

S  
L  
O  
B  
E

Pattern of Tree Squirrel Distribution in th  
OSMP Studies 4321

Study



Slobe, Brian

Pattern of Tree Squirrel Distribution in the Boulder Mountain Parks:  
a 10-Year Follow-up Study



by

Brian Slobe

Honors Thesis Submitted to the Department of Environmental, Population,  
Organismic Biology at the University of Colorado -- Boulder

April, 1994

Brian Slobe

Department of EPO Biology

**Pattern of Tree Squirrel Distribution in the Boulder Mountain Parks:  
a 10-Year Follow-up Study**

**ABSTRACT**

The Boulder Mountain Parks (BMP) provide a mosaic of habitats, perhaps unique within North America, in which to observe three species of diurnal tree squirrels. As a 10-year follow-up to a previous study, two species of long-term natural inhabitants, *Sciurus aberti* and *Tamiasciurus hudsonicus*, and one relative newcomer, *Sciurus niger*, were observed. The presence of *Sciurus niger* in BMP was made possible through deliberate introduction along the Front Range in the early 1900s and perhaps more importantly through natural expansion into habitats on the Great Plains altered by human activities (i.e., fire suppression and flood control). Where sample sizes were adequate, there was a significant difference between habitats of species. *S. aberti* was found primarily in ponderosa pine forests, *S. niger* in riparian woodlands, and *T. hudsonicus* in Douglas-fir forests. These results are consistent with those of earlier researchers. I recommend that this unique area be studied further, which may provide insight into processes of competition, invasion, and habitat selection for the three species of coexisting tree squirrels.

## INTRODUCTION

The Boulder Mountain Parks (BMP) are one of the only places in North America where three tree squirrels, *Sciurus aberti*, *S. niger*, and *Tamiasciurus hudsonicus*, coexist (Hall, 1981, Havlick, 1984) (Fig. 1). BMP includes many different habitat types from grassland to ponderosa pine stands and even talus rock (Fig. 2). Not only vegetation, but many other factors probably influence the presence of each species of squirrel.

This introduction presents information on habitat and geographical range, home range and territoriality, and feeding patterns for each species. These variables may play a major role in how the species coexist. I also discuss the role of invasion, competition, and habitat selection, as they are potentially relevant processes in this situation. This study was not intended as a definitive study of the coexisting squirrels, but rather a 10-year follow-up survey to Havlick (1984), in which I emphasize ecological distribution. Numerous questions remain, of course. For example, what effect does the non-native fox squirrel have on the native species? How does increasing foot traffic in BMP influence the pattern of squirrel populations? How does the influx of ornamental, non-native plant species affect fox squirrel distribution in BMP.

### *Invasion*

Species' limits are dynamic on all time scales. Therefore, one must ask, what constitutes invasion? Is an invasion an actual physical entrance into another species' habitat or could invasion be a minor change at a level only noticeable to animal rather than to human observers? To clarify these questions I briefly examine four topics: (1) how an area may be invaded, (2) examples of mammalian invasions, (3) which species may be considered "invaders" in BMP, and (4) the circumstances that make it possible for such an occurrence. Invasion is a process of importance on this study site.

Elton (1958) wrote, "it will be noticed that invasions most often come to

cultivated land, or land much modified by human practice." BMP has been under constant human pressure since the 1860s, when it was logged for timbers used in mining and early city structures (Veblen and Lorenz, 1991). In addition, BMP rivals Yellowstone National Park in the number of annual visitor days, with figures reaching over one million people. While Yellowstone has approximately 0.11 visitors/ha, BMP has 625 visitors/ha, thus representing a six thousand fold difference in visitor density. This many visitors compounded with the proximity of BMP to the city of Boulder has caused disturbance to the area.

Successful invading species often fill in environments which are highly disturbed by humans (Groves and Burdon, 1986). For example, invading species of birds in Australia were most often human commensals and generalist feeders (Groves and Burdon, 1986). Normally, natural communities are composed of a number of coexisting species which utilize a common resource base. There are two types of disturbance (Fox, 1986), which can occur in such communities, endogenous (i.e., wildfires or population explosions of herbivores) or exogenous (i.e., human-induced through change of fire regime or removal of native animals). One example of such invasion within Australia involved *Mus musculus*, the house mouse. In a post-fire, endogenous, community *M. musculus* was introduced and wasn't forced out by the native species, *Pseudomys novaehollandiae*, New Holland mouse; instead they coexisted. Fox (1986) concluded the two were, "ecologically similar species (which) are separated principally by their microhabitat requirements."

A classic example of *Sciurus* introduction and subsequent invasion is the *S. carolinensis* (American gray squirrel), which has displaced the native *S. vulgaris* in many parts of England. The timing of the process ranged from about 2-15 years, and in the Midlands and the southern part of the country there has been almost complete displacement (Elton, 1958).

Recently, Kenward and Holm (1993) suggested that the gray squirrel's success can be attributed to "conservative demographic traits combined with feeding competition." This stems from a failure of *S. vulgaris* to exploit areas where oaks occur in greater than 14% density within British forests. In addition, they reported that local coppiced hazel populations have decreased in post-war times, leading in some areas to a decline in the number of *S. vulgaris*.

Within the BMP, which species can be considered native and which should be labeled invader(s)? Both *S. aberti* and *T. hudsonicus* are native to western coniferous forests whereas *S. niger* is native to eastern North America, and the Midwest, and thus is the invader. Such an introduced species can generally fall into one of Elton's (1958) "outbreaks in populations" whereby a new species invades a native habitat.

The introduction and subsequent invasion by the fox squirrel, in Colorado, has only occurred within the last 90 or so years (Armstrong, 1972). The two major hypotheses why *S. niger*, did eventually make it to the BMP were first, the deliberate stocking by humans which occurred within the South Platte river drainage of northeastern Colorado in the 1900s and 1910s and second, migration that occurred as the squirrel followed the development of irrigation westward since the 1880s. This irrigation has provided a riparian corridor for the fox squirrel as the natural processes of prairie fire and floods have been reduced through human involvement (Gurnell, 1987, Hoover and Yeager, 1953, MacClintock, 1970).

As the fox squirrel has started to move into Boulder County there have been the typical animal/human clashes. As a result the Boulder Humane Society has captured *S. niger*, along with other eastern species including *Procyon lotor*, raccoon, and *Mephitis mephitis*, striped skunk, and released these animals into BMP from the 1970s until as recently as three years ago. These introductions combined with the invasion of ornamental shrubs and

citation?

trees into riparian areas within BMP, have served as a corridor for the invasion of *S. niger* (Armstrong, A., pers. comm.).

The effect the species, *S. niger*, has on BMP is a question that awaits further study. But it is important to note that the BMP represents a fragile area which has all the components necessary (i.e. human and vegetational disturbance) for an invading species to exist and possibly succeed.

### *Competition*

Competition is a central feature of Darwin's theory of natural selection, so it has long figured prominently in the thinking of biologists studying the evolution of biodiversity. From competition among large mammals on the plains of Africa to interaction among corals on the Great Barrier Reef their studies almost always touch upon some area considered to be competition. Consider Darwin's thoughts on the subject: "We have reason to believe that species in a state of nature are limited in their ranges by the competition of other organic beings quite as much as, or more than, by adaptation to particular climates," and he adds, "As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera" (Darwin, 1859).

Obviously, this is not the place for a thorough review of competition. For now I will examine some related concepts to this process: (1) niche, (2) competitive exclusion, and (3) exploitation vs. interference.

Many researchers early in this century found that when species coexisted there were ecological differences between them in microhabitat (Diamond, 1978), such as the way vegetation was used as cover or how food sources were exploited. This suite of resource requirements has come to be

known as the "niche." The niche can be defined as "the resources a species uses, where it finds them and the strategy by which it harvests them" (Diamond, 1978). In the present case I have not tried to determine what each species' niche is within the BMP, but it serves as a convenient term on which to base a discussion of the different factors which may be involved in competition.

A principle that has arisen from the niche concept is competitive exclusion. Diamond (1978) attributes this term to Hardin (1960) and goes on to state, "the separation of niches observed in nature is the outcome of the interspecific competition that Darwin stressed." The problem with competitive exclusion is, how do you prove it is actually occurring? Examples of fighting, resource depletion, and even changing another species' reproductive efficiency have all been mentioned (Birch, 1957, Cockburn, 1991, Diamond, 1978, Ferner, 1974). Diamond concluded that these factors are not reflected in daily battles among species. Rather an equilibrium is reached where coexistence or even complete exclusion occurs between species.

Another differentiation which has been made is exploitative vs interference competition. Exploitative competition occurs when one organism is so much better at using a resource that it actually excludes other organisms from its use. Interference competition, occurs when an animal directly intervenes (by threats or fighting, for example) with another species' use of a resource (Cockburn, 1991).

These types of competition are difficult to demonstrate because they may actually occur over a short period of time, but they may then be reflected in patterns of populations found decades (if not centuries) later. Competition occurs only when resources are in limiting supply. Thus, it is almost impossible to substantiate its occurrence without some kind of experimental manipulation (Armstrong, D., pers. comm., Cockburn, 1991).

These are examples in the literature of interactions between several

pairs of tree squirrel species: *S. niger* and *S. carolinensis*, *T. hudsonicus* and *S. carolinensis*, and *T. hudsonicus* and *S. aberti*. Armitage and Harris (1982) studied coexisting fox and gray squirrels. They found that, "spatial patterning of a species is a result of spatiotemporal distribution of ecological factors such as resources, predators and competitors, and the sociological response of the species to these factors." They hypothesized that this occurred because of microhabitat differences they did not detect or possibly the presence of one species affected the spatial patterning of the other.

Riege (1991) studied an area where the ranges of red and gray squirrels overlapped. Each species exhibited differences in habitat specialization which affected their distribution. He observed minimal interspecific aggression and came to the overall conclusion that the factor which determined the density of both squirrel populations was seed production, conifer seeds for *T. hudsonicus* and nuts for *S. carolinensis*.

Perhaps the example of squirrel interaction most relevant to the present study was done by Ferner (1974). He conducted his study on the same area of the BMP which I did, but 20 years previously. He saw 24 of 25 *T. hudsonicus* in Douglas-firs, whereas 13 of the 14 *S. aberti* were in ponderosa pines. A general overlap of the two species' habitats was noted, where a transition of pine and Douglas-fir existed. Within Abert's squirrel habitat the chickaree would generally not be found. In areas of ponderosa pine where *S. aberti* was absent the chickaree could be commonly found. He concluded that the reason that habitat separation occurred was because of competitive exclusion. This may possibly be explained further by direct interference (i.e., threats or fighting) between the two species.

Again, my study was not designed to elucidate patterns or processes of competition, but simply to document patterns of distribution, for comparison with earlier studies. Nonetheless, competition remains a possible factor



influencing the local distribution of tree squirrels on BMP.

### *Habitat Selection*

"Where do species occur" and "why do they occur there" are two fundamental questions of ecology, often discussed as habitat selection. These actually are complex questions involving both, pattern and process. The pattern of distribution that a species exhibits may be easy to describe. Cockburn (1991) stated, "The habitat of an organism describes the properties of the environment in which the organism lives." This definition suggests patterns can be observed. For the three species of tree squirrels that live in BMP, distributional patterns have been reported as follows: *Sciurus aberti* lives in ponderosa pine forests, *S. niger* lives in riparian woodlands, and *Tamiasciurus hudsonicus* lives in mixed conifer forests (Gurnell, 1987, Heaney, 1984, MacClintock, 1970).

The second part of habitat selection, the process, is much harder to determine. This process may include different variables (e.g., cover available, food proximity and stability, access to water) which affect a species' occurrence in an area. While certain biological aspects such as canopy cover and mast production can be measured, we often cannot directly attribute a species' presence to one factor or another. Also, factors which are difficult to measure in a natural environment (i.e., competition and invasion) may also influence this process. Finally, relevant cues or stimuli of behavioral "mechanisms" of habitat selection are mostly unknown.

