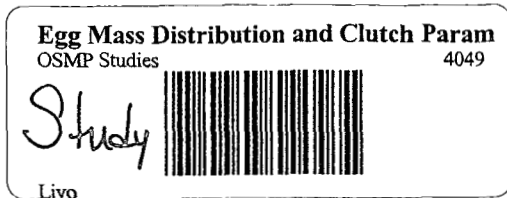


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SOCIAL BEHAVIOR AND ECOLOGY OF ABERT SQUIRRELS
(SCIURUS ABERTI)

by

MARGARET ELIZABETH HALLORAN

B.A. California State University, Chico, 1982

M.S. San Diego State University, 1988

A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
Department of Environmental, Population,
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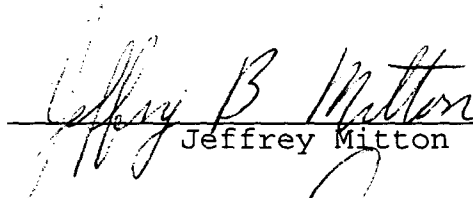
This thesis for the Doctor of Philosophy Degree by
Margaret Elizabeth Halloran
has been approved for the
Department of
Environmental, Population and Organismic Biology
by



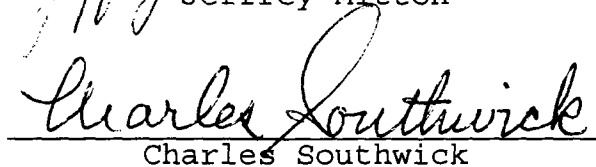
Marc Bekoff



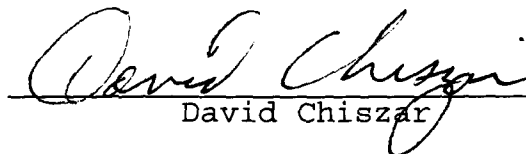
Anne Bekoff



Jeffrey Mitton



Charles Southwick



David Chiszar

Date April 27, 1993

Halloran, Margaret Elizabeth (Ph.D., E.P.O. Biology)
Social Behavior and Ecology of Abert Squirrels
(Sciurus aberti).

Thesis directed by Professor Marc Bekoff

The social behavior and ecology of Abert squirrels (Sciurus aberti) was studied in the foothills of the Rocky Mountains in Boulder, Colorado. Topics on which I focused my attention included nesting behavior, seasonal changes in home range and activity patterns, cheek rubbing, and reproductive behavior. Seasonal differences in nest use indicate that Abert squirrels may be selecting nest site locations to 1) maximize the number of entry and escape routes; 2) inhibit detection by predators; and 3) maximize structural stability which may provide protection from wind and rain. Thermoregulation does not seem to play a role in nest site selection. Only females were observed building nests, although both males and females maintained nests once they were built. Communal nesting by Abert squirrels was rare, but the majority of the observed nest sharings involved unrelated male and female pairs.

Analysis of space use showed that there was no significant differences in overall home range size among males and females, but that males occupied significantly larger home ranges than females during the mating season. Home range sizes did not significantly change with seasonal variations in diet. As photoperiod and ambient temperatures increased from winter to summer, the number of hours during which squirrels were active outside of their nests also increased. Seasonal changes in activity budgets were also observed.

My results suggest that cheek rubbing by Abert squirrels is a form of self-grooming to remove food residue and not active scent marking. Feeding and carrying food or grooming usually preceded cheek rubbing. Cheek rubbing did not predominantly occur at home range boundaries or at nest sites.

Some aspects of reproductive behavior were also studied. Litter size was related to the date on which a female mated. Females who mated earlier had smaller litters than females who mated later in the year. Data suggest that litter size may vary with food availability at the time of estrus, whereas juvenile survival may depend on food availability at the time

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of emergence from the nest. The timing of estrus may be a reproductive pattern that is dependent on these two factors.

DEDICATION

This thesis is dedicated to my father,
Dr. Thomas Halloran, who introduced me at a young age
to the world of academics, and never doubted my
abilities to succeed within that world.

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Several undergraduate field assistants helped me collect data for this project, including Shelly Brown, Jon Mauer, Craig Miller, and Camille Ciccioni. I was extremely fortunate to have Caroline Roeckl working with me for an entire year. Caroline's never ending patience and detailed fieldnotes contributed a large portion of this database. Susan Townsend, my academic sibling and friend, spent a summer working with me before starting her own disseration project. Dr. Ann Kohlhaas got up very early on several mornings to hold squirrels while I attached radio transmitter collars, and Christy Tharenos did a fantastic job on the artwork for this manuscript.

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CHAPTER I
INTRODUCTION

An exciting area of research entails identifying ecological factors that have a role in shaping the social behavior of a species. For animals that are active throughout the year, ecological variables such as seasonal food availability, weather conditions, and appropriate nesting sites may be critical for overwinter survival and for determining seasonal activity patterns and home range size. This study analyzes interrelationships between ecological and behavioral variables by examining the social behavior of Abert squirrels (Sciurus aberti), and by evaluating the habitat in which they live.

Natural history of Abert squirrels

Abert squirrels are large tree squirrels ranging in weight from 500 - 800 grams and are considered by many to be the "most handsome tree squirrel in North America" (Goldman, 1928, p.127; Hall, 1981, p.6; Keith, 1965; p.150). They show many color morphs; varying from grey with a white ventrum to being completely melanistic (black). One of their most

distinguishing morphological characteristics is the tufts of fur that extend out from the pinnae of their ears. These tufts, or "tassels" as they are commonly called, give rise to their other common name, tassel-eared squirrels (Figure 1.1).

Sciurus aberti are in the family Sciuridae, and is the only species in the subgenus Otosciurus. There are six valid subspecies including S. a. ferreus, True; the subspecies that is found along the Front Range of the Rocky Mountains in Colorado (Hoffmeister and Diersing, 1978). Abert squirrels are only found in mountain regions of North America. In the United States their range extends from extreme south-central Wyoming to New Mexico and Arizona (Brown, 1965; Hoffmeister and Diersing, 1978; McKee, 1941). Abert squirrels are limited to the Ponderosa pine (Pinus ponderosa) forests in which they feed and build their nests.

Abert squirrels are diurnal and active year round; even in severe winter weather they leave their nests for a short time to feed (Keith, 1965). They are considered to be non-territorial. Home ranges are large and there is overlap among individuals within a population (Farentinos, 1979; this study).

Figure 1.1. Line drawing of an Abert squirrel (Sciurus aberti).



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Social dominance and reproductive behavior. Previous to the present study, the most extensive field research on Abert squirrels was performed by Robert Farentinos (1972a), who first described patterns of social dominance and the mating activities of Abert squirrels. He discovered that a dominance hierarchy was formed among members of a group of 4 - 12 males, most of whom attempted to participate in mating bouts with one female. Invariably, there was one dominant male who chased away subordinate males who approached the female. The title "dominant male" was assigned to the squirrel who positioned himself between the female and the other males, an act that limited other males' access to the female. Females would bite, bark at, and threaten dominant males as they approached her (Farentinos, 1972a). However, females were generally less aggressive towards subordinate males than towards the dominant male.

Often, while the dominant male was busy chasing one subordinate male, another male approached the female and attempted to copulate with her. During observed mating bouts, the female copulated an average of 12 times (range = 7-15). Although the dominant male copulated first and most often with the female (57% of

observed matings), subordinates were responsible for 43% of all observed copulations (Farentinos, 1972a; 1980). In some cases females were observed to solicit copulations from subordinate males (Farentinos, 1980).

Mating bouts usually lasted about 11 hours, from early morning (shortly after sunrise) until dusk. The mating season started as early as mid-February and continued until early June. After a gestation period of about 40 days, an average of 2.9 pups are born (litters range in size from 1 - 5 young; Farentinos, 1972a; this study). Young squirrels were altricial and first emerged from the nest at about 7 - 10 weeks of age (Keith, 1965; Nash and Seaman, 1977). They remained around their natal nest for about two months after emergence, and then left the natal nest and occupied one of their own (Farentinos, 1972a).

Feeding habits. Many of the studies completed on Abert squirrels have focused on their selective herbivory. During winter months squirrels depend on Ponderosa pine phloem (inner bark) for a large part of their diet (Stephenson, 1974). Abert squirrels appear to select particular trees on which to feed; trees that squirrels eat may be extensively defoliated as a

result of Abert squirrel herbivory, whereas nearby trees of similar size and appearance remain unutilized (Snyder, 1990). Preference for feeding on selective trees has been noted by Farentinos (1972b), Goldman (1928), Hall (1981), Keith (1965), Patton (1974), and Snyder (1990).

