

Food Availability

There was no great difference in foods used by black and fox squirrels in East Lansing, and this agreed with the findings of J. Allen (1952) and Bakken (1952). While many exotic horticultural varieties of trees and shrubs were available to they fed mainly on those species also used by rural squirrel populations. Robinson and Cowan (1954) and Thompson and Thompson (1980) also noted this for the park and cemetery gray squirrel populations they studied and concluded that gray squirrels were basically conservative in their choice of foods.

Thompson and Thompson (1980:708) mentioned that "the only type of seed which was seen to be cached was the husked nuts (hickory, oak, horse-chestnut); none of the various samaras was buried,". This behavior was also noted for the East Lansing squirrels. During the mast crop failure in the Fall of 1978, the bumper crop of sugar maple seeds was vigorously attacked in the trees and later foraged for on the ground, but not once was a squirrel observed to bury any of these seeds.

Hicks (1949) reported that snow more than two inches deep impeded squirrel activity. Yet Brown and Yeager (1945) presented photographic evidence that both fox and gray squirrels readily dug through a foot or more of snow to reach food. Experiments by Cahalane (1942) and Thompson and Thompson (1980) indicated that smell was the major faculty used by the gray squirrel to locate buried nuts. East Lansing squirrels, however, were never observed to have dug through more than two inches of snow for buried nuts. It was quite possible, due to the availability of food at supplemental feeders in residential areas, that it was not worthwhile for the squirrel to dig through more than two inches of snow for a buried nut, even if it could be located by smell.

Sharp (1979) observed that at times of mast crop failures, squirrels began deserting his study area by August. J. Allen (1952) and Longley (1963) reported that during times of food scarcity in late winter and early spring, the squirrels stripped bark from trees for food. Neither of these behaviors was ever observed in the East Lansing area, again probably because of the presence of supplemental feeders in residential areas.

Robinson and Cowan (1954) reported that about one-third of the squirrels in the 60 acre study area in their park made some use of artificial food sources. Particularly during winter, a time of food scarcity and the onset of the breeding season, unnatural foods were found to be more sought after than at any other season.

Thompson and Thompson (1980) reported that no "handouts" were sought or received by squirrels in their Toronto cemetery study. Bakken (1952), however, noted that the squirrels in his Madison, Wisconsin, cemetery study were unfed except for one winter feeding station in a backyard bordering the cemetery. This, he said, was heavily used by both gray and fox squirrels in January and February. Black and fox squirrels in the East Lansing study area also relied heavily on the supplemental feeders during winter, and the presence of these feeders markedly changed the foraging behavior of the squirrels.

Pack et al. (1967) suggested that in years of mast scarcity when food was limited in quantity and concentrated in a small area, subordinate squirrels possibly could be refused access to food. The presence of supplemental feeders in residential areas might, therefore, have influenced the structure of the social system of urban squirrels and the subsequent allotment of food.

Interspecific Aggressive Behavior

Pack et al. (1967) and Thompson (1978a) studied the social systems of gray squirrel populations and Bernard (1972) did the same for fox squirrels. Bakken (1952) investigated the interrelationships of gray and fox squirrels in mixed populations, but mentioned little of the actual aggressive interactions between species, mostly because of the low number of fox squirrels in the cemetery. In the course of a year, he recorded only fourteen instances of gray squirrels chasing fox squirrels and nine instances of fox squirrels chasing gray squirrels (1952:159). No reports could be found in the literature concerning the aggressive interactions of these two species.

In the natural condition where food was dispersed under trees or scatter-hoarded by squirrels, Thompson (1978a) found that intraspecific aggression among gray squirrels was virtually absent during winter because a stable dominance heirarchy had been established. Bakken (1952), however, noted that in feeding groups, individual aggression, based on signaling and chasing, was more evident at winter feeding stations on private property adjoining the cemetery than in the natural feeding areas. Bernard (1972) reported that dominant fox squirrel individuals on an artificial feeder, located about six feet up a tree trunk, did not allow others access to the feeder. On the ground, however, aggressive activity was displayed less frequently, with as many as three or four animals feeding peaceably in close proximity to one another.