I have concentrated on the patterns each species of squirrel exhibits in BMP, and have not directly examined the process of habitat selection in this study, although the processes may play a vital role in the coexistence of the three species of squirrels within BMP.

## *Attributes of Species*

### *Sciurus aberti*

*Geographical range and habitat* -- *S.aberti*, commonly known as Abert's squirrel, is native to a band of western states including Arizona, Colorado, New Mexico, Utah, Wyoming and northern parts of Mexico (Gurnell, 1987, Nash and Seaman, 1977). The local subspecies, *S. a. ferreus*, was named by True in 1894 and is distributed from extreme south-central Wyoming south through Colorado into New Mexico east of the Rio Grande (Hoffmeister and Diersing, 1978). It is confined to a very specific habitat type, ponderosa pine (*Pinus ponderosa*) forest and rarely ventures outside these stands (Armstrong, D., 1972, 1975, Gurnell, 1987, Heaney, 1984, MacClintock, 1970, Snyder, 1992, 1993, Snyder and Linhart, 1993).

*Territoriality* -- Gurnell (1987) stated that most squirrels of the genus *Sciurus* have overlapping home range systems that follow a dispersed social organization based on an inter-individual distance. This was documented within the BMP study site by Farentinos (1972) who noted that *S. aberti* remained solitary during the non-mating season and observed intraspecies interaction only when competing for food or when the females defended nest territories. In addition, he mentioned that established squirrels seldom moved to other parts of the forest during his observation period of 1000 hours. On average, the home range of Abert's squirrel is 2-13 ha depending on season, age, and gender (Nash and Seaman, 1977).

*Feeding pattern* -- Of the three species studied, Abert's squirrel has the most specialized feeding pattern. Its main sources of food come from ponderosa pine in the form of seeds, inner bark, apical buds, and staminate flowers (Farentinos, 1972). This foraging pattern extends to preference for individual trees based upon low levels of particular monoterpenes (Capretta et al., 1980, Snyder, 1992, 1993, Snyder and Linhart, 1993). This leads to the

establishment of feeding trees which are conspicuous in the stand because of their obvious lack of the parts of many branches and the abundance of these parts lying on the ground below (Fig. 3). The squirrels occasionally eat fleshy fungi, dandelions, and wildflowers (Farentinos, 1972). This use of fungi, with their high water content and their nutritional value, has been suggested as a major reason why Abert's squirrels are able to maintain their presence in ponderosa pine forests of the Southwest (Sanford and States, 1984).

### *Sciurus niger*

*Geographical range and habitat* -- Perhaps the most common tree squirrel known to Americans is the fox squirrel (*S. niger*). Originally a native of the East and Midwest it has spread westward via stocking and migration along irrigation ditches and river bottoms (Hoover and Yeager, 1953). The subspecies which occurs locally is *S. n. rufiventer*.

Hoover and Yeager (1953) reported finding eight reliable stocking records of *S. niger* within Colorado. The first, occurred prior to 1908 midway along the South Platte drainage near Greeley. Others occurred near Sterling, in 1921, near Fort Collins before 1927 and the rest occurred within the Platte river valley until 1927. In addition, the fox squirrel has moved to the north and west from its ancestral distribution in Nebraska by following the development of irrigation of the South Platte tributaries (Hoover and Yeager, 1953).

The fox squirrel is very adaptable to many different habitats from its normal eastern deciduous broadleaf forests to mixed forests including pines. It thrives in semi-natural areas like city parks, large estates and college campuses (Gurnell, 1987, Heaney, 1984, MacClintock, 1970, Wiegl et al., 1989).

*Territoriality* -- Their home range is very similar to *S. aberti* except that there occurs a movement of home areas during the breeding season (Gurnell, 1987, Heaney, 1984, Hicks, 1949). Baumgartner (1943) mentioned there is

normally thought to be a population pressure correlated with a shortage of food, yet he observed the most movement of squirrels when food amounts were at their highest. He attributed this to "intra-species intolerance." He supported this notion by stating "that no record of excessive fox squirrel population either in literature or in field could be authenticated." His own field work showed about two squirrels per acre (4.9 per ha) on a study site in Ohio. ? How dense? - urban pop?

*Feeding pattern* -- The fox squirrel feeds on the buds of a variety of trees including: *Populus deltoides* (cottonwood), Ulmaceae spp. (elm), box elder, maple, *Quercus* spp. (oaks), *Carya* spp. (hickories), *Fraxinus pennsylvanica* (green ash), and *Salix fragilis* (crack willow) (Armstrong, A., pers. comm., Farentinos, 1972). The cones of conifers are also eaten with fruit and berries added in the summer. It has been reported fox squirrels will also eat mycorrhizal fungi as a subsidiary food source thus acting in forest maintenance (Gamroth and Weigl, 1987). But since human introduction of grains, these have become a main staple which has served to facilitate the western migration of the species by following new settlement and farming (Weigl et al., 1989).

### *Tamiasciurus hudsonicus*

*Geographical range and habitat* -- A variety of common aliases -- red squirrel, pine squirrel, chickaree -- are all used for the same species, *Tamiasciurus hudsonicus*. They range from northern Alaska throughout Canada and the northeastern United States and southward, along the Rocky Mountains, to New Mexico (Hall, 1981). The chickaree's habitat is coniferous forests.

*Territoriality* -- Gurnell (1987) noted that this is the most territorial of all North American tree squirrels. He added that home ranges overlap and territories are circular which makes it easier to accumulate and defend their cone caches. This hoarding of food (i.e. conifer cones) ties in directly with the territoriality of this species, and is one of the main reasons why an area would be defended (Glanz, 1984, Gurnell, 1987, Heaney, 1984, Hurley and Robertson,

1990). Gurnell (1987) reported that in most coniferous forests throughout their range each territory is exclusive, being defended year round. Overall, he concluded their territoriality is tied to economically defensible food supplies in mature, boreal and temperate coniferous forests, while in deciduous forests (at the southern limit of range) the chickaree was not territorial, much like *S. niger*. This theory is supported by many others (Kemp and Keith, 1970, Price et al., 1990, 1993, Riege, 1991).

*Feeding pattern* -- Smith (1981) noted that pine squirrels were either fungi or conifer seed specialists. He stated, "overriding emphasis of selection on both species of *Tamiasciurus* has been for the efficient storage of foods that are ephemerally suitable for harvest rather than for the ability to forage for and digest a specific type of food." He added that there would be too large an increase in effort and time expended while carrying the food to make any specialization advantageous. Riege (1991) stated that *Sciurus* species were more suited to deciduous habitats producing large nuts, whereas *T. hudsonicus* was better suited to habitats producing smaller seeds (i.e. maple, elm and various conifers) based on their "reported distribution in eastern hardwood forests."

## METHODS

Boulder Mountain Parks, Boulder County, Colorado include an area where three species of tree squirrels coexist: *Sciurus aberti*, *Sciurus niger* and *Tamiasciurus hudsonicus*. The squirrels in this area were studied by Ferner and Farentinos in the 1970s and have been investigated more recently by Havlick (1984), and Rooth (1992). In an attempt to see how the passage of 10 years has affected Havlick's findings I have tried to replicate her study in as much detail as possible.

The study area includes several broad types of vegetation: ponderosa pine (*Pinus ponderosa*) stands, riparian woodlands, and Douglas-fir

(*Pseudotsuga menziesii*) stands (Fig. 2). Since Havlick conducted her research, Jones (1990) has made a comprehensive vegetational map of the area. On this map he differentiated between ponderosa pine and Douglas-fir forests by the amount of canopy cover and percentage of mature trees. To qualify as ponderosa pine forest, the canopy cover must exceed 50% and more than 75% of the mature trees must be ponderosa pines. To be considered a Douglas-fir forest, 75% of the mature trees must be Douglas-firs. He also broke down the riparian areas into two categories: cottonwood/willow and box elder/maple. By separating the transect route into 250 m sections and examining these following Jones's guidelines, I was able to standardize Havlick (1984), Rooth (1992), and my own study into one vegetation map of uniform scale (Fig. 2), thereby setting the basis of habitat type to a standard rather than leaving it to the judgment of the observer. In addition, the two riparian woodlands, Jones listed, are clumped into one area, thereby consistent with the three vegetation types used in the previous studies. The sightings from all three studies could then be compiled into one comparative data set. The areas are now broken down into riparian (1.2 km of trail), ponderosa pine forest (3.1 km), and Douglas-fir forest (0.6 km).

Through Havlick (pers. comm.) I was able to adjust the current trail system, reflecting 10 years of land management, to one that closely represented her original transect area. The following trails, or sections thereof, were surveyed: Enchanted Mesa, McClintock, Mesa, Skunk Canyon and Wood's Quarry (Fig. 4) as listed in "1993 Trail Map: Boulder Mountain Parks and Nearby Open Space" (Bereck, 1993) (initially derived from USGS 7.5 minute topographic maps of Boulder, Eldorado Springs, Louisville, and Niwot quadrangles). The section of Royal Arch Trail which Havlick included in her study I omitted because it was not clear from Havlick (pers. comm.) how many times she covered that section each season. Elevation of the study area ranged

from 1771 m (5800 ft) at the bottom of Skunk Canyon to 1910 m (6400 ft) at Wood's Quarry.

I walked the transect during three seasons: summer (August 1993), early winter (December 1993/January 1994) and late winter (February/March 1994). For each season a total of ten (10) passes was made on the transect. Following Havlick's example, these were done within one hour of sunrise with each lasting approximately three hours. Total field time was 90 hours.

To determine the number of squirrels within the area, the transect was walked slowly, taking time to scan the ground and among the branches of the trees with 7x35 binoculars. I stopped frequently to listen for vocalization or movement by the squirrels. *T. hudsonicus* was the most vocal; many times I would hear their chattering call even before seeing them. For *S. aberti* telltale signs were piles of terminal ends of ponderosa pine branches beneath trees or the sound of falling cone scales as the squirrels ate conifer seeds. Once an animal was located the following were recorded: species, number of individuals, general habitat type, location and other characteristics including food (if eating) and behavior. To pinpoint the location of each squirrel I used a grid system developed by Farentinos (1972) which marked ponderosa pine trees throughout much of the area with small metal tags. By transferring this grid system onto the general area map a location could be determined within 10 m. All of the above data were recorded on a separate field observation chart and study site map (Appendix A).

## RESULTS AND DISCUSSION

Because a major focus of my study is follow-up comparison with a study by Havlick (1984), my field results are merged with general discussion. I (1) describe patterns of distribution, (2) report numbers of squirrels per hour, and (3) discuss various factors which may influence these observations.

During the summer season (August 10-22, 1993) a total of 13 Abert's

squirrels, 23 fox squirrels, and 10 pine squirrels were observed (Fig. 5). All of the Abert's squirrels were seen in ponderosa pine habitat. Of these, seven were in ponderosa pine trees, one was in a Douglas-fir tree, and five were on the ground. Seven Abert's squirrels were observed eating or in the process thereof (three on ponderosa pine cones, three carrying such cones and one chewing on a unknown kind of conifer cone):

Of the 23 fox squirrels observed, eight were in ponderosa pine trees (two were eating ponderosa pine cones), 10 were located in the backyards of the homes which line the beginning of the Enchanted Mesa Trail, and five were located in deciduous trees (where one was eating chokecherries). Ten pine squirrels were observed within Skunk Canyon, eight of which were in ponderosa pine trees and two were foraging on the ground.

Figure 6 shows a general increase in the number of squirrels per hour for the summer season, 1984 to 1994, for all three species. Squirrels/hour observed by Havlick (1984), Rooth (1992) and I are, respectively: *S. aberti* = 0.18, 0.38, 0.43; *S. niger* = 0.25, 0.58, 0.77; and *T. hudsonicus* = 0.1, 0.33 (*T. hudsonicus* was not studied by Rooth, 1992). At first glance this seems to indicate that the overall population of squirrels within BMP is on the rise, but several factors must be considered before making this assumption. Squirrel populations fluctuate from year-to-year with availability of cones and seeds (MacClintock, 1970). In 1984 cone production of ponderosa pine was low (Havlick, 1984; Snyder, M., pers. comm.) Therefore the base year, 1984, may not have been a "typical" year upon which to base an assumption of increasing population size.