Several studies have compared aspects of the trees on which Abert squirrels feed with other Ponderosa pines on which squirrels do not feed (Capretta and Farentinos, 1979; Capretta et. al., 1980; Farentinos et. al., 1981; Pederson and Welch, 1985; Snyder, 1990). The results are equivocal. Capretta and Farentinos (1979) and Farentinos et. al. (1981) reported that twigs from selected Ponderosa pines contained smaller amounts of monoterpenes than trees that Abert squirrels do not eat. However, Pederson and Welch (1985) found no difference in monoterpene levels between trees that Abert squirrels select and trees that Abert squirrels do not select, and suggested that squirrels prefer trees with inner bark that is easily peeled from twigs. The most recent research indicates that Abert squirrels select Ponderosa pines on the basis of xylem oleoresin flow rate, monoterpene composition, and concentrations of

non-structural carbohydrates, sodium, iron, and mercury in the phloem (Snyder, 1990).

Description of the study site

The area in which squirrels were studied was a 72 hectare region of Ponderosa pine forest located 0.7 km west of Boulder, Colorado (elevation about 1940 meters above sea level) in the Front Range of the Rocky Mountains. This property is commonly known as Enchanted Mesa and is under the jurisdiction of the City of Boulder Mountain Parks Department. Enchanted Mesa is transected by several major hiking trails that are maintained by the City of Boulder. The area is restricted to day-use only and is used extensively by hikers and joggers, especially on the weekends. Most of the visitors abide by park rules; they stay on the trails and have limited impact on the study area.

Boulder is classified as semi-arid, with an annual precipitation of 46 cm. Most of the precipitation occurs from March through July of each year. The average annual snowfall is 221.3 cm. Snow is often found on Enchanted Mesa from the middle of September to late April; March usually has the most snowfall (Lanham, 1974). December is the coldest month

with a mean daily temperature of -0.9 °C, and July is the warmest month with a mean daily temperature of 21.7 °C.

The study area has natural boundaries consisting of ravines to the north and south containing mixed deciduous vegetation including box elder (Acer regundo) and cottonwoods (Populus angustifolia), an open grassland to the east, and a rock quarry to the west. All of these areas are unsuitable habitats for Abert squirrels. Enchanted Mesa is a relatively pure all age stand of Ponderosa pine (Snyder, 1990) with a few Douglas fir (Pseudotsuga menziesii) and red cedar (Juniperus virginiana) present. The grassy understory contains sagebrush (Artemesia frigida), prickly pear cactuses (Opuntia compressa) and many colorful wildflowers during the spring and summer months. The area was subjected to selective cutting in 1981 and 1982, primarily to control outbreaks of Dendroctonus bark beetles and is therefore relatively open (Snyder, 1990).

In addition to Abert squirrels, Enchanted Mesa is inhabited by fox squirrels (Sciurus niger) introduced into the area in the mid-1970's. Boulder city residents who were seeking to rid their back

yards of fox squirrels would trap them and release them in the foothills (Littlefield, 1984). The niches of the two species do not appear to overlap. Abert squirrels primarily use pure Ponderosa pine habitat, whereas fox squirrels use several deciduous tree and Ponderosa pine-Douglas fir regions found on the edges of the study site (Littlefield, 1984; pers. obs.).

Enchanted Mesa is of particular historical significance in the study of Abert squirrel biology. Robert Farentinos first used this site to study the behavioral ecology of Abert squirrels from 1970 to 1971 (Farentinos, 1972a; 1972b; 1974; 1979). The same area was used by Victoria Littlefield from 1980 to 1983 (Littlefield, 1984), and by Marc Snyder from 1985 to 1990 in his work on selective herbivory by Abert squirrels (Snyder, 1990; Snyder, 1993). The grid transect system was first installed in 1969, and recreated for this study from remaining tree tags and Farentinos' notes.

Purpose

Although this is the fourth study investigating Abert squirrel biology using the Enchanted Mesa study site in 20 years, I am the first person to observe a

marked population of these squirrels for longer than one year on this study site or any other study site. Therefore, the information obtained from this study will significantly add to the existing data base for Abert squirrels, and provide a unique opportunity to compare these data with data obtained 20 years ago.

This thesis is written as a series of manuscripts. Therefore, the reader should be advised that there is some duplication among chapters 2 - 6, primarily in the methods section of each chapter. This study examines five different areas of Abert squirrel behavior and ecology. In chapter two, I present data on the first study that compares trees utilized by Abert squirrels for building nests with a control group of trees selected at random. I also examine patterns of nest use and how they may influence site selection. In chapter three, I examine space use by Abert squirrels during different times of the year when different foods are available. I also compare home range data obtained in this study with home range sizes from a previous study on this site. In chapter four, I examine changes in activity patterns between seasons, comparing day length and changing diet. In chapter five, I examine the context of cheek rubbing,

and I explore several hypotheses about its possible function. Chapter six is a brief one in which I explore the relationship between the time of year when a female is in estrous with the number of offspring she subsequently produces.

CHAPTER II
NEST SITE SELECTION AND NEST USE BY ABERT SQUIRRELS
(Sciurus aberti).

ABSTRACT

Nest site selection and nest use by Abert squirrels (Sciurus aberti) were studied in the foothills of the Rocky Mountains in Boulder County, Colorado. Fourteen variables were used to evaluate 49 nests inhabited by Abert squirrels from May 1988 to June 1991. All nests were located in Ponderosa pine (Pinus ponderosa) trees. The majority of nests were constructed of twigs and located in the upper one-third of the canopy, near the trunk, on the southeast side of the tree. Trees with nests were predominantly located in closed stands. Nest trees were compared to control trees, which were equally accessible to squirrels, but were not used by squirrels for building nests. Nest trees were significantly different from control trees in five out of the nine variables selected for comparison. Nest tree crowns intertwined with a larger number of adjacent tree crowns than did control tree crowns. Nest trees were also

significantly taller than control trees, but subdominant to adjacent trees within a stand. Seasonal difference in nest utilization indicates that Abert squirrels do not choose nest locations on the south east sides of trees to facilitate behavioral thermoregulation. Rather, Abert squirrels may be selecting nest site locations to 1) maximize the number of entry and escape routes; 2) inhibit detection by predators; and 3) maximize structural stability which may provide protection from wind and rain.

Only females were observed building nests, although both males and females maintained nests once they were built. Communal nesting by Abert squirrels was rare, but the majority of the observed nest sharings involved unrelated male and female pairs.

INTRODUCTION

The selection of a nest site may influence an animal's reproductive success and survival (Bekoff et.al., 1989; Rothwell, 1979). Nests are used by arboreal sciurids for sleeping at night, and sometimes during the day (Farentinos, 1972b; Keith, 1965;

Koprowski, 1991a; Thompson, 1978; Wauters and Dhondt, 1990a). Arboreal squirrels are active year round and depend on their nests for protection from bad weather (Farentinos, 1972b). In addition, they use their nests to raise their young and to evade predators.

There are three major categories into which most arboreal squirrel nests can be placed. They are 1) outside nests constructed of leaves or twigs, built within the branches of a tree; 2) den nests which are located within tree cavities; and 3) underground nests. Nests are usually lined with soft material such as grass clippings or spongy tree bark.

Descriptive studies of nest structure and nest site selection have been completed for many arboreal squirrel species including Mexican red-bellied squirrels (Sciurus aureogaster; Brown and McGuire, 1975), eastern grey squirrels (S. carolinensis; Fitzwater and Frank, 1944; Robinson and Cowan, 1954; Sanderson et. al., 1976; Uhlig, 1956), California grey squirrels (S. griseus; Ingles, 1947; Merriam, 1930), fox squirrels (S. niger; Baumgartner, 1943; Moore, 1957), European red squirrels (S. vulgaris; Tittensor, 1970), red-bellied tree squirrels (Callosciurus erythraes; Setoguchi, 1991), pine squirrels

(Tamiasciurus hudsonicus; Hatt, 1943; Layne, 1954; Murie, 1927; Rothwell, 1979), Douglas squirrels (Tamiasciurus douglasii; Vahle and Patton, 1983), northern flying squirrels (Glaucomys sabrinus; Harestad, 1990), and the semi-arboreal rock squirrel (Spermophilus variegatus; Ortega, 1987; 1988).

Abert squirrel nests

Abert squirrels (Sciurus aberti) build two different types of outside nests in Ponderosa pine trees (Pinus ponderosa). The most common type is the "bolus" nest that is constructed of a ball of cut twigs. The second type is the "broom" nest, so named because it is built in preexisting dwarf mistletoe, or "witch's broom" patches, within a tree (Farentinos, 1972b). Although two descriptive studies of Abert squirrel nest sites have previously been completed, Farentinos (1972b) and Patton (1974) only looked at characteristics of the nest trees themselves and did not study the features of non-nest trees that were equally accessible to squirrels.