This behavior was also frequently observed at East Lansing feeding stations which were in an elevated position. While one squirrel would dominate the elevated platform, a number of others might be tolerantly feeding on the scattered droppings below the feeding station. When a feeding station was at ground level, however, one individual at a time used it, and others waited their turn or went elsewhere to forage. These observations suggested that food sources in nature were dispersed in such a manner that it would not be advantageous, or maybe not possible, for an individual exclusively to dominate a large feeding area. When food was presented in a small area that could be easily dominated, however, as occurred at artificial feeders, aggressive interactions increased as individuals attempted to secure a food source for themselves.

Bakken (1952:131) observed that "intolerance increased noticeably in both species in autumn. The beginning of the greater intolerance varied from year to year and appeared to correlate with the size of the mast crop, as it occurred earlier during years of poor mast production." An increase in aggressive behavior at this time of the year was also observed in the East Lansing squirrels. However, it was not only related to the success or failure of the fall mast crop, but was also modified by the severity or mildness of the winter weather.

Bernard (1972:21) noted that severe winter weather prompted an early formation of a dominance heirarchy among fox squirrels and this led to very consistent behavior patterns. "Interactions were always swiftly accomplished and the victor nearly always took his position on the feeder." Pack et al. (1967) reported a rigidity in the social heirarchy established by the gray squirrels which resulted in its stability. Actual physical combat was rarely observed at the feeder, with most social interactions being settled by bluffing. Throughout the winters in the East Lansing research area, intra- and interspecific interactions at the feeders tended to be a mixture of mild, moderate and severe encounters. While some individuals appeared to establish their dominance at a feeder, they frequently had to reaffirm it with chases. No rough-and-tumble combats, however, were ever observed. Some individuals were not dominant at all feeders. If the feeder they dominated became empty, they moved to another where they were sometimes subordinate.

Although the presence of a social heirarchy was not investigated, some form of a complex interspecific dominance heirarchy was suspected to exist.

Bernard (1972:22) noted that "while dominants would feed to repleteness in one hour and then depart, low ranking animals would sometimes remain three or four hours eating discarded fragments and awaiting access to the feeder." Smith and Follmer (1972:89) stated "since the nest serves as insulation for tree squirrels, which have a thin fur and high critical temperature (Hicks, 1949; Irving, Krog, and Monson, 1955; and Muul, 1968), their winter energy requirements for maintaining a constant body temperature will increase in proportion to the time spent out of the nest." Black squirrels in East Lansing were often observed to displace fox squirrels at feeders, which then waited in nearby trees for the black squirrels to finish feeding. By dominating in encounters at the East Lansing supplemental feeders two or three times as often as the fox squirrels, the black squirrels were believed to have secured a more constant food supply for themselves, while at the same time they reduced their exposure to winter weather. This certainly must have enabled the black squirrels to maintain a healthier physical condition through the winter than that of the less frequently dominant fox squirrels.

Weather and Winter Weight Fluctuations

The weights of black and fox squirrels in the East Lansing study during the summer and fall compared favorably with those reported in studies of rural squirrel populations (D. Allen, 1943; Brown and Yeager, 1945; Bakken, 1952; Robinson and Cowan, 1954; Havera, 1977). During the winter months, however, a difference was noted. The average winter weight of the East Lansing adult fox squirrels (about 750 g) was less than that (average = 800 g) reported by Bakken (1952) and the winter weights of the East Lansing adult black squirrels (between 580 - 630 g) was heavier than that (between 410 - 500 g) reported by J. Allen (1952) or by Bakken (average = 500 g; 1952).