Another factor to consider is the months when the studies occurred (Havlick, June, Rooth, June/July, Slobe, August). This difference may influence numbers seen and also help explain the shifting of the general area in which squirrels were sighted. Havlick observed Abert's squirrels solely on the



Enchanted Mesa, pine squirrels only in upper Skunk Canyon, and fox squirrels in Bluebell Canyon (in the border area between ponderosa pine and riparian habitat). Rooth observed Abert's squirrels in two areas on Enchanted Mesa. She also saw fox squirrels near the base of Enchanted Mesa Trail and on the section of Mesa Trail between McClintock and Skunk Canyon trails where they overlapped with Abert's squirrels. My sightings place Abert's and pine squirrels in the same area as Havlick, and Abert's squirrels in a location similar to that reported by Rooth, but there was a difference in the area occupied by fox squirrels. Havlick's sightings were around the junction of Mesa and McClintock trails in upper Bluebell Canyon, whereas my sightings were grouped lower in the canyon along the beginnings of Enchanted Mesa and McClintock trails. In addition, I did not see any overlap in habitat between fox and Abert's squirrels as reported a year earlier by Rooth (1992). Havlick's and Rooth's studies (done in June/July) may represent times when the diet of fox squirrels includes fruit and berries of plant species that live higher in the canyon. By August, the plant species found lower in the canyon may be producing more food and thus the squirrels follow their food supply.

During the early winter season (December 31, 1993-January 23, 1994) four Abert's, 13 fox, and five pine squirrels were observed (Fig. 7). All Abert's squirrels were seen in ponderosa pine habitat with two foraging on the ground and two in ponderosa pine trees. A possible feeding tree was discovered within 10 m of the two squirrels seen in the trees. This tree showed obvious signs of being vigorously fed upon (Fig. 3). With its many missing terminal branch parts, it fit the characteristics of a "feeding tree" as outlined by Snyder and Linhart (1993).

Of the 13 fox squirrels observed, 12 were within 30 m of a backyard bird feeder located in the beginning of the Enchanted Mesa Trail. Of these, nine were spotted directly under the feeder foraging for dropped seeds and three

were in deciduous trees near the feeder. The only one not seen near the feeder was on the slope between Bluebell Canyon and Enchanted Mesa, where it was having a vocal interaction with a black-billed magpie (*Pica pica*) which occupied the same ponderosa pine tree.

On the fourth of 10 passes over the early winter transect a pine squirrel midden was discovered on the north-facing side of Skunk Canyon. Five pine squirrels were observed after this find. Each was located within 20 m of the midden, two in Douglas-firs and three in ponderosa pines. One was observed eating strips of ponderosa pine bark (2 cm long) from the tops of branches (10-20 cm in diameter). Two possible nests were in a Douglas-fir located directly above the midden.

During the winter season Havlick (1984) observed almost <sup>0.4</sup>~~4.0~~ Abert's/hour whereas I saw fewer than <sup>0.15</sup>~~1.5~~/hour (Fig. 8). Various factors may influence this including the fact *S. aberti* stays in the nest during harsh weather for up to 10 days (MacClintock, 1970). The study site was covered by snow for the whole period in which I made my search. Indeed, the only two days that Abert's squirrels were spotted the weather was sunny and clear; with no sightings occurring on cold, cloudy days. Havlick (1984) observed 0.1/pine squirrels per hour compared with my 0.17/hr (Fig. 8). The factor which seemed to most heavily influence these numbers was the discovery of the location of middens. Havlick reported only seeing pine squirrels near their middens in winter and that a discovery of a third midden in spring increased her sightings by one-third. This corresponds with my observations of pine squirrels only after the location of a midden during the early winter transect. This is consistent with reports of the importance of food caching and the proximity of pine squirrels to their middens in winter (Gurnell, 1987; Kemp and Keith, 1970; MacClintock, 1970).

The biggest difference occurred in the observation of fox squirrels

during the early winter season. I saw a total of 13 in 30 hours of field time whereas Havlick did not observe any in the 40 hours she spent on the study site (Fig. 8). She attributed this to the lack of food present during the winter in BMP and added that most squirrels would ". . . retreat to the private bird feeders which are amply supplied with grains and seeds by City of Boulder residents." This hypothesis seems to be supported by the fact that 12 of the 13 fox squirrels I observed were within 30 m of backyard bird feeders. Snyder also conducted some trapping and telemetry work on fox squirrels on Enchanted Mesa and in Bluebell Canyon in the early 1980s which suggested that during the winter most squirrels would only be found in areas near backyard feeders (Snyder, M., pers. comm.).

During the late winter season (February 20, 1994-March 10, 1994) three Abert's, eight fox and zero pine squirrels were observed (Fig. 9). All Abert's squirrels were seen foraging on the ground within ponderosa pine habitat. One had a gray coat, versus the black coat which I normally observed on the other *Sciurus aberti*. Farentinos (1972) mentioned distribution of coat color, on the BMP study site, to be about one to one (black: 56.7% to gray: 43.3%) but only 1 of 20 (5%) Abert's squirrels I observed exhibited gray coloration.

All eight of the fox squirrels observed were within the riparian habitat. Of these, five were foraging near the bird feeder mentioned previously and three were in deciduous trees located within the riparian habitat but further than 30 m from the feeder. No pine squirrels were observed during the late winter transect.

The number of all three species observed per hour decreased from my early winter to late winter transects (Figs. 8, 10). Abert's squirrel sightings went from <sup>0.15</sup>1.5/hour to 0.1/hour, which is also lower than Havlick's (1984) observations of almost <sup>0.4</sup>4.0/hour. Harsh weather may again be a factor in the

decreased amount of sightings, with the only observations coming on sunny days. The number of pine squirrels per hour also decreased from 0.17/hr to no observations from early to late winter transects. Therefore, the midden located previously seemed to have no effect on sightings during late winter transect. In addition, the fox squirrel sightings per hour decreased, but once again the majority (5 of 8) were seen within 30 m of backyard bird feeders. Figures 11, 12, and 13 which show the total number of squirrels sighted by each observer will not be discussed but were included for general reference within the paper.

The general habitats of each squirrel species have been observed over the last ten years as follows (Havlick, 1984, Rooth, 1992): Abert's squirrel populations have been found only in ponderosa pine stands, pine squirrels have stayed within the confines of upper Skunk Canyon (which supports a Douglas-fir habitat), and fox squirrel occurrence in ponderosa pine has stayed fairly consistent (and low) but has increased in the riparian woodlands (Fig. 2). These patterns are consistent with the reports of others (Farentinos, 1972, Ferner, 1974, Gurnell, 1987, MacClintock, 1970, Snyder, 1992, 1993, Snyder and Linhart, 1993). For my study the null hypothesis of no difference between habitats of species was rejected for the summer transect (Table 1). The hypothesis may again be rejected during the early winter transect except for within the ponderosa pine habitat (Table 1). One reason for significant difference in species occurrence in ponderosa pine was that the numbers involved (five sightings) are small enough to fall into the range where error may occur in a Chi-square test (Marks, M., pers. comm.). The null hypothesis may again be rejected for the late winter transect except for within the Douglas-fir habitat (Table 1). No squirrel species were sighted and thus no statistical analysis could be completed. Both previous studies, (Havlick, 1984, Rooth, 1992), reported a significant difference between areas inhabited and

squirrel species for each of three seasons (Spring, Summer and Winter).

### CONCLUSIONS

The unique habitat and range overlap which occurs within the BMP provides an excellent opportunity to study three species of coexisting tree squirrels. This study served to follow-up Havlick's (1984) work and add new field data following her initial methods. In the summer season, 1993, all three species of squirrels were observed. The number of squirrels observed per hour has increased over the past 10 years but this may be attributed to various factors, including year-to-year fluctuation in squirrel populations and seed production. During the early winter transect, once again all three species were observed, although, compared with Havlick's data, there apparently has been a tremendous increase in the number of fox squirrels. The vast majority (12 of 13) of these sightings were within 30 m of backyard bird feeders which according to Havlick (1984) are a stable food supply for fox squirrels during winter. This is a possible reason for difference between the studies. There was a similarity between Havlick's study and mine in the number of pine squirrels observed and the finding of middens. She mentioned that her sightings increased upon location of middens which corresponds with my observations, which increase from none before a midden was located to five after its discovery. During the late winter transect both *S. aberti* and *S. niger* were observed, while no *T. hudsonicus* were sighted. For the three species, the number of sightings per hour have decreased from the early winter transect (1994) and Havlick's (1984) findings. The increased amount of snow fall and lower temperatures during surveying may explain these differences.

The relationship that exists between habitat type and species was significant where sample sizes were adequate. All observations of *S. aberti* occurred within ponderosa pine forests, *S. niger* was mainly seen in riparian woodlands, and *T. hudsonicus* was found in Douglas-fir forest. These results

also correspond with previous studies (Havlick, 1984, Rooth, 1992), which showed significant difference between habitat types of species. One difference between the present study and previous ones is that I observed little overlap in habitat between fox squirrels and the other two species. One reason for this may be attributed to different months of surveying and the corresponding fruiting patterns of vegetation, especially within Bluebell Canyon.

A number of interesting questions are raised by the three sympatric species on BMP. These include the processes by which the species came to coexist, invasion of a non-native species, *S. niger*, and possible competition for resources and habitat. Unfortunately, these concepts are not easy to investigate in this situation and will require more study before any conclusion may be reached.

I recommend that the unique situation found on this study site not be overlooked. Further study may provide some insight into the processes by which these species came to coexist. In addition, questions concerning the effect of the fox squirrel on *S. aberti*, the role of vegetational invasion in BMP on the species, and the effect of increasing human disturbance, should be addressed.

## ACKNOWLEDGMENTS

Without the guidance, knowledge and wisdom of Dr. David M. Armstrong my completion of this study would not have been possible. I wish to thank him for helping me fulfill the most rewarding educational experience of my undergraduate career. I thank the staff of the Boulder Mountain Parks, especially Ann Armstrong, for support of my efforts and the provision of many needed resources throughout this study. In addition, Dr. Mark Snyder and Val Havlick were both very helpful in providing advice pertinent to my research. Finally, I thank Dr. Allan C. Collins for allowing me the use of his computer facilities and Dr. Michael Marks for his assistance with statistical analysis.

\*\*\* Printed on recycled paper \*\*\*

## BIBLIOGRAPHY

- Armitage, K. B., and K. S. Harris. 1982. Spatial patterning in sympatric populations of fox and gray squirrels. *American Midland Naturalist*, 108:389-397.
- Armstrong, D. M. 1972. Distribution of mammals in Colorado. Monograph, University of Kansas Museum of Natural History, 3:1-415.
- , 1975. Rocky Mountain mammals: a handbook of mammals of Rocky Mountain National Recreation Area, Colorado. Rocky Mountain Nature Association, Inc., Estes Park, CO. 174 pp.
- Baumgartner, L. L. 1943. Fox squirrels in Ohio. *Journal of Wildlife Management*, 7:193-202.
- Bereck, D. 1993. 1993 Trail map Boulder Mountain Park and nearby Open Space. The Boulder Group, Colorado Mountain Club, Boulder, Colorado.
- Birch, L. C. 1957. The meaning of competition. *American Naturalist*, 91:5-18.
- Capretta, P. J., R. C. Farentinos, V. M. Littlefield, and R. M. Potter. 1980. Feeding preferences of captive tassel-eared squirrel (*Sciurus aberti*) for ponderosa pine twigs. *Journal of Mammalogy*, 61:734-737.
- Cockburn, A. 1991. An introduction to evolutionary ecology. Blackwell Scientific Publications, London, 356 pp.
- Darwin, C. 1859. On the origin of species. John Murray, London, 490 pp.
- Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. *American Scientist*, 66:322-331.
- Elton, C. S. 1958. Ecology of invasions. Butler and Tanner, Limited, London, 181 pp.