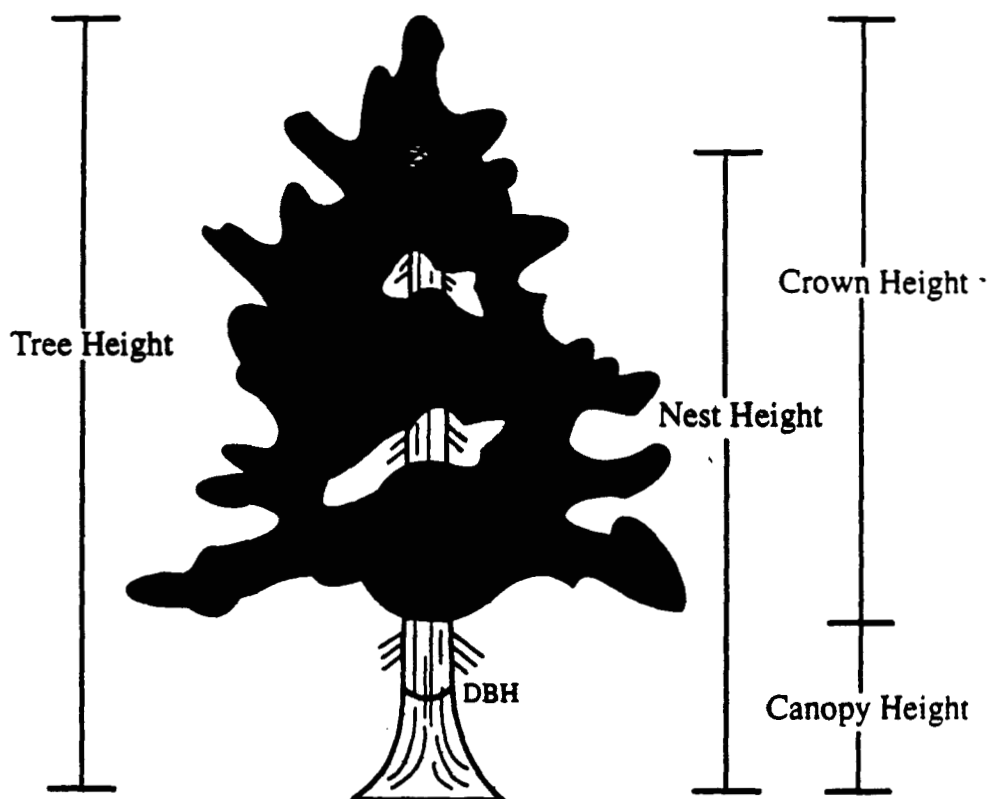
If Abert squirrels are selecting individual trees in which to build their nests non-randomly, one would expect that nest trees would differ from the

other trees on the study site in at least one characteristic. These features may be intrinsic to the tree itself, such as tree height or the height of the crown, or be extrinsic characteristics such as the tree's location within a stand or the number of trees within a stand. On Enchanted Mesa, there are regions in which many nests are built within a single plot and there are other regions where many adjoining plots do not contain any nests. The purpose of this portion of the study was to 1) describe the nests built and used by Abert squirrels on Enchanted Mesa; and 2) determine if trees in which squirrels build their nests differ from a random set of non-nest trees with respect to intrinsic and extrinsic variables.

Nest use

Adult arboreal squirrels of the genus Sciurus are generally not territorial and home ranges overlap extensively (Benson, 1980; Koprowski, 1991a; Thompson, 1978a). An individual may use more than one nest, and the same nest may be used by different squirrels sequentially or simultaneously: sometimes two adult squirrels will be found together in a nest (Wauters and Dhondt, 1990a; Wiegl et al, 1989). The genetic

Variables for Nest-Tree Selection Comparisons



$$\text{Live Crown Ratio} = \frac{\text{Crown Height}}{\text{Tree Height}} * 100$$

$$\text{Nest Height Ratio} = \frac{\text{Nest Height}}{\text{Tree Height}} * 100$$

DBH= diameter of the tree trunk @ ~4' from ground

determine which independent variables best classify the trees used by Abert squirrels for building nests.

Nest use by Abert squirrels

Squirrels were trapped using Tomahawk #202 live traps baited with peanut butter and sunflower seeds. Squirrels were permanently marked with an ear tattoo and a freeze brand using "quik-freeze" brand liquid cryogenic. Dye marks were also used as temporary visible identifiers. The squirrels' age, weight, and sex were recorded.

Between May 1989 and October 1991 squirrels were observed year round from sunrise until one half hour before sunset, or when it was determined that all squirrels had entered their nests for the evening. Days were normally divided into two sampling periods; 1/2 the number of daylight hours in duration. Dawn to dusk observations were attempted at least one day per week.

Once marked squirrels were found, they were followed and their behavior patterns were recorded using focal animal sampling (Altmann, 1974). Their location on the study site was recorded using grid markers as reference points. Marked squirrels were

observed with 10 x 50 binoculars using trees as natural blinds. Nests were also watched beginning at dawn to observe squirrels as they emerged. Squirrels habituated to the observers' presence and squirrels did not appear to alter their activities when followed. Behavioral data were spoken into a microcassette recorder and later transcribed into notebooks. Data were then subsequently entered into a computer for analysis.

Survival analysis for nest longevity was completed using the product - moment survival analysis method (BMDP, 1990; program 1L). Univariate tests on nest use were completed using Chi-square analyses and Mann-Whitney U tests (Minitab, 1991). Significant transitions within contingency tables were identified by using a simple approximation derived from Castellan's (1965) method of partitioning contingency tables as adapted by Lefebvre (1981).

Home ranges were calculated using the 95% minimum convex polygon method (Bekoff and Mech, 1984; Mohr and Stumpf, 1966). Home range sightings for seven females and six males were plotted using the x and y grid coordinates. The area of home ranges were then calculated using a digitizing tablet and the computer

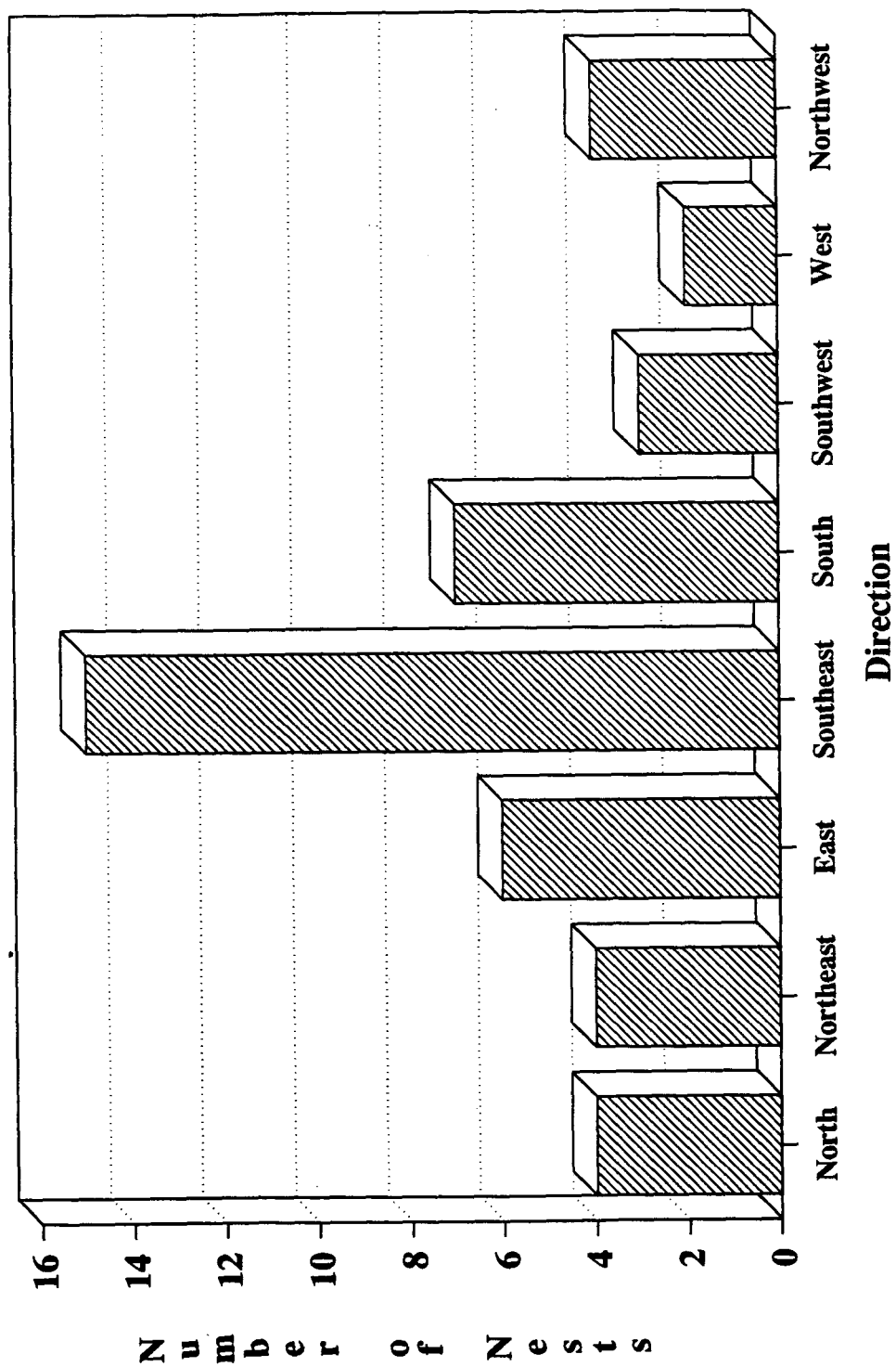
program JAVA™ (Jandel Corp, 1991). Home ranges were measured three times and the average of these measurements was recorded. Correlations of nest size with home range size and amount of time a squirrel was observed in the field were calculated using Spearman's rho (Minitab, 1991). For a more detailed discussion of the methods used to calculate home ranges see Chapter III.