Packard (1956:46) reported that a food shortage in the Winter of 1954-55 reduced the weight of both the gray and fox squirrels in Kansas. From December through March, he found that adult fox squirrels lost 10-18 g/month, while young of the previous year lost 20.5 g/month. In contrast, adult gray squirrels lost 6 g/month and young of the previous year lost 7.5 g/month. Adult fox squirrels in the East Lansing study averaged a loss of between 35-40 g/month during the winter. No data were obtained for fox squirrel juveniles or black squirrel adults during the winter, but the black squirrel subadults averaged a gain of almost 3 g/month and the black squirrel juveniles averaged a gain of almost 40 g/month. Overall, the black squirrels of East Lansing fared better during the winter than rural gray squirrel populations, and East Lansing fox squirrels fared worse than rural fox squirrel populations. It should be noted that these recorded weight fluctuations of black and fox squirrels occurred during a mild winter. It was suspected that the difference in weight gain/loss between the species may have been much greater during the severe Winter of 1978-79 which followed a fall mast crop failure.

D. Allen (1942:365) reported that poor health may impede the breeding of a squirrel. J. Allen (1952:58) observed that no pregnant females were trapped and few males appeared to be in breeding condition in Janaury, February and March of 1947, following the fall mast crop failure in 1946. As buds became available in March and April of 1947, squirrel weights increased and by May, males were found in breeding condition and females in estrus. All were capable of breeding, but were four months behind schedule.

Havera (1977:293) felt it was possible that some minimum level of body fat may be needed for fox squirrels to enter estrus and that a subnormal body condition may explain their lack of breeding. He also suggested that a fox squirrel population with a low percentage of carcass fat during the winter breeding season may be expected to show reduced reproduction in the spring and perhaps a decline in abundance or an increase in disease. It is suspected that the East Lansing fox squirrels may have been failing to maintain a minimum of body fat during severe winters while the black squirrels maintained their weight. That the black squirrels had an edge in reproductive success the following year evidently was due to their ability to compete successfully for winter foods.

Nests

Overwinter Leaf Nests Sites

While Fitzwater and Frank (1944) and Robinson and Cowan (1954) found that squirrels in their study areas built the majority of leaf nests in conifers, most other researchers reported a strong preference for oak trees: black oaks held 3/4 of the nests in Allegan County, Michigan (D. Allen, 1942); most nests were in oaks in an Illinois study (Brown and Yeager, 1945); all of the summer and most of the winter nests in Berkshire, England, were observed in oaks (Shorten, 1951); J. Allen (1952) discovered 2/3 of the nests in an Indiana study were located in oak, hickory and maple trees (40% in oak); Uhlig (1956) noted 2/3 of the nests in West Virginia were in beech, maple and oak trees. Bakken (1952) reported nest building by squirrels in a Madison, Wisconsin, cemetery appeared to follow a feeding succession: late spring in elms, summer nests in oak and hickory, and autumn and winter in white oak.

Nest building in response to localized food availability appeared to occur among the East Lansing squirrel population only during the hickory "nut cutting" time of early fall. Most of these nests fell into disrepair during winter, after they were abandoned in late fall by juveniles which built them in the summer and early fall. The observed preference among East Lansing squirrels for oaks as nesting sites was probably due to the overwinter retention of leaves by the trees. Squirrels were observed to gather these leaves throughout the winter to use as added insulation in leaf nests. Even squirrels with nests in other tree species were observed gathering oak leaves.

The preferential use of the oak region for winter nesting sites was more impressive when considering the facts that the maple region was about twice as large (see Figure 3) and contained a higher density of supplemental feeders than the oak region (see Figure 16).

The 50% increase in leaf nest numbers between the Winter of 1978-79 and the Winter of 1979-80 occurred mostly in maple trees. Not only did this result in more nests in the maple trees in the oak and elm regions, but also in all the trees in the maple region. This suggested that the oak trees may have been fully occupied and the squirrels had to locate in less preferred sites, choosing maples over elms.

Winter Nesting Aggregations

Bakken (1959) frequently observed nesting aggregations which were more apparent during non-breeding periods. Uhlig (1956) generally found one gray squirrel for each leaf nest in late fall, while Shorten (1954) mentioned finding as many as nine together in a nest in January. Bakken (1952), however, found the largest number of fox squirrels in a nest to be only four, with seven for gray squirrels. The most fox squirrels observed to be sharing a nest in the East Lansing study area was three, while black squirrels were frequently found four to a nest.