- Farentinos, R. C. 1972. Social dominance and mating activity in the tassel-eared squirrel (*S. a. ferreus*). Unpubl. PH.D. dissert., University of Colorado, Boulder, 73 pp.
- Ferner, J. W. 1974. Habitat relationships of *Tamiasciurus hudsonicus* and *Sciurus aberti* in the Rocky Mountains. *Southwestern Naturalist*, 18:470-473.
- Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pp. 57-66. in *Ecology of biological invasions* (R. H. Groves, and J. J. Burdon, eds.). Cambridge University Press, Cambridge, 149 pp.
- Gamroth, M. S., and P. D. Weigl. 1987. Mycophagy and the southeastern fox squirrel (*Sciurus niger*). 67th Annual Meeting, American Society of Mammalogists, Albuquerque, NM, Abstract 261.
- Glanz, W. E. 1984. Larderhoarding vs. scatterhoarding by red squirrels in Maine. 64th Annual Meeting, American Society of Mammalogists, Arcata, CA, Abstract 209.
- Groves, R. H. and J. J. Burdon. 1986. Foreward. P. vi in *Ecology of biological invasions* (R.H. Groves, and J. J. Burdon, eds.). Cambridge University Press, Cambridge, 149 pp.
- Gurnell, J. 1987. The natural history of squirrels. Facts-on-file Publications, New York, 184 pp.
- Hall, E. R. 1981. The mammals of North America, second ed. John Wiley & Sons, New York, 2 vols.
- Hardin, G. 1960. The competitive exclusion principle. *Science*, 131:1292-1297.

- Havlick, V. H. 1984. A population index and habitat relationships of three species of tree squirrels in the Boulder Mountain Parks. Unpubl. Master of Basic Science paper, University of Colorado, Boulder, 30 pp.
- Heaney, L. R. 1984. Climatic influences of life-history tactics and behavior of North American tree squirrels. Pp. 43-62 in The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 456 pp.
- Hicks, E. A. 1949. Ecological factors affecting the *S. n. rufiventer*. Ecological Monographs, 19:287-302.
- Hoffmeister, D. F. and V. E. Diersing. 1978. Review of the tassel-eared squirrels of the subgenus *Otosciurus*. Journal of Mammalogy, 59:402-413.
- Hoover, R. L. and L. E. Yeager. 1953. Status of the fox squirrel in northeastern Colorado. Journal of Mammalogy, 34:359-365.
- Hurley, T. A., and R. J. Robertson. 1990. Variation in food hoarding behavior of red squirrels. Behavioral Ecology and Sociobiology, 26:91-98.
- Jones, S. R. 1990. Managing Boulder Mountain Park ecosystems for bird and mammal populations. Boulder, Colorado, 118 pp.
- Kemp, G. A., and L. B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology, 51:763-774.
- Kenward, R. E., and J. L. Holm. 1993. On the replacement of the red squirrel in Britain: a phytotoxic explanation. Proceedings of the Royal Society of London, Series B, Biological Sciences, 251(1332):187-194.
- MacClintock, D. 1970. Squirrels of North America. Van Nostrand Reinhold Company, New York, 169 pp.

- Nash, D. J., and R. N. Seaman. 1977. *Sciurus aberti*. *Mammalian Species*, 80:1-5.
- Price, K., S. Boutin, and R. Ydenberg. 1990. Intensity of territorial defense in red squirrels: an experimental test of the asymmetric war of attrition. *Behavioral Ecology and Sociobiology*, 27:217-222.
- Price, K., and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. *Behavioral Ecology*, 4:144-150.
- Riege, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. *Journal of Mammalogy*, 72:152-162.
- Rooth, J. 1992. Are fox squirrels extending their range to ponderosa pine forests in the Colorado Front Range? Unpubl. paper, University of Arizona, 20 pp.
- Sanford, C. A., and J. S. States. 1984. Food habits of the Abert squirrel--The importance of fungus consumption. 64th Annual Meeting, American Society of Mammalogists, Arcata, CA, Abstract 76.
- Smith, C. C. 1981. The indivisible niche of *Tamiasciurus hudsonicus*: an example of nonpartitioning of resources. *Ecological Monographs*, 51:343-363.
- Snyder, M. A. 1992. Selective herbivory by Abert's squirrel mediated by chemical variability in ponderosa pine. *Ecology*, 73:1730-1741.
- 1993. Interactions between Abert's squirrel and ponderosa pine: the relationship between selective herbivory and host plant fitness. *American Naturalist*, 141:866-879.
- Snyder, M. A., and Y. B. Linhart. 1993. Barking up the right tree. *Natural History*, 102(9):44-49.
- Veblen, T. T., and D. C. Lorenz. 1991. *The Colorado Front Range: a century of ecological change*. University of Utah, Salt Lake City, 186 pp.

Weigl, P. D., M. A. Steele, L. J. Sherman, J. C. Ha, and T. L. Sharpe. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina (U.S.A.): implications for survival in the southeast. *Bulletin of Tall Timbers Research Station*, 1:1-93.

Figure. 1. Distribution of three species of tree squirrels in North America. Adapted from Hall, (1981), by Havlick, (1984.)  
( - - - - = *Sciurus aberti*; ----- = *Sciurus niger*,  
———— = *Tamiasciurus hudsonicus* )

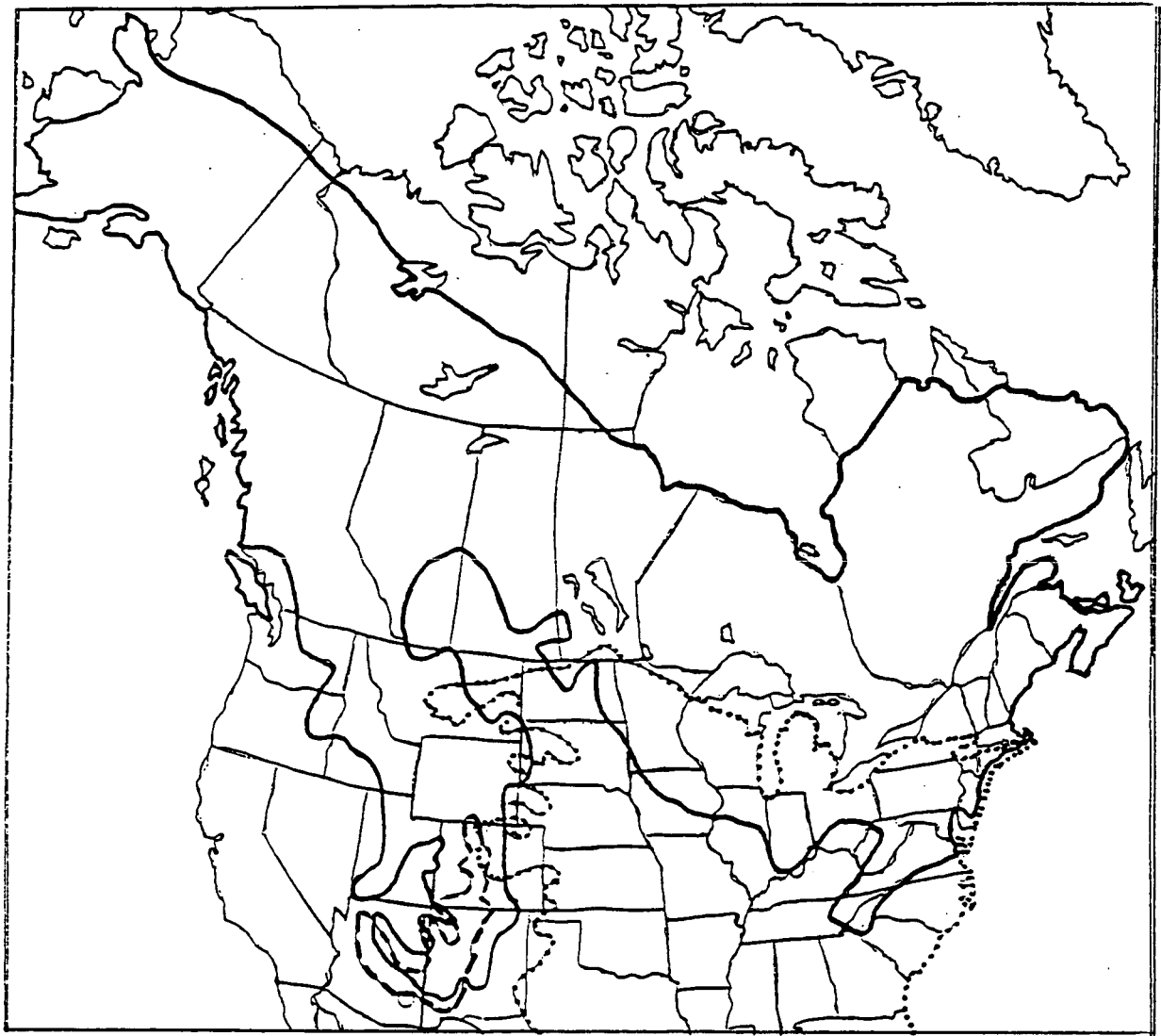
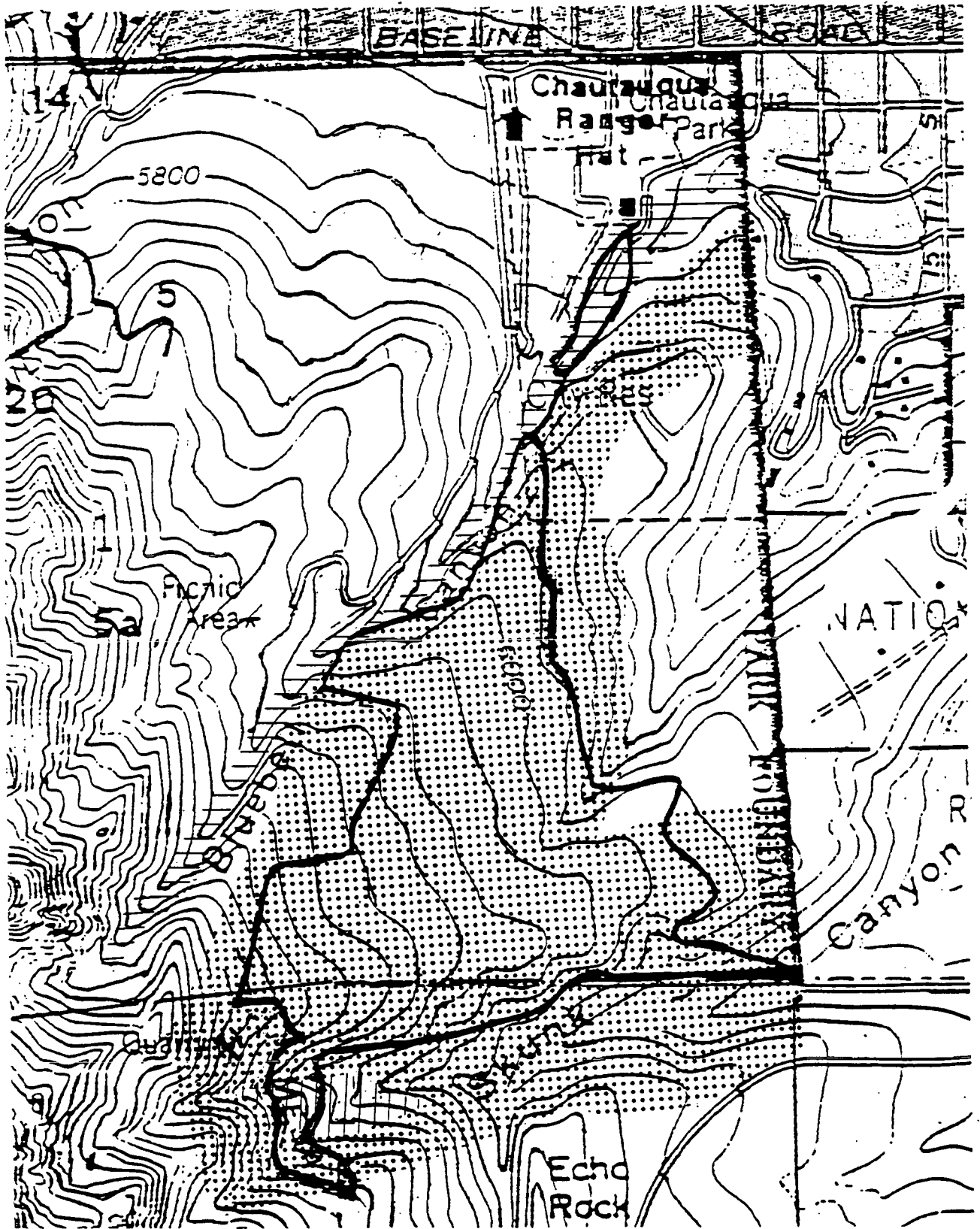


Figure. 2. Map of vegetation types on the study site.