RESULTS

Characteristics of Abert squirrel nests

The majority of nests built by Abert squirrels on Enchanted Mesa were bolus type (48/49 nests; 98%) and were built next to the trunk (45/49 nests; 92%). Fifteen (33%) of the bolus nests were built on the southeast side of the tree (112.5° to 157.5°) which is significantly more than would be expected by chance (Chi-square = 21.06, df = 7 p < 0.005; Figure 2.2). Nests were built in the upper one-third of the canopy; their mean height was 13.6 ± 2.9 s.d. meters from the ground. The average nest height to tree height ratio was 0.72.

Figure 2.2. Compass orientation of nests built by Abert squirrels (Sciurus aberti) on Enchanted Mesa from 1989 to 1991. N = North, NE = Northeast, E = East, SE = Southeast, S = South, SW = Southwest, W = West, NW = Northwest (n = 49).



Characteristics of trees in which Abert squirrels
build nests

Abert squirrel nest trees differed from non-nest trees in three out of the four selected intrinsic variables. Abert squirrels build nests in trees that are significantly taller (mean = 19.0 ± 2.7 m) than non-nest trees (mean = 13.5 ± 5.1 , $t = 6.47$ $df = 89$ $p < 0.001$; Figure 2.3). The diameter at breast height (DBH) of nest trees (mean = 37.5 ± 7.5 cm) is significantly larger than non-nest trees (mean = 28.9 ± 11.6 ; $t = 4.23$ $df = 89$ $p < 0.001$). The crown height of nest trees (mean = 12.1 ± 2.8 m) is also significantly greater than that of non-nest trees (mean = 8.5 ± 3.9 ; $t = 5.1$, $df = 89$ $p < 0.001$), but there is no significant difference in live crown ratio of the two groups (64% for nest trees vs 63% for non-nest trees).

Nest trees differed from non-nest trees in two out of the five selected extrinsic variables. There was a significant difference in the number of access routes between nest trees and non-nest trees. There was an average of 2.8 (± 1.2) access routes to nest trees, but only an average of 1.6 (± 1.2) access routes to non-nest trees ($t = 5.49$, $df = 89$, $p < 0.01$;

Figure 2.3. The height of the trees used by Abert squirrels (Sciurus aberti) for building nests (n = 49), and a set of trees selected at random that were equally accessible, but did not contain Abert squirrel nests (n = 41).

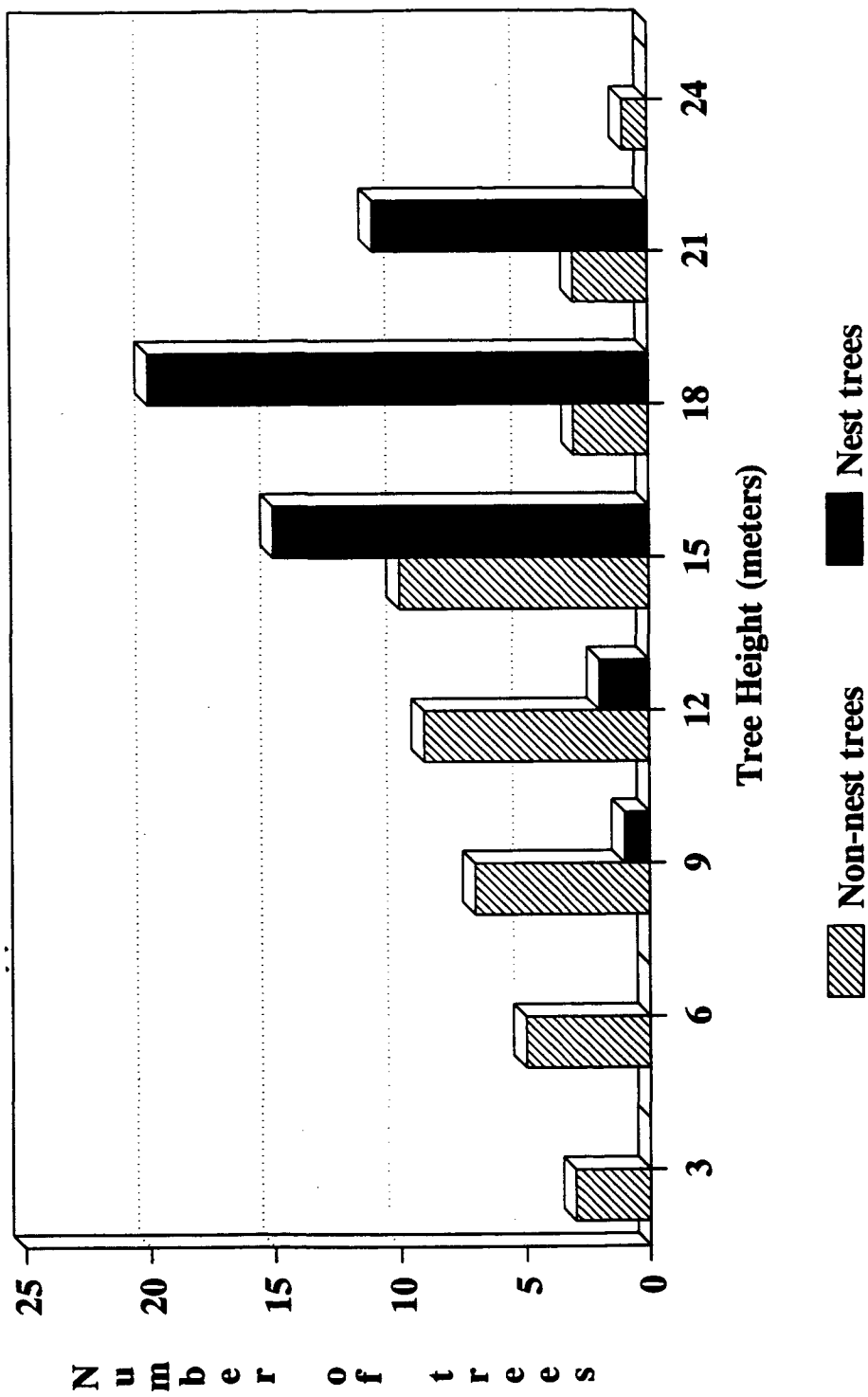


Figure 2.4). Although there is no significant difference between the total number of trees per quadrat, quadrats with nest trees have significantly more ponderosa pines greater than seven meters in height (mean = 24.3 ± 10.5) than non-nest tree quadrats (mean = 19.4 ± 10.7 ; $t = 2.15$, $df = 89$, $p < 0.05$; Figure 2.5).

Nest trees did not differ significantly from non-nest trees with respect to crown dominance. Crown dominance for the majority of trees sampled in both groups was sub-dominant. Squirrels seldom built nests in trees that were isolated or overtopped (Figure 2.6). Nest trees also did not differ significantly from non-nest trees with respect to spatial relationship. Squirrels generally built nests in trees that were on the interior of the stand (Figure 2.7).