The size of winter nest aggregations was initially believed to be primarily an adaptation for reducing energy loss during the winter, adjustable to meet the needs of the situation. Were this correct, the average nest aggregation would be expected to be significantly different during severe winters or possibly during winters preceded by food shortages. This, however, was not observed. The average sizes of the black squirrel or fox squirrel winter nest aggregations were not significantly different (at the .05 level) during severe winters (1977-78 and 1978-79) compared to a mild winter (1979-80), nor were they significantly different during a winter preceded by a food shortage (1978-79) compared to a winter preceded by abundant food (1977-78).

It was a distinct possibility that the abundance of food available during winter at the supplemental feeders moderated the impact of the severe winter or food shortage. If so, this could result in similar winter nest aggregation sizes for black and fox squirrels from year to year. It seemed likely, however, that energy conservation was just one of a number of factors determining aggregation size.

Other factors may have been physical, health related or social-familial in nature. A maximum size to the nest may be dictated by the physical limitations of the tree to support the nest, and the thickness of the insulation needed in a given climate may limit the internal occupancy space. An increased chance of spreading ectoparasites among nestmates might also limit larger aggregations. Many of the larger aggregations observed appeared to have been sibling subadults with an adult female which were still nesting together while the single nests were often occupied by adult males. The effect of these social aspects on aggregation size merit further investigation.

Interactions with People

The major unique feature of the urban environment was the presence of abundant food, found mostly at supplemental feeders. The majority of these feeders was intended to be used exclusively by birds and much effort was expended by some residents in attempts to squirrel-proof the feeders. While these efforts discouraged many squirrels, no feeder in the research area ever succeeded in being totally squirrel-proof for long, although two did succeed in discouraging all but one individual squirrel. The resourcefulness of the squirrels which frustrated the residents' efforts was often admired and provided a source of pleasurable competition between man and beast.

The management of individual nuisance squirrels could be accomplished by habitat manipulation to make an area unsuitable for squirrels or by the animal-proofing of buildings. Solving the nuisance problem by the removal of an entire species from a large area, however, would seem unlikely to succeed. Flyger (1970) suggested the introduction of fox squirrels into urban communities to replace the gray squirrels, which appeared to be more prone to nest in houses. From the experience of Marshall, Michigan, and the evidence from this study, however, it can be expected that just the opposite would occur.

For most people in the East Lansing research area, the presence of black and fox squirrels added to the quality of life in the urban environment. An appreciation for the values of squirrels was shown by drivers who would stop their cars for squirrels crossing residential streets or swerve to avoid hitting them. It was also demonstrated by a few residents who put up nest boxes for them. But most of all, it was expressed by those residents who conscientiously maintained supplemental feeders during winter. On the area studied, humans greatly altered the environment, benefiting both species of squirrel and probably a number of other urban wildlife species as well.

SUMMARY

The ecology of an urban squirrel population was studied and compared with data on rural squirrel populations. The squirrel population in a 200 acre residential area of East Lansing, Michigan was composed of fox squirrels (Sciurus niger) and melanistic gray squirrels (S. carolinensis). The latter were introduced during the late 1950's and early 1960's. During the 36 month study (June 1977 - May 1980), 128 squirrels (81 black and 47 fox) were individually marked with dyes and observed for more than 4,000 hours.

The main body of the black squirrel population occupied much of East Lansing. An additional eleven isolated populations were scattered throughout the Greater Lansing area. Black squirrels were translocated by residents wishing to have them in their neighborhoods. Their dispersal was aided also by the indiscriminate release of captured nuisance squirrels by animal control agents.

Marked and unmarked black and fox squirrels were counted during periodic winter surveys which followed a predetermined course through a 50 acre trapping area within the research area. Population estimates were derived from these data using Bailey's modified formula of the Petersen estimator. East Lansing squirrel densities were greater than most rural gray and fox squirrel densities. Total (black and fox) squirrel densities measured during three winters ranged between 1.6 and

2.4/acre. Squirrel densities in the autumns preceding those winters were believed to have been between 2.0-4.0/acre.