(Area enclosed by horizontal lines = riparian woodlands; stipled = ponderosa pine stands; vertical lines = Douglas-fir stands.)





---

Figure. 3. **Top:** ponderosa pine used as *Sciurus aberti* feeding tree (Note other trees within 10m have complete branches.)  
**Bottom:** terminal ends of branches scattered below feeding tree.

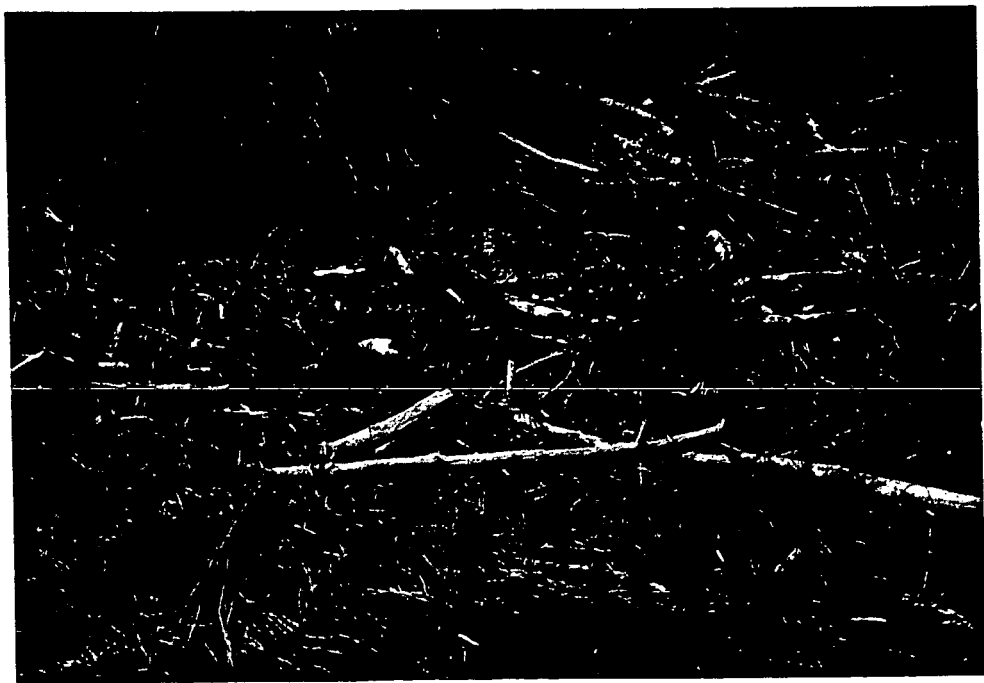
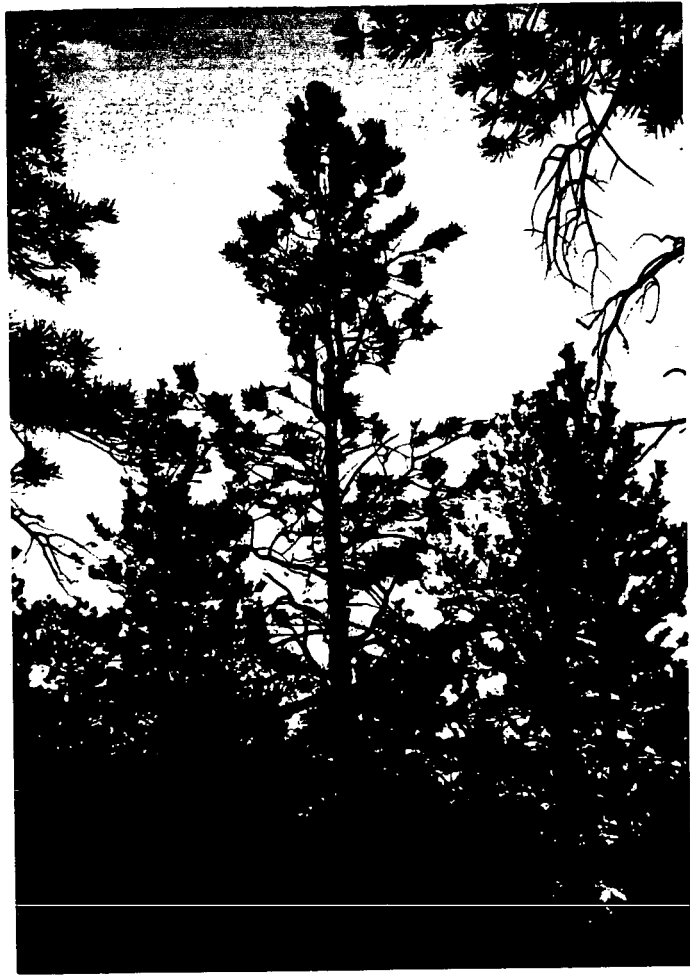


Figure. 4. Map of study site ( ——— = indicates transect route.)

Scale 1:37,000.

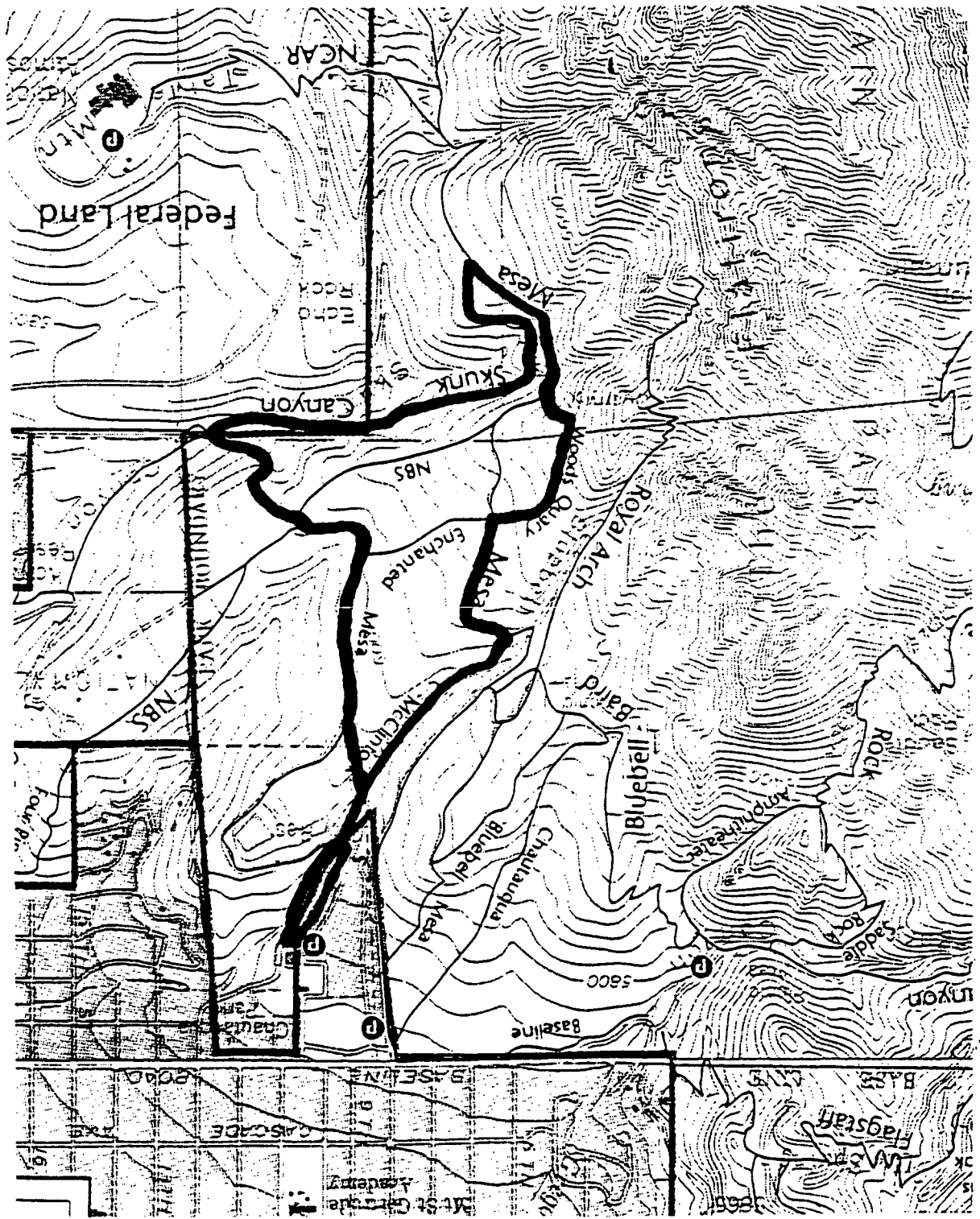


Figure. 5. Map of study site indicating location of squirrel sightings during summer month of August, 1994 (Triangles = *Sciurus aberti*; circles = *Sciurus niger*; squares = *Tamiasciurus hudsonicus*.)