Stepwise discriminant analysis correctly classified 91.8% of nest trees and 80.5% of non-nest trees using the independent variables of tree height, access routes, and crown dominance (Table 2.1).

Nest use by Abert squirrels

The distribution of nests on the study site is illustrated in Figure 2.8. The average density of

Figure 2.4. The number of access routes for trees that contain Abert squirrel nests ($n = 49$) and a set of trees selected at random that were equally accessible, but did not contain Abert squirrel nests ($n = 41$).

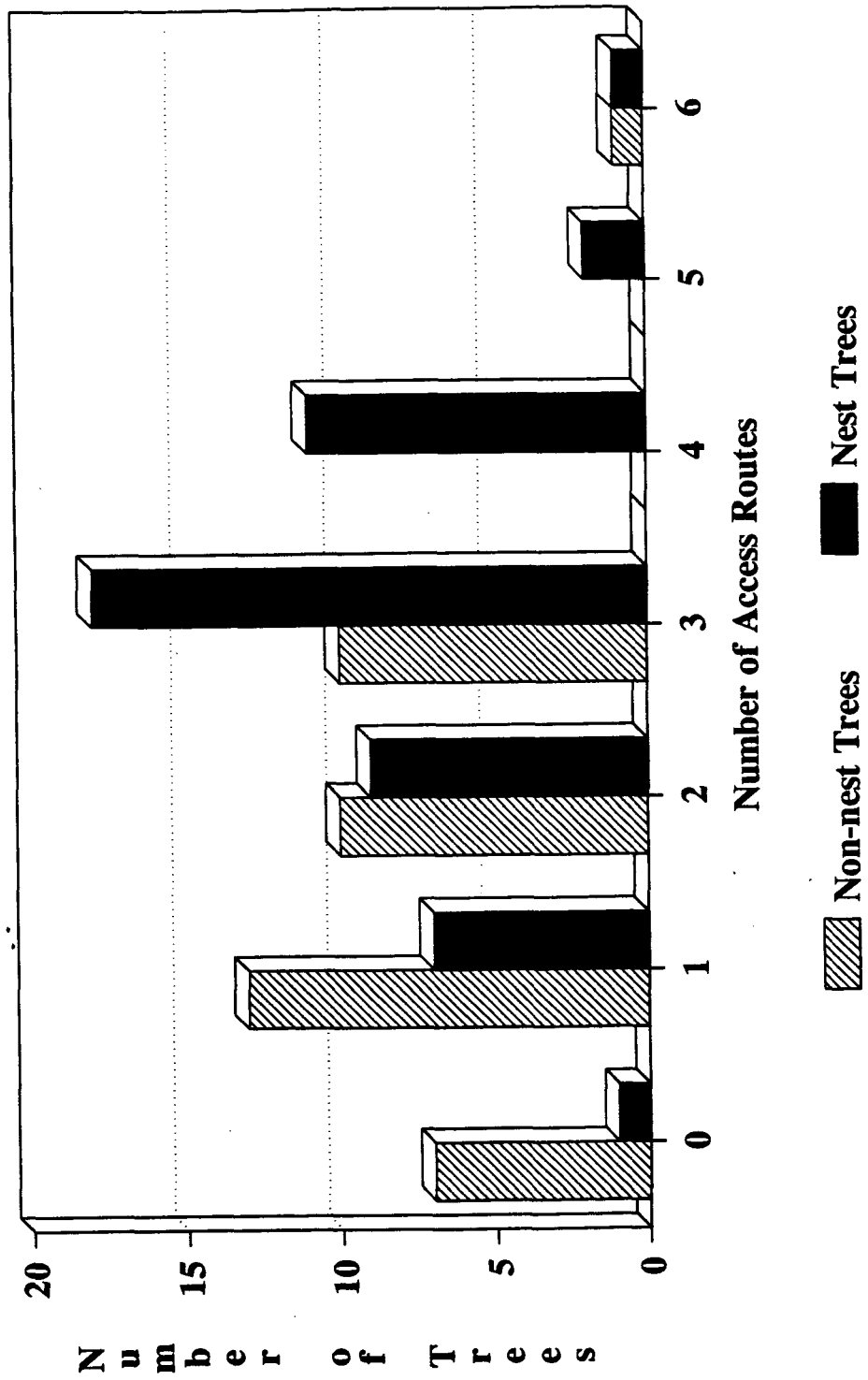


Figure 2.5. Distribution of the number of pine trees greater than seven meters per plot for plots that contain Abert squirrel nests (n = 41) and a set of plots selected at random that were equally accessible, but did not contain Abert squirrels nests (n = 41). Plot size = 30 x 30 meters.

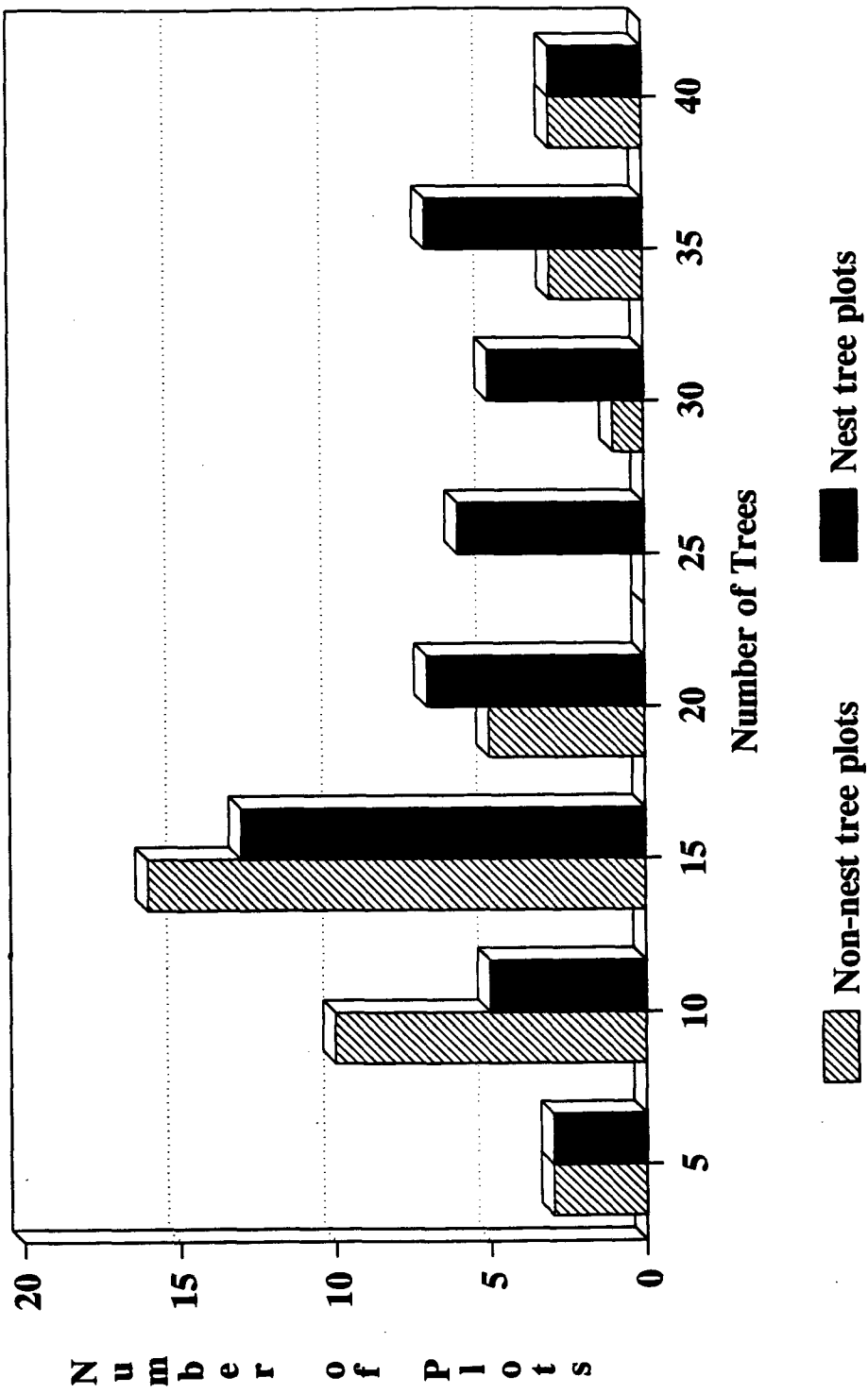


Figure 2.6. Distribution of canopy types for trees that contain Abert squirrel (Sciurus aberti) nests (n = 49) and a set of trees selected at random that were equally accessible, but did not contain Abert squirrel nests (n = 41).