Average black squirrel litter size ($3.16 \pm .16$) was larger than that reported for rural gray squirrel populations, and the average fox squirrel litter size ($2.66 \pm .16$) was comparable to that reported for rural fox squirrel populations. The mean sizes of black and fox squirrel litters were not significantly different in the Springs of 1978 or 1980. Following a fall mast crop failure and a severe winter, however, the average black squirrel litter in the Spring of 1979 was significantly (.001 level) larger than the average fox squirrel litter. Also during the Spring of 1979, both black and fox squirrel young emerged from the nest significantly (.001 level) later than they had in the Springs of 1978 and 1980. While both species had late litters that spring, the fox squirrel litters were even later than the black squirrels (significant at the .001 level).

Road kills and cat predation were the major sources of squirrel mortality in this urban area. Black and fox squirrels appeared equally susceptible to being killed by automobiles. This may have been influenced, however, by a greater proportion of black squirrels in the total population during the last year of the study. Not all cats preyed upon squirrels and the squirrels apparently learned to distinguish the individual cats which were non-hunters. Malnutrition and mange were evident during late winter and were suspected of contributing appreciably to squirrel mortality during severe winters.

Daily activity levels of East Lansing squirrels were much higher throughout the year than reported for rural squirrel populations. Both black and fox squirrels were similar in their activity patterns, showing high levels of activity from 9 AM - 5 PM. It was suspected these high levels were an accomodation of the high density urban squirrel population to an abundant food supply. Some individuals might have been feeding at other than the prime times found to be typical of rural squirrel populations so as to avoid or reduce urban intra- or interspecific confrontations.

The home ranges of East Lansing black and fox squirrels (5-10 acres in size) were smaller than that reported for rural squirrel populations. It was believed this was due to the more constant food supply provided by the urban environment throughout the year, not only from a greater concentration of uncrowded trees with large canopies, but also from supplemental feeders maintained by residents.

There was no great difference in food species eaten by black and fox squirrels in East Lansing. In spite of the presence of many exotic horticultural varieties of trees and shrubs, urban squirrels fed mainly on those native species also used by rural squirrel populations. East Lansing squirrels did not desert the area at a time of mast crop failure and were never observed to strip bark from trees or dig through more than two inches of snow during the winter. These traits were attributed to the abundance of food supplied by the ubiquitous supplemental feeders. Over 30% of the residents in the research area maintained such feeders, an average of 1.25 feeders per acre. This supplied almost every squirrel nesting overwinter in the research area with at least five feeders within its home range from which to supplement its natural food supply.

During late spring, summer and early fall, urban squirrels fed tolerantly in mixed groups on naturally occurring food sources which tended to be dispersed over large areas (thousands of square feet). Once snow had accumulated to more than two inches, however, squirrels turned to the more easily obtainable supplies at supplemental feeders. These concentrated food sources were easily dominated by individual squirrels and during winter, the levels of interspecific aggression increased dramatically. Black squirrels excelled at dominating feeders, driving away or warning off fox squirrels two or three times as often as they were driven away or warned off by fox squirrels. Although the presence of a social heirarchy was not investigated, some form of a complex interspecific dominance heirarchy was suspected to exist.

Weight fluctuations of the East Lansing squirrel population were followed through the Winter of 1979-80. Black squirrel success in maintaining weight during winter was attributed to their ability to dominate at the supplemental feeders.

Oak trees were preferred for overwinter leaf nest sites, probably because the winter retention of dead leaves trees offered a continual source of insulating material during winter. Maples appeared to be second in preference for leaf nest sites.

Average winter nest aggregation size for black squirrels was significantly (.01 level) larger than that of the average fox squirrel. The average sizes of black and fox squirrel winter nest aggregations did not significantly (.05 level) change in response to more severe winter weather or to food shortages preceding the winter. The availability of food at supplemental feeders during winter were believed to have moderated the impact of these factors.