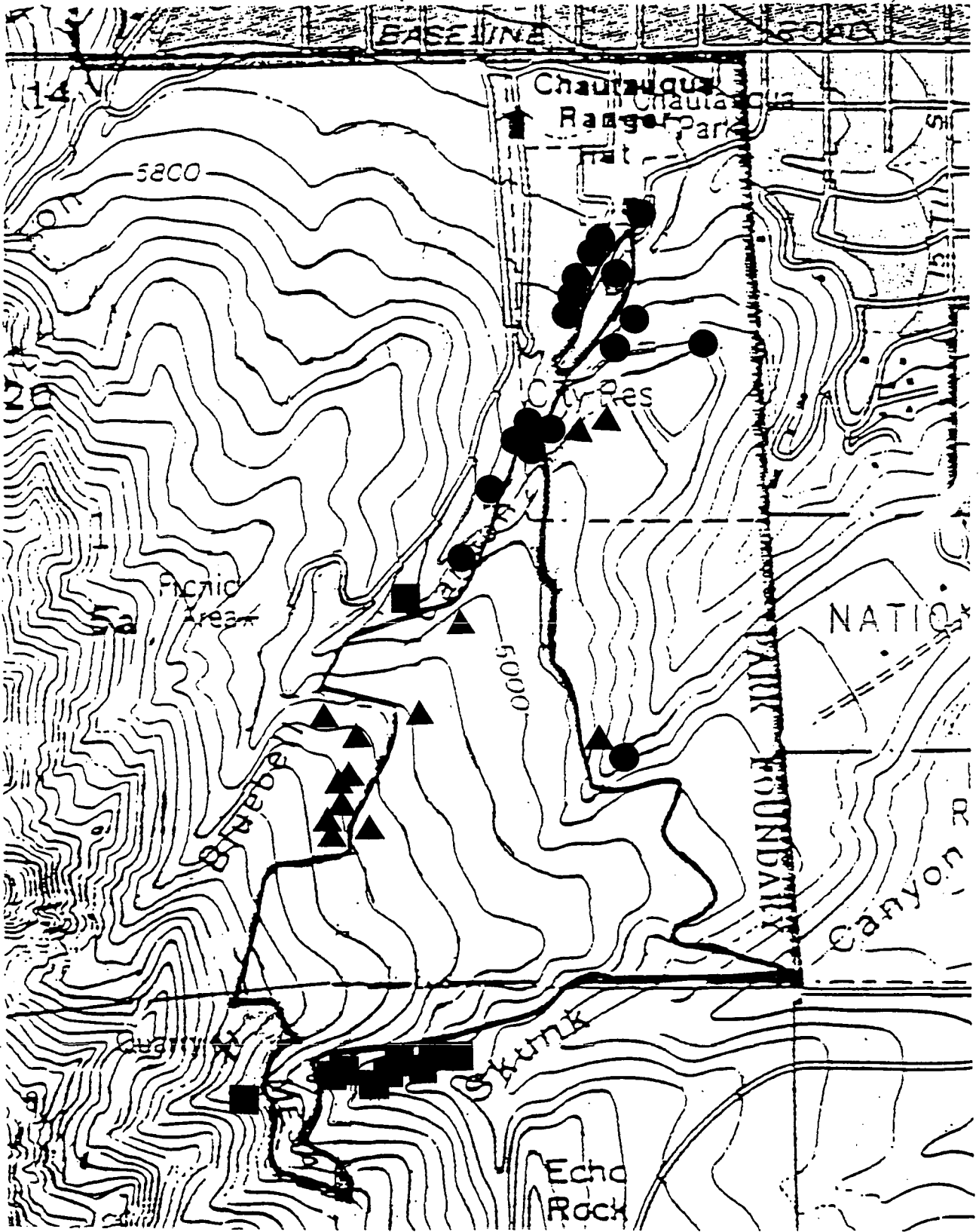


Figure. 6. Comparison of numbers of squirrels observed per hour in each study during summer season. (observation time: Havlick, (1984), 40 field hrs; Rooth, (1992), 50 hrs; present study, 30 hrs.) (Rooth, (1992), studied only *Sciurus aberti* and *Sciurus niger*, therefore no record of *Tamiasciurus hudsonicus* sightings exists.)

NUMBER OF SQUIRRELS PER HOUR

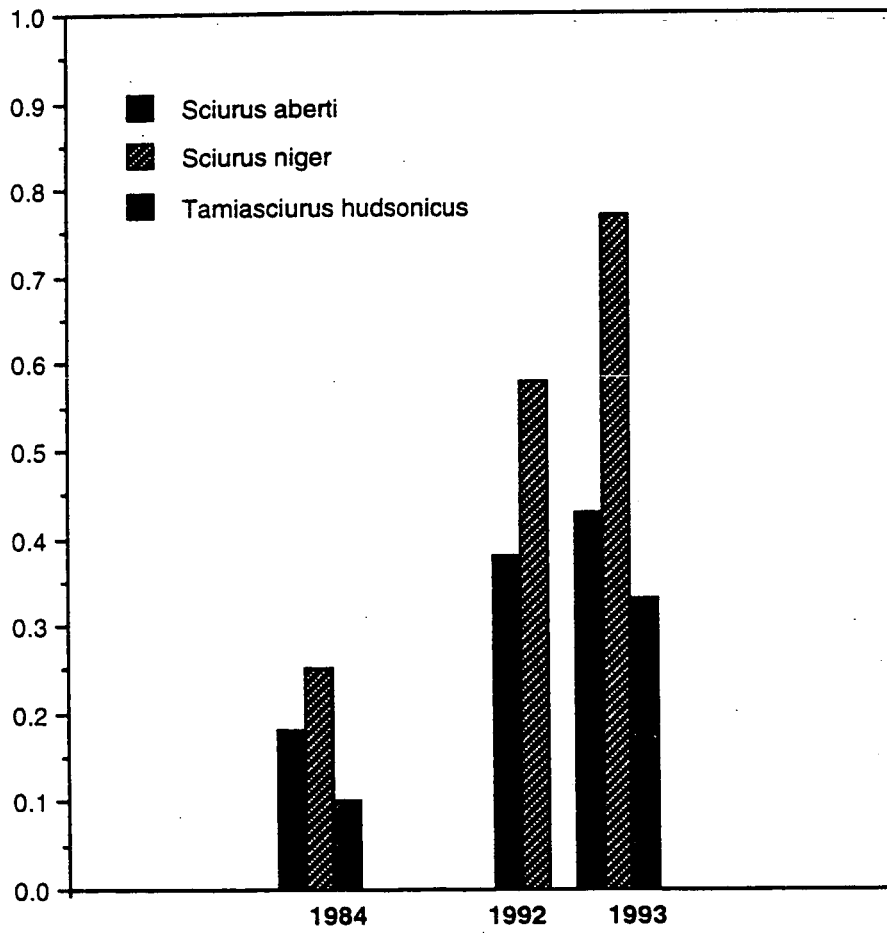




Figure. 7. Map of study site indicating location of squirrel sightings during winter months of December/January, 1994 (Triangles = *Sciurus aberti*; circles = *Sciurus niger*; squares = *Tamiasciurus hudsonicus*.)

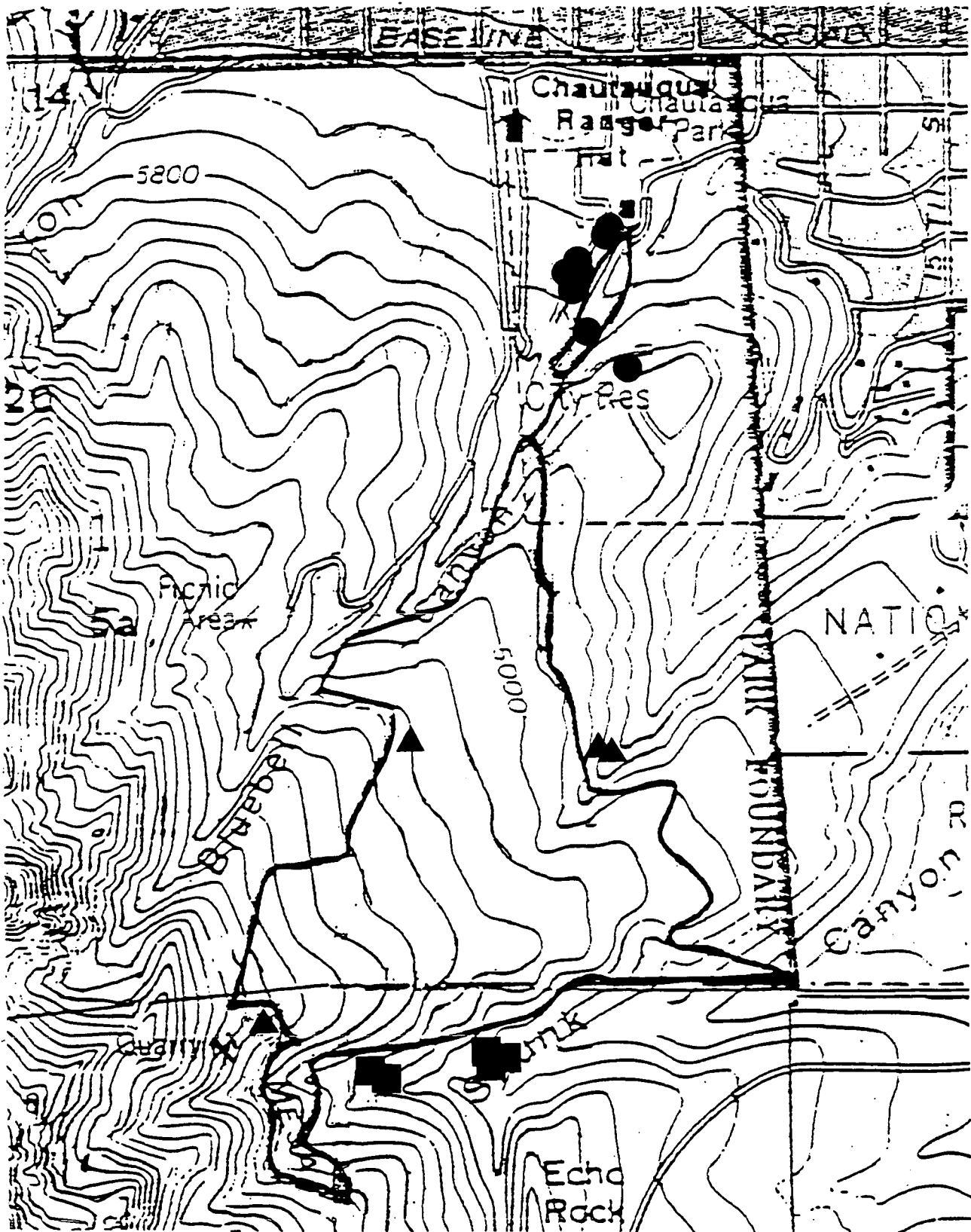


Figure. 8. Comparison of total numbers of squirrels observed per hour in each study during early winter season (observation time: Havlick, (1984), 40 field hrs; present study, 30 hrs.)

NUMBER OF SQUIRRELS PER HOUR

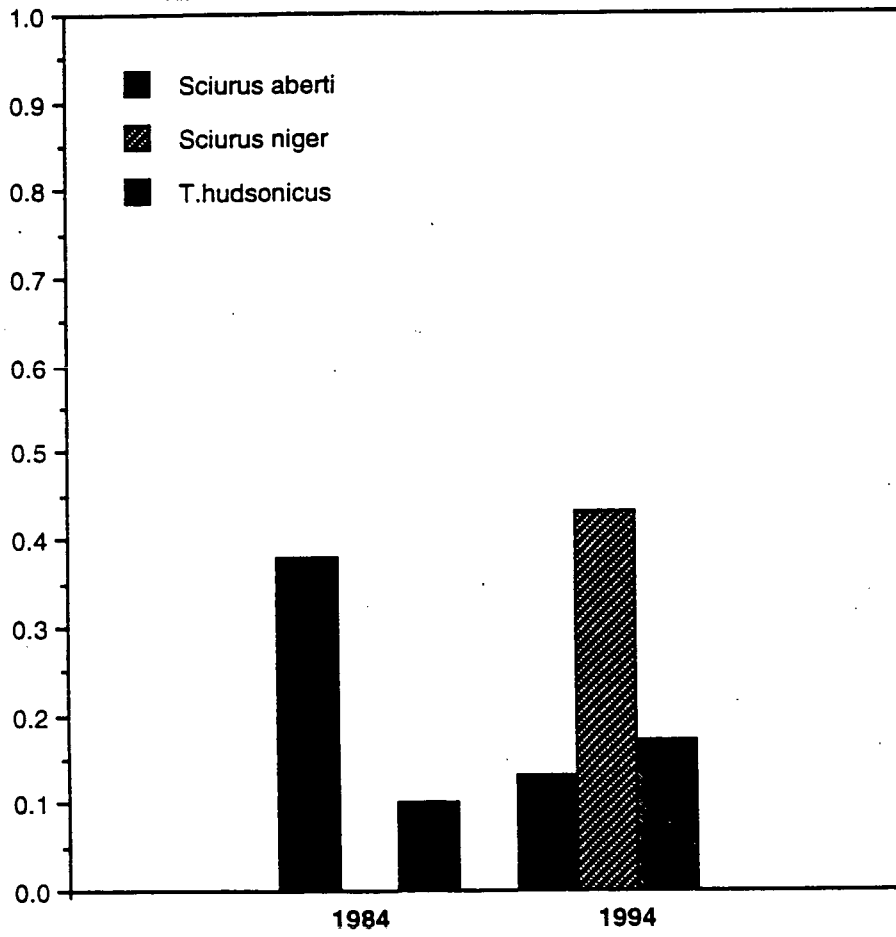


Figure. 9. Map of study site indicating location of squirrel sightings during late winter months of February/March, 1994 (Triangles = *Sciurus aberti*; circles = *Sciurus niger*; squares = *Tamiasciurus hudsonicus*.)