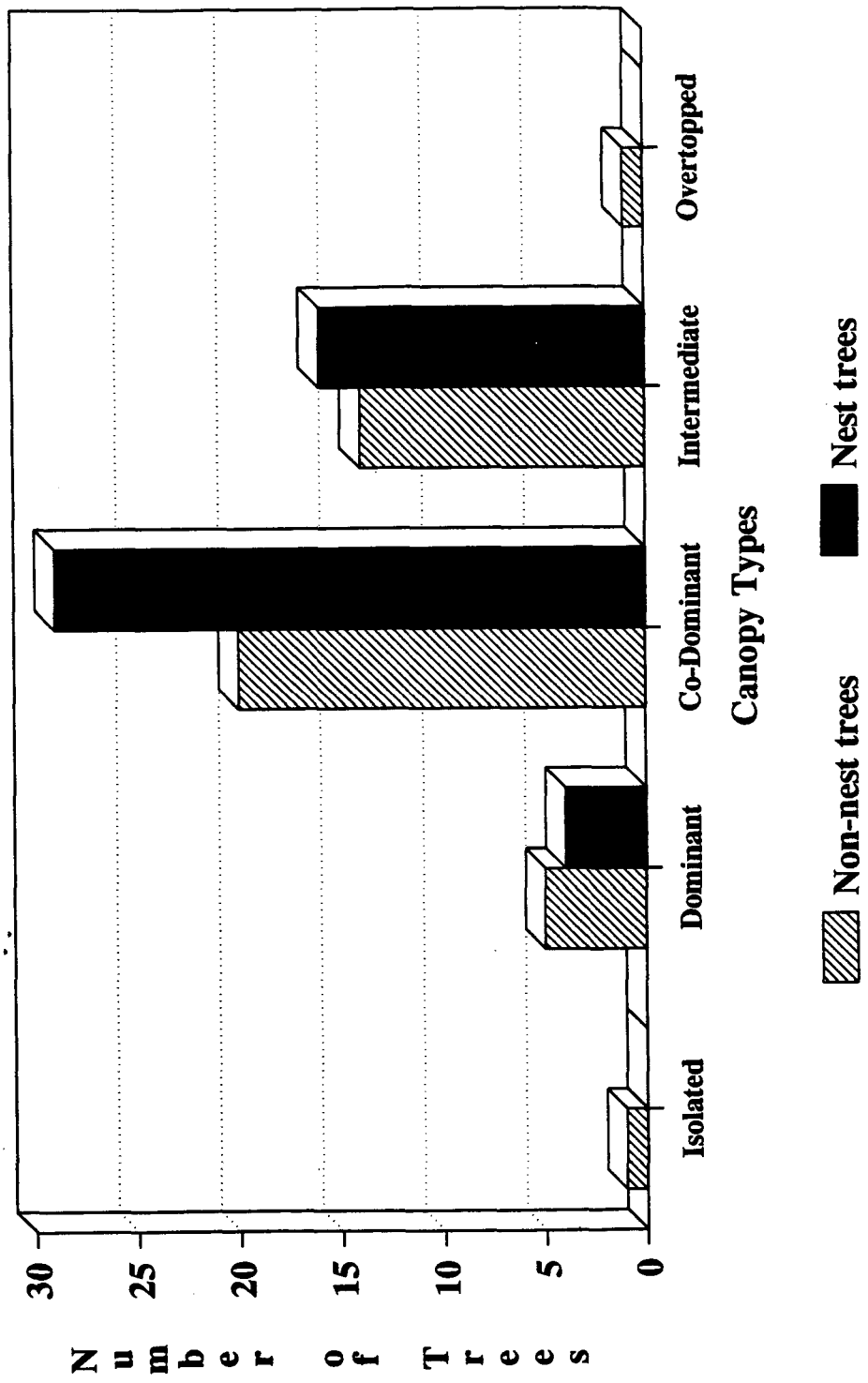
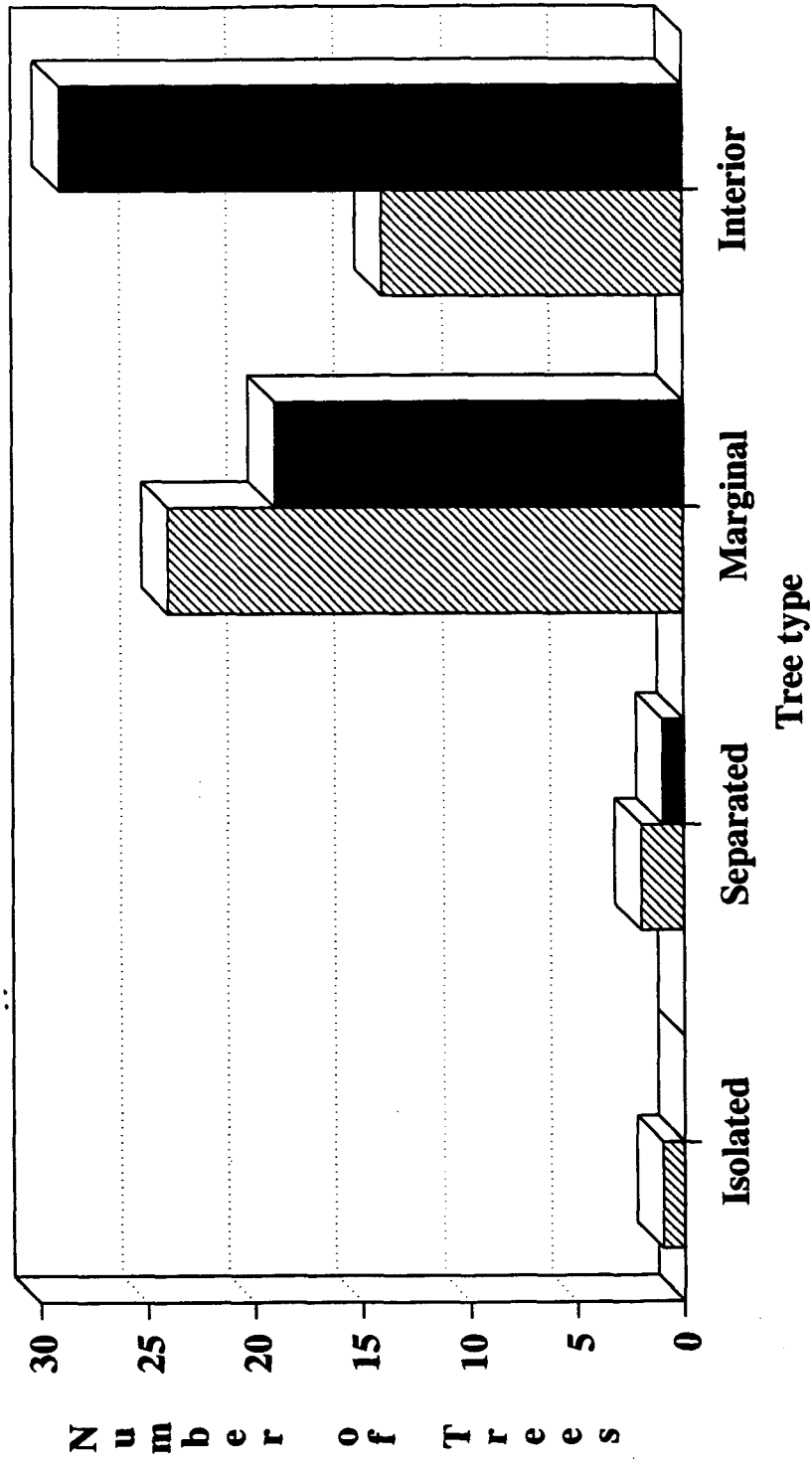


Figure 2.7. Distribution of the spatial relationship for trees that contain Abert squirrel (Sciurus aberti) nests (n = 49) and a set of trees selected at random that were equally accessible, but did not contain Abert squirrel nests (n = 41).