RECOMMENDATIONS

Management

1) The increasing desire of urban residents to observe wildlife near their homes may lead to unplanned translocations of animals native to other parts of the state or to introductions from out-of-state. Local governments should work with the State Department of Natural Resources to clarify state regulations pertaining to urban wildlife. Local ordinances to prohibit introductions without prior study of the potential consequences may be required.
2) While unrestricted movements of cats in some urban areas may assist in mouse and rat control, it can also result in predation upon some desirable wildlife species (both birds and mammals). In such communities, cat-leash, confinement or impoundment laws should be considered to protect small wildlife species from excessive predation.
3) Animal control departments responsible for controlling nuisance animals in urban areas should set a policy of releasing such captured individuals only into those areas where they are already found.

Future Research

1) Red squirrels. Red squirrels now appear to be abundant enough in East Lansing residential areas to be a factor influencing black and fox squirrel populations. A study to investigate their relationships to black and fox squirrels at the supplemental feeders, to determine whether competition for nesting sites occurs, and to assess whether their territorial nature affects the non-territorial black and fox squirrels should be conducted.

2) Black squirrels on the MSU campus. A study could determine how human activity levels on campus compare with those in residential areas and whether this is a likely factor in the failure of black squirrels to establish themselves on campus. The investigation might also determine what happens to black squirrels which come on campus during the "fall shuffle" and whether juveniles could be introduced on campus and induced to stay. The status of black squirrels in Sanford Woodlot and whether they are spreading on the eastern part of campus could must also be examined.

3) Population comparisons. The distribution and abundance of black squirrels in East Lansing and the Greater Lansing areas should be determined along with population estimates and the population composition (black:fox) in the same 200 acre residential area. Comparisons with 1977-80 data could indiate whether black squirrels are displacing the fox squirrels as occurred in Marshall, Michigan.

4) Social heirarchy. A wintertime study should be conducted involving a number of supplemental feeders and all three squirrel species (red, black and fox) in which every individual is identifiable to determine whether a stable interspecific social heirarchy is established.

5) Daily activity. A study could be made to determine whether all individuals are active throughout the day or only at different time periods selected to avoid confrontations. The influence of an individual's intra- or interspecific social position upon its time of activity might also be investigated.

6) Mortality causes. An intensive study on cat predation should determine whether they contribute more to urban squirrel mortality than do automobiles. The fate of mangy, under-nourished individuals prevalent during late winter must also be determined.

7) Reproductive success. The present study concentrated on average litter size and the time of appearance of spring litters. No information was obtained on the number of females having two litters per year. An improved measure of average reproductive success conducted to determine whether there are significant differences between black and fox squirrels in an urban area is desirable.

8) Nesting. A study of the nesting preferences of urban squirrels could determine whether there is a significant difference between black and fox squirrels in their use of homes and other man-made structures.

APPENDIX A

APPENDIX A

Research explanation sheet distributed to residents of research area at beginning of East Lansing squirrel study

My name is John Fogl and I'm doing research on the behavioral and ecological interactions between fox squirrels (*Sciurus niger*) and black squirrels (*Sciurus carolinensis*, melanistic phase) in the urban environment of East Lansing. The situation here is unique in that one species (black squirrel) has been introduced into a habitat already occupied by a closely related species (fox squirrel) having nearly identical requirements and has managed to increase its population in the face of competition from this established species.

I am interested in what the black squirrel is doing that has resulted in this remarkable increase since its introduction on the MSU campus 20 years ago. Recent observations have indicated there is no aggressive behavior displayed during feeding, each species either ignoring or avoiding the other. I, therefore, suspect the factor most influencing this population increase in black squirrels may be nesting behavior.

The females mate in Dec-Jan and have their litters in Jan-Feb. After nursing them in the nest for 10 weeks, the young of this spring litter come out on their own in March, April, and May. The females may then mate again to produce a summer litter which will be on their own by October. A study relating to squirrel nesting behavior must therefore be conducted through this entire period.