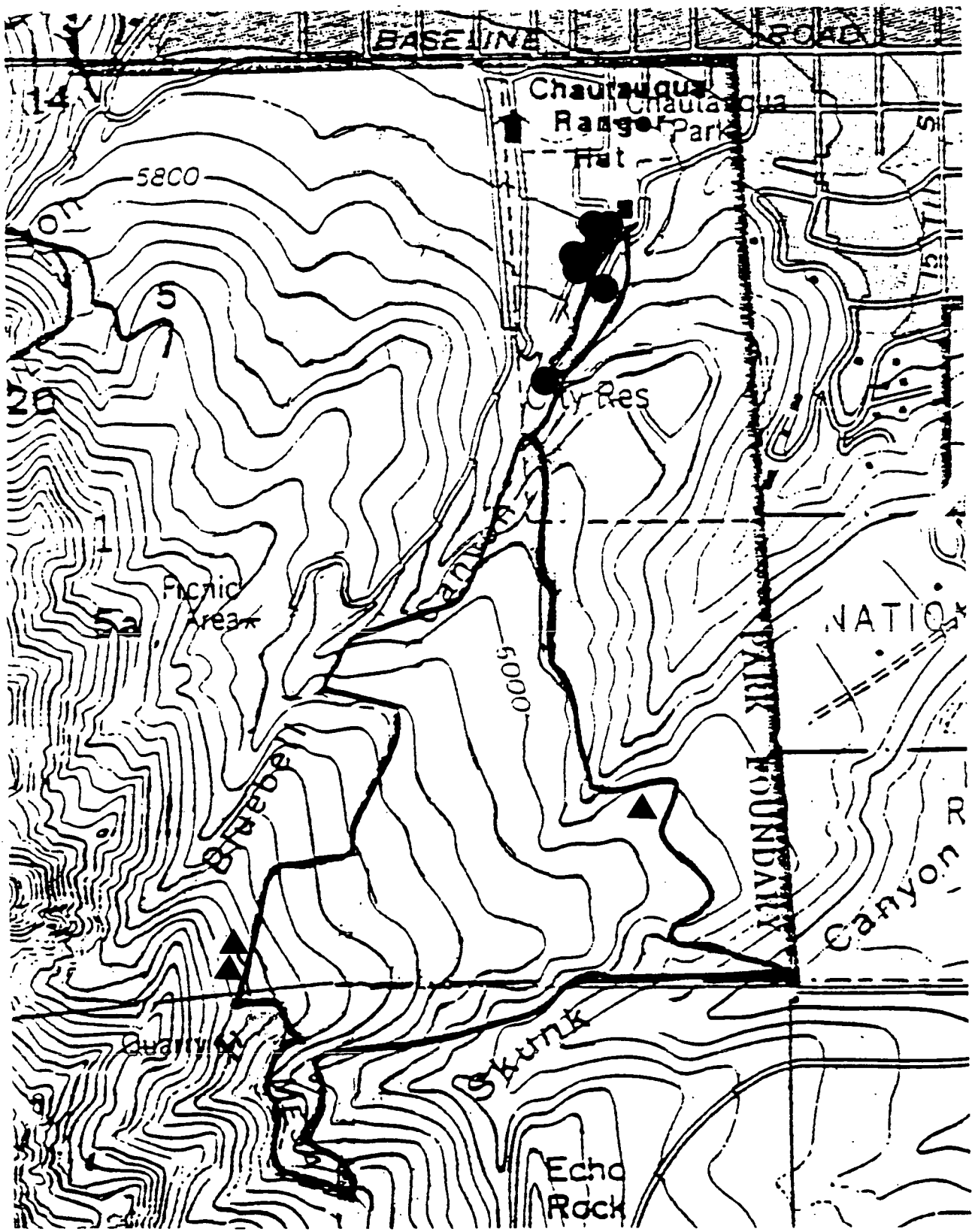


Figure. 10. Comparison of total numbers of squirrels observed per hour in present study during late winter months of February/March, 1994 (observation time: present study, 30 field hrs.)

NUMBER OF SQUIRRELS PER HOUR

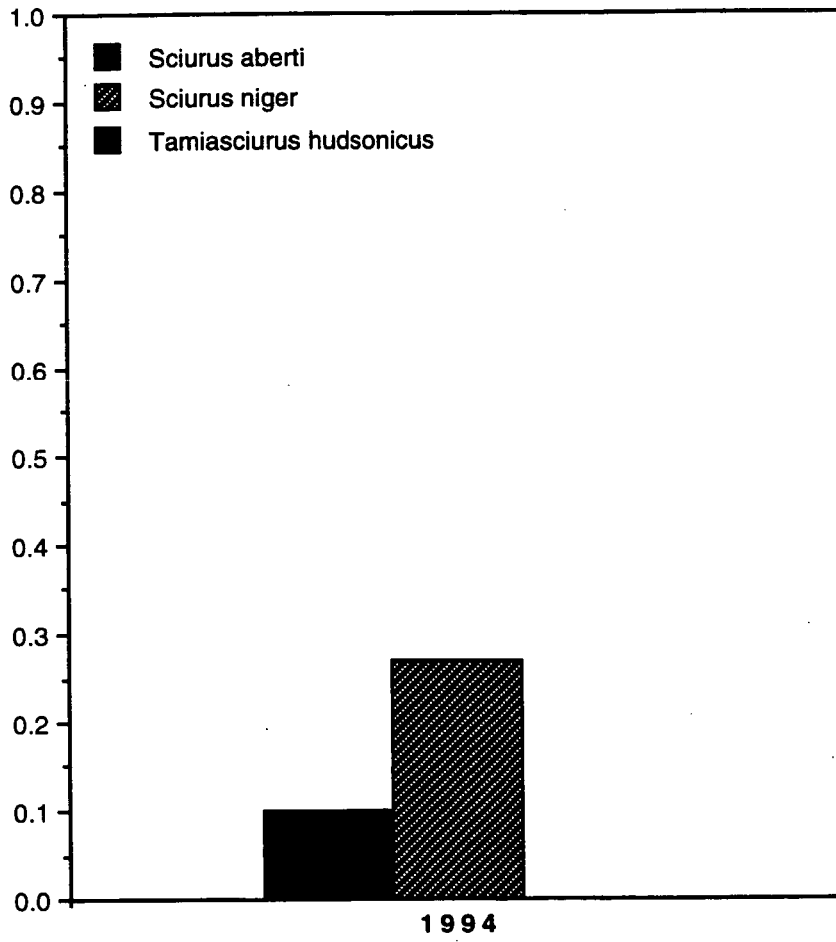
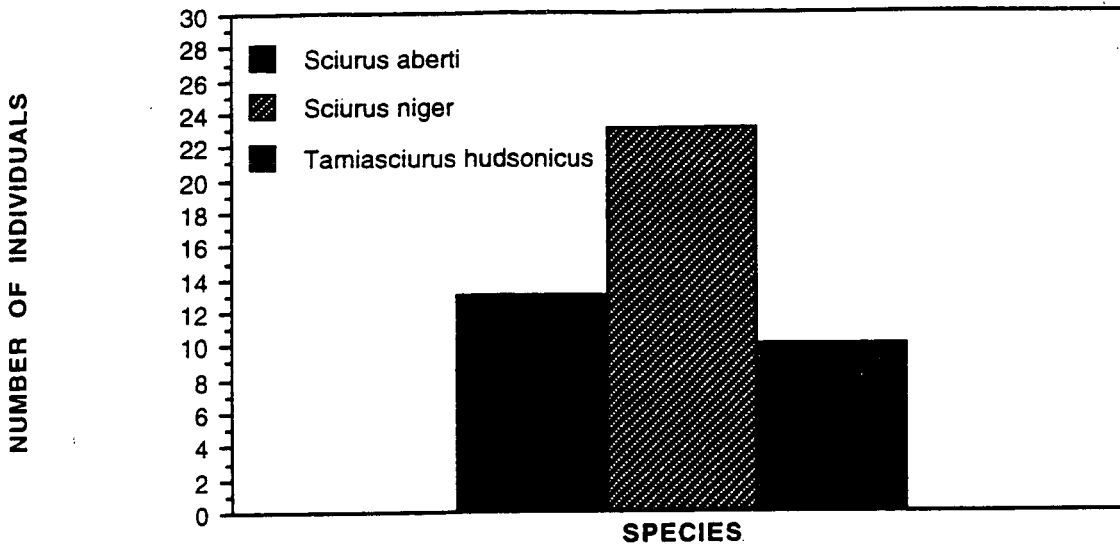


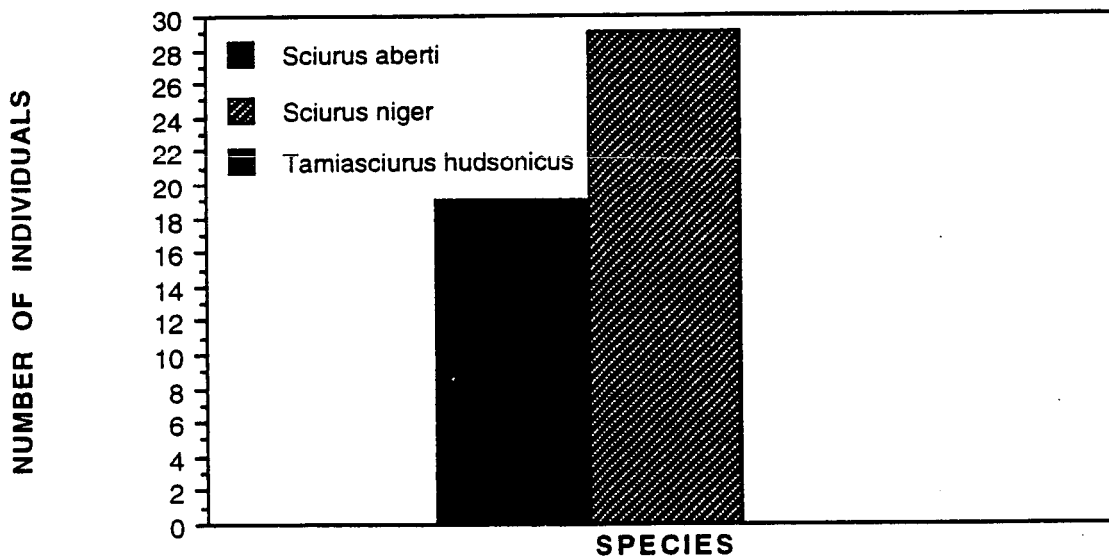


Figure. 11. Comparison of total numbers of squirrels sighted during summer by three observers (observation time: Havlick, (1984), 40 field hrs; Rooth, (1992), 50 hrs; present study, 30 hrs.)