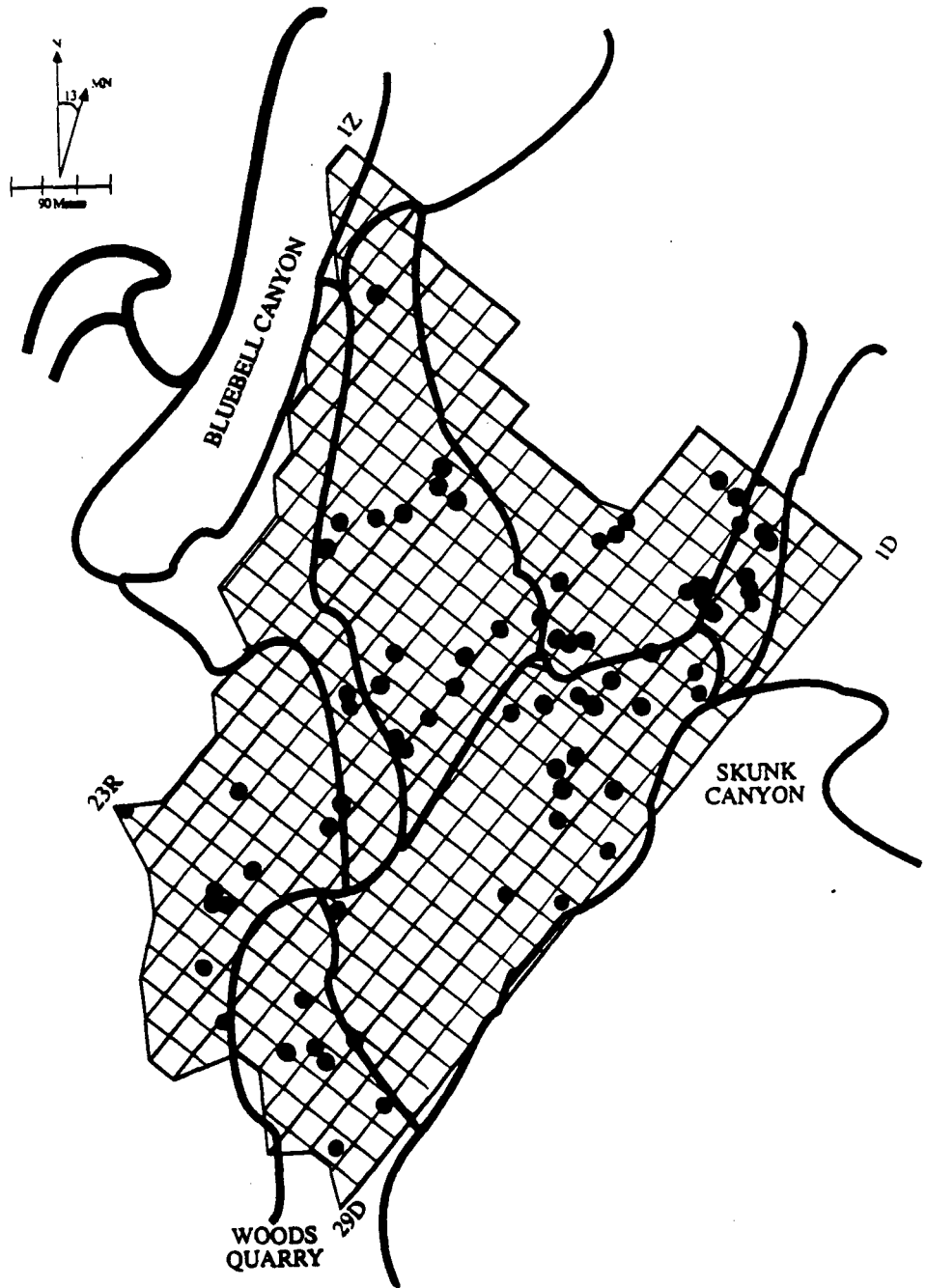


■ Non-nest trees ■ Nest trees

Table 2.1. Classification Matrix: The number of nest trees and non-nest trees correctly classified by Discriminant Function Analysis.

Tree type	Classification		Percent Correct
	Nest tree	Non-nest tree	
Nest tree	45	4	91.8
Non-nest tree	8	33	80.5

Figure 2.8. A map of Enchanted Mesa with nest site locations indicated.



nests per hectare on Enchanted Mesa was 0.47. There was no significant difference in the number of nests located on the study site between years (Chi-square = 4.47, $df = 2$, $p > 0.05$; Table 2.2).

Of the 24 nests discovered in 1989, 16 (67%) were still being used in 1990 and eight (33%) were still being used in 1991. Of the 24 additional nests discovered in 1990, 10 (42%) were still in use in 1991 (Table 2.3). The date a nest was first observed in the field was compared with the census date when a nest was first observed to be missing, using the product moment survival analysis method (BMDP, 1990) for the 68 nests located from May 1989 to June 1991. The median nest survivorship was estimated at 2.0 ± 0.1 standard error. These data suggest that nests are used by squirrels for approximately two years before they deteriorate.

I recorded 363 observations of nest use by 17 adult Abert squirrels were made. Individual squirrels used an average of 7.6 (± 6.1) nests each. There was no significant difference between the number of nests used by male (mean = 7.0 ± 5.4) and female (mean = 8.8 ± 6.4) Abert squirrels ($U = 55.5$, $p > 0.05$). There was also no significant difference between the number of

Table 2.2. The number and density of nests per hectare found on Enchanted Mesa from May 1989 to June 1991.

Year	Number of nests	Nests/Hectare
1989	24	0.33
1990	40	0.55
1991	38	0.53

Table 2.3. The number of new nests counted in consecutive years. The percentage of nests still in use after one and two years is given in brackets.

Year	# of new nests counted	# of nests still present	
		1990	1991
1989*	24	16 (67%)	8 (33%)
1990	24	--	10 (42%)
1991	20	--	--

* 1989 was the first year of the study; not all nests found in 1989 were necessarily built during that year.

observations of nest use by males (mean = 17.9 ± 15.3) and females (mean = 26.3 ± 26 ; $U = 59.8$, $p > 0.05$; Table 2.4).

The number of nests used by Abert squirrels on Enchanted Mesa was not correlated with home range size ($r_s = 0.56$, $n = 13$, $p > 0.05$). Overall home range size was not correlated with the number of total hours a squirrel was observed ($r_s = 0.41$, $n = 13$, $p > 0.01$). However, the number of nests a squirrel used was significantly correlated with the amount of time a squirrel was observed in the field ($r_s = 0.82$, $n = 13$, $p < 0.01$; Table 2.4). Squirrels that were observed for a longer period of time used more nests than those observed for a shorter amount of time, but squirrels generally used the same number of nests per year.

There were no significant differences between the number of times males frequented nests during the day (mean = 8.4 ± 7.41) vs the number of time females frequented nests during the day (mean = 5.8 ± 7.82 ; $U = 60.5$, $p > 0.05$; Table 2.5) exclusive of nest building and maintenance. However, 98% ($n = 51/52$) of all observations of female nest use occurred during the summer months when females returned to their nests to nurse their young, and female squirrels who did not

Table 2.4. The number of nests built by, and home range sizes of, adult Abert squirrels (*Sciurus aberti*) from May 1989 to October 1991 (N = 13; F = female, M = male).

Squirrel	Sex	Number of Nests ^a	Hours Observed ^b	Home Range size (hectares)
GBH	F	7	31.7	20.71
BBMH	F	3	25.9	12.16
BLH	F	9	59.1	17.04
BBH	F	8	51.8	19.55
GRH	F	18	103.9	12.89
BRH	F	20	136.3	22.02
BRMH	F	9	138.6	17.32
BLF	M	2	12.5	14.35
BLFM	M	6	34.9	21.50
BRF	M	8	59.1	17.99
GRF	M	4	65.4	18.83
BBF	M	13	120.7	25.77
BRFM	M	15	127.3	26.31
average	F ^c	8.8	61.2	17.38
std dev		5.4	53.3	3.76
average	M	7.0	61.2	20.79
std dev		6.4	47.9	4.66

^aThe correlation between the number of nests a squirrel occupied and home range size was not significant ($r_s = 0.56$; $p > 0.05$). Whereas the number of hours squirrels were observed in the field and the number of nest sites was significant ($r_s = 0.82$; $p < 0.01$).

^bThe correlation between the number of hours squirrels were observed in the field and the home range size was not significant ($r_s = 0.41$; $p > 0.05$).

^cNo significant differences were obtained between males and females for the number of nests, the number of hours observed, or home range size.

Table 2.5. Incidence of daytime nest use by adult Abert squirrels (*Sciurus aberti*) from May 1989 to October 1991 (N = 16; F = female, M = male).