In order to gather specific data about nesting, it will be necessary to identify squirrels as individuals. This will be accomplished by capturing, tagging and marking as many squirrels as possible. Squirrels have never been injured by the box trap to be used in this study, and have only died of shock when left in the trap overnight or harassed by a predator (cat, dog or human). By checking the traps after the morning activity period and also shortly before sunset, I hope to avoid any loss of squirrels.

A numbered tag will be placed in each ear of every captured squirrel, a process as painless as getting your ears pierced. Since these tags are rarely lost, a tagged squirrel can be identified when handled again or when its body is recovered. The fur on certain body regions will be bleached with hydrogen peroxide, along with a combination of numbers and letters. This code bleached into the animal's side fur should be easily discernible at a distance. Since squirrels molt in late spring, they will have to be retrapped during summer, identified by ear tag number and re-bleached.

Hopefully, this research will be accomplished within the next year. Your assistance in the following ways would contribute greatly to this research project.

1. Discourage children, cats and dogs from disturbing the traps or harassing any squirrels already in the traps.
2. Recover any fox or black squirrels recently killed in your neighborhood. Place it in a plastic bag along with a note on

when, where and how it was killed. The teeth can be used to accurately age it, the reproductive organs of the female can give information about size of recent litters, and the skeleton and skin preserved in the MSU Museum collection. (Don't bother with a squirrel if the body is badly crushed and/or decomposed as it would most likely be useless.)

3. Contribute information about squirrel activity near a nest or other interesting behavior of squirrels that was observed.

Should you wish to get in touch with me, my office phone is 355-1725 (8 AM - 5 PM) and my home phone is 351-4212. I also will be checking traps an hour or two before sunset and would be happy to talk with you at that time.

Your cooperation is greatly appreciated.

John Fogl

APPENDIX B

APPENDIX B

News release prepared by the Michigan State University Office of Information Services which appeared in local newspapers during July, 1980.

EAST LANSINGITES ASKED TO COUNT SQUIRRELS

In the late 1950s and early '60s, 20 black squirrels were released on the MSU campus. They promptly moved off campus into the city of East Lansing.

Today, their descendants are being found throughout the Lansing area. And there's some concern that the more aggressive black squirrels may be gradually displacing the larger fox squirrels, as they have in Marshall and some other Michigan cities.

Unfortunately, no one surveyed the fox squirrel population before the black squirrels were released, so no one knows for sure whether the black squirrels are displacing the fox squirrels here or merely coexisting with them.

"What we do know," says John Fogl, a doctoral candidate in the Department of Fisheries and Wildlife at MSU," is that once we had 100 percent fox squirrels. Now we have a mix of black and fox squirrels that are competing for food and nesting sites."

Fogl is studying the distribution of black squirrels in the Lansing-East Lansing area to find out how the introduced black squirrels are succeeding in relation to the fox squirrels. He hopes to establish a benchmark which later researchers can use to monitor changes in the squirrel population. To do this, he is trapping and marking squirrels with ear tags, dye and bleach and asking local residents to let him know where black squirrels are.

Drop him a postcard in care of the MSU Department of Fisheries and Wildlife, he asks, telling him how many black squirrels can be found in your vicinity, and give a street intersection. He'll take it from there.

"With enough information, I could document where they are now and to what extent they have been spread," Fogl says. "Then future researchers will have some data to compare to."

Another aim of this project is to identify topics for future studies. Why the squirrels prefer East Lansing to the campus is an obvious question. How the squirrels have spread so far away from the release point is another. (Fogl surmises that squirrels trapped as nuisances in East Lansing have been haphazardly -- and purposefully -- released in other areas).

The role of bird feeders in the success of the black squirrel's adaptation is something Fogl is particularly interested in. He suspects that the black squirrels, which tend to be more aggressive in defending a food source, dominate bird feeders in the winter. In a harsh winter when natural food is in short supply, this dominance would result in their coming through the winter in better condition than the less aggressive fox squirrels. This, in turn, would give them a reproductive advantage: they would probably breed earlier and produce an extra litter of young per year. Over time, that could give them the advantage of numbers.

Leslie McConkey

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