### DATA COLLECTED FROM SUMMER 1993



### DATA COLLECTED FROM SUMMER 1992



### DATA COLLECTED FROM SUMMER 1984

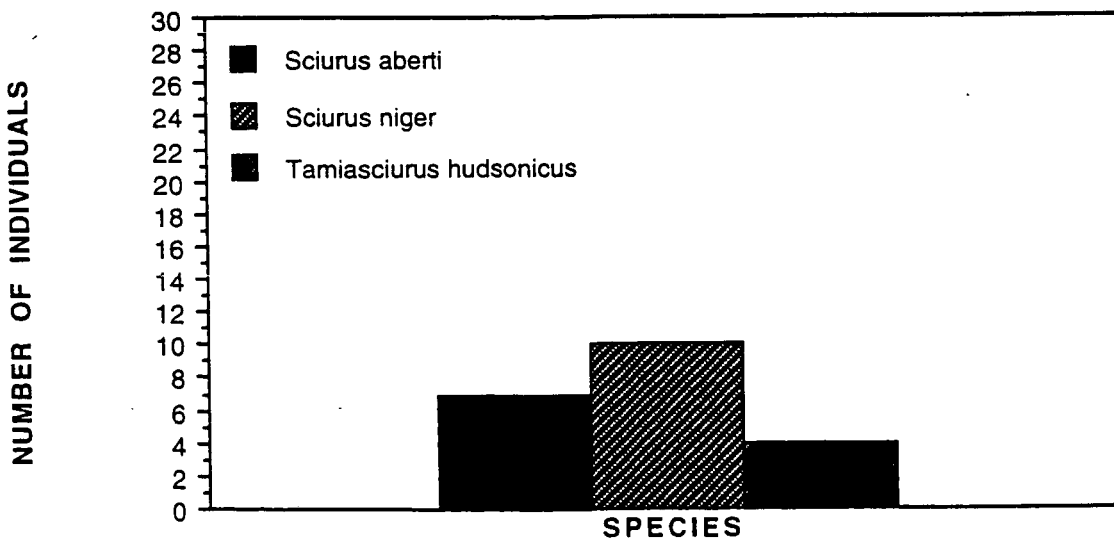
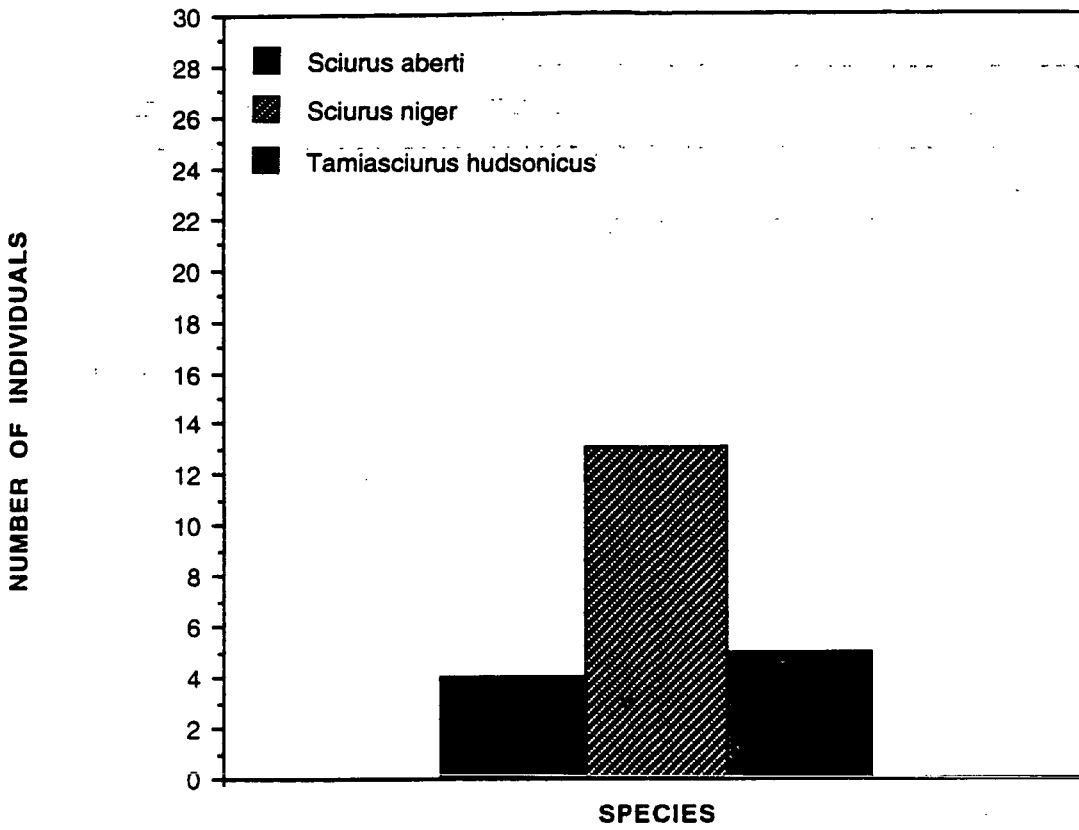


Figure. 12. Comparison of total numbers of squirrels observed during early winter by two observers (observation time: Havlick, (1984), 40 field hrs; present study, 30 hrs.)

### DATA COLLECTED FROM WINTER 1994



### DATA COLLECTED FROM WINTER 1984

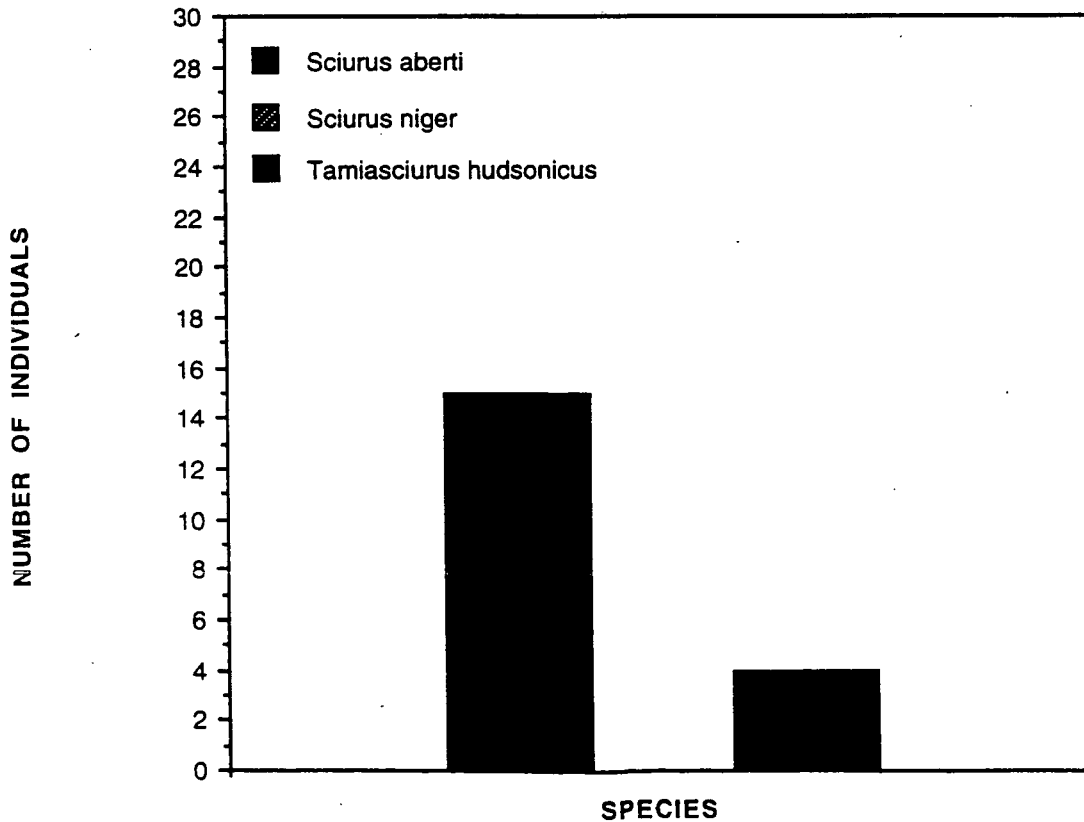


Figure. 13. Comparison of total numbers of squirrels observed in present study during late winter (observation time: present study, 30 hrs.)

### DATA COLLECTED FROM LATE WINTER 1994

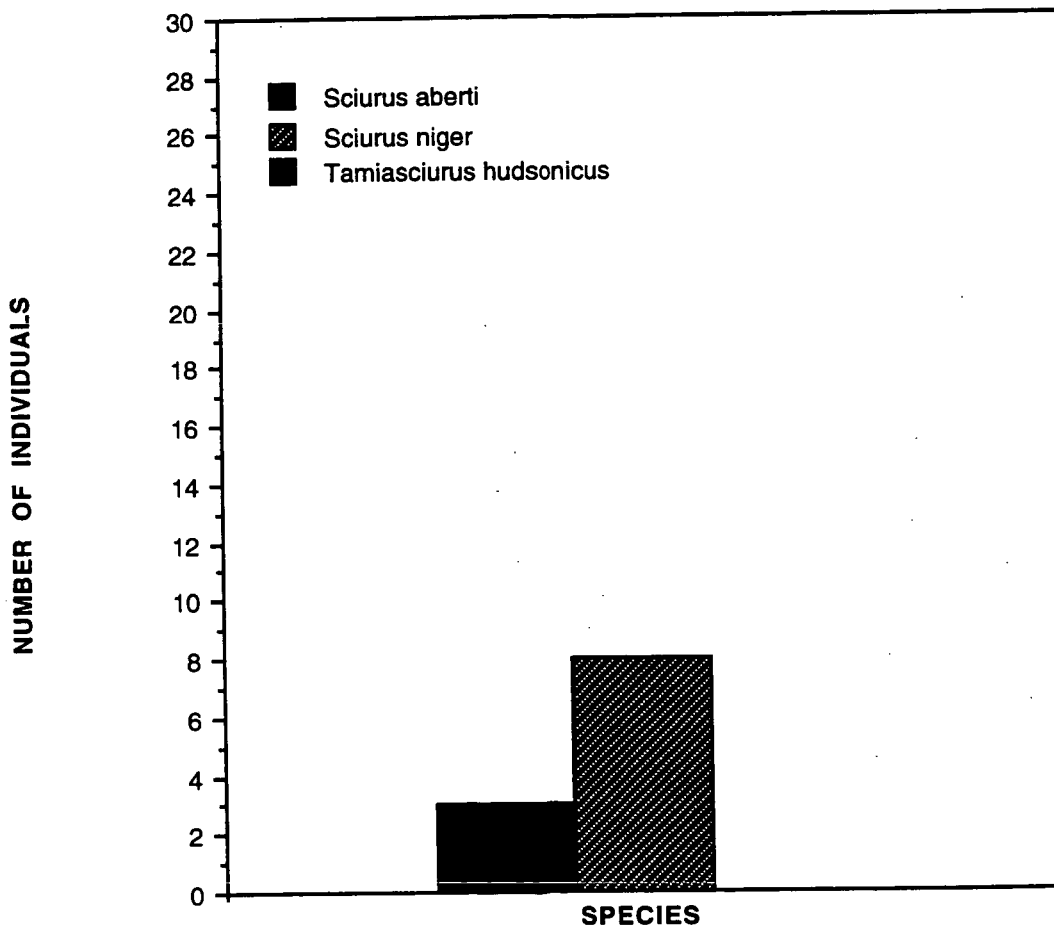


Table. 1. Comparison of frequency of sightings of three species of tree squirrels in three different habitats. (Expected frequencies for Chi-square based on hypothesis of no difference in squirrels between habitats.)

Squirrel species	August	Dec./Jan.	Feb./March
<b>Ponderosa pine</b>			
<i>S. aberti</i>	13	4	3
<i>T. hudsonicus</i>	0	0	0
<i>S. niger</i>	8	1	0
	---	---	---
Total	21	5	3
Chi-square	12.28**	5.19 (n.s.)	6.0*
<b>Douglas-fir</b>			
<i>S. aberti</i>	0	0	0
<i>T. hudsonicus</i>	9	4	0
<i>S. niger</i>	0	0	0
	---	---	---
Total	9	4	0
Chi-square	18.0**	8.02*	N/A
<b>Riparian</b>			
<i>S. aberti</i>	0	0	0
<i>T. hudsonicus</i>	1	0	0
<i>S. niger</i>	15	12	8
	---	---	---
Total	16	12	8
Chi-square	26.39**	24.0**	15.98**

\* Significant to  $p < 0.05$

\*\* Significant to  $p < 0.01$



**Appendix. A. Field observation chart.**