Squirrel	Sex	^a Day use	^a Maintenance	Building
GLMH	F	0	1	0
BBM	F	0	3	0
BLH	F	0	2	2
BRH	F	17	8	3
BRMH	F	17	5	0
GRH	F	14	9	5
GRHLH	F	0	0	0
GBH	F	4	0	0
BBF	M	5	7	0
BRF	M	9	2	0
BLFM	M	4	2	0
BRFM	M	22	2	0
GRF	M	9	8	0
GLF	M	0	0	0
BLF	M	0	0	0
Mean	F	5.78	3.11	1.25
Std. Dev.		7.82	3.48	1.91
Mean	M	8.43	3.00	0
Std. Dev.		7.41	3.21	0

^aNo significant differences were found between males and females for either day use or maintenance.

produce litters were never seen using nests during the day. Males seldom entered nests for periods greater than 2 minutes in length ($n = 3/59$; 5%) and most day use activity observed ($n = 56/59$; 95%) occurred during the mating season; males would enter and exit several nests in succession as they traveled around the study site in the early part of the day.

Nest maintenance, which includes the addition of bedding materials or cut twigs to an existing nest, was observed 48 times from May 1989 to October 1991. Six females and five males were observed to perform this behavior 29 and 19 times, respectively. There was no significant difference between the frequencies with which these behaviors were performed by the two sexes ($U = 67.0$, $p > 0.05$; Table 2.5).

The building of 10 nests was observed. All nests were built by either pregnant or lactating females from May to August of each year. These data suggest that nest building is not performed by males, juveniles, or females outside of the breeding season (Table 2.5).

Seasonal differences in nest use was documented for 35 nests ($n = 153$ observations). There was a significant difference in the percentage of time a

squirrel occupied a south or southeast facing nest when compared to other nests facing different directions ($X^2 = 102.5$, $df = 9$, $p < 0.01$; Table 2.6). In fact, squirrels were more likely to occupy a southeast facing nest during the warmer summer months (46% of all summer observations) than during the winter months, and they were also more likely to occupy a north to northwest facing nest during the winter months (52% of all winter observations) than during the summer. This suggests that squirrels do not use different nest orientations to thermoregulate behaviorally.

Of the 68 nests on Enchanted Mesa, 21 (31%) were observed to be used by an adult squirrel once, and seven (10%) had only two incidents of nest use recorded. For those nests with more than two nest use observations ($n = 40$; 59% of all nests), patterns of nest sharing and exclusive use were analyzed. Of these 40 nests, eight (20%) were used by one squirrel exclusively and 32 (80%) were used by more than one squirrel, either sequentially (at different times) or by two or more squirrels communally (Table 2.7). There was no significant difference for the number of

Table 2.6. Seasonal use of nests by adult Abert squirrels (*Sciurus aberti*). Data are presented as the number of observations (N) of use per season and compass direction, and as a percentage (%) of seasonal observations for each direction.

Compass Direction	Winter		Spring		Summer		Autumn	
	N	%	N	%	N	%	N	%
NW-N	15	52 ^a	13	46 ^a	12	26	7	14 ^a
NE-E	5	17	6	28	13	28	18	37
SE-S	7	24	9	46	21	46 ^a	11	22
SW-S	2	7	0	0 ^a	0	0 ^a	13	27 ^a
Total	29	100	28	100	46	100	49	100

^aThese cells are significantly different from the results that would be expected by chance ($p < 0.05$) using Castellan's method of partitioning contingency tables.

Table 2.7. The number of nests used by different numbers of squirrels from May 1989 to October 1991, based on a random sample of 363 nest use observations. Only data for nests observed used more than three times is presented. Exclusive nests are those nests used only by one squirrel, shared nests are those nests used by more than one squirrel sequentially, or communally. (N = the number of nests; # solitary = the number of observations with one squirrel in a nest; # communal = the number of observations with more than one squirrel in a nest; mean = the mean number of observations per nest.)

Nest type	N	# solitary	# communal	Mean
Exclusive	8	67	0	8.4
Shared	32	237	24	8.2
Total	40	304	24	8.2

observations per nest between exclusive nests and shared nests ($U = 67.5, p > 0.05$).

Communal nest sharing by adults was rare and observed only 24 times (6.6% of all nest use observations) in 15 (37.5%) of the nests. All occurrences of communal nest sharing took place in nests that were also used by more than one individual sequentially. Communal nesting by adult Abert squirrels was significantly more common in the autumn (25%) and winter (63%) than in the spring (4%) and summer (8%; Chi-square = 20.4, $df = 3, p < 0.01$). The most common group composition was unrelated male and female pairs which accounted for 16 (67%) of the pair aggregations, significantly more than would be expected due to chance (Chi-square = 17.9, $df = 2, p < 0.01$). There were no all male pair aggregations, and 6 (27%) all female pair aggregations; three were young of the year females who had returned to their natal nest during the winter, and three were young of the year females sharing a nest with an unrelated female. Although juvenile development was not looked at specifically in this study, all juveniles did leave their natal nest after weaning, before the onset of winter. Only two incidents of aggregations greater

than two squirrels sharing one nest communally were observed. One of these took place in the summer when a male shared a nest with an unrelated female and her offspring, and the other consisted of two unrelated males and an unrelated female.

DISCUSSION

Types of nests built by Abert squirrels

Abert squirrels usually build bolus nests having a framework constructed of cut twigs, each twig having been cut individually by a squirrel (this study, Farentinos, 1972b; Hall, 1981; Keith, 1965; Patton, 1974). Broom nests, also used by Abert squirrels, have a ready made framework constructed of tree branch shoots caused by dwarf mistletoe (Arceuthobium vaginatum). Although it may be an advantage, in terms of energy expenditure, to build a nest in a pre-existing framework, Abert squirrels on Enchanted Mesa rarely built broom nests in dwarf mistletoe infections (1/49 nests; 2%). The incidence of dwarf mistletoe infection on Enchanted Mesa from 1989 to 1991 was rare but there were patches of dwarf mistletoe that did not house squirrels. Patton (1974) reported 15% of Abert

squirrel nests in Arizona to occur in dwarf mistletoe, in an area where 6% of the trees had some infection. The costs of building a broom nest (in terms of the amount of energy necessary to complete the nest) may be less than the advantages of selecting a position within the tree to build a nest.

In contrast to eastern grey squirrels (Sciurus carolinensis) that often use tree dens (Sanderson, et. al. 1976), only one tree den was discovered on Enchanted Mesa from 1989 to 1991, and it was not included in data analyses due to small sample size. No other use of tree dens has been published for Abert squirrels. One reason that reports of tree dens by Abert squirrels are rare is that Ponderosa pine trees, in which Abert squirrels exclusively build nests, are resistant to rot and seldom have cavities of a size suitable for dens (Keith, 1965). Dens may be found in dead trees, but most occur in live trees and in a variety of species in mixed deciduous woodland rather than conifers (Sanderson, et. al. 1976).

Nest placement within a single tree

Behavioral thermoregulation. The tendency of Abert squirrels to build their nests on the south or southeast side of a tree has been explained by the thermoregulatory benefits of heat conservation (Farentinos, 1972b). On Enchanted Mesa the sun remains in the south for the majority of the day. Thermal benefits of solar radiation may be beneficial to a small non-hibernating mammal during the winter. If squirrels are using nest placement as a means of behavioral thermoregulation, one would expect a disproportionate use of nests that are on the warmer side of the tree (south-southeast) during the winter months. However the present results show significant differences in seasonal nest use opposite the trend that would be expected. Fifty-two percent of all winter nest use sightings were of nests that are located on the north and northwest (shady) sides of trees, whereas in the summer, 46% of nest use observations were of nests on the south - southeast (sunny) sides of the tree. An experiment performed on northern flying squirrels (Glaucomys sabrinus) demonstrated that they showed no preference for nest

boxes that were placed on either the north or south sides of trees (Harestad, 1990).

Abert squirrels are diurnal mammals who generally leave their nests within 1 - 2 hours after sunrise. They return to nests in the late afternoon or early evening after the sun has dropped behind the mountains to the west of the study site. With the exception of lactating females, Abert squirrels do not spend considerable amounts of time within their nests during daylight hours except during periods of very inclement weather (heavy rain or snow). Therefore, squirrels are generally not in their nests during the times of day when they would benefit from the direct thermoregulatory effects of solar radiation on nests. Overnight carry-over effects of daytime solar radiation have not been investigated for arboreal squirrel nests.

Nest walls retain metabolic heat given off by arboreal squirrels and arboreal squirrels can greatly reduce their metabolic costs of thermoregulation by being in a nest (Gurnell, 1987). Red squirrels (Sciurus vulgaris) in Finland maintain nest temperatures of 20 - 30 °C above ambient temperatures after an initial warmup period (Havera, 1979).

Therefore, Abert squirrels may depend more on the insulating properties of nests, rather than solar radiation warming nests, during winter.

The data presented here on nest use indicate that Abert squirrels were more likely to share nests in aggregate groups during winter rather than during summer months. Similar data have been reported for fox (*S. niger*) and grey squirrels (*S. carolinensis*) that show an increase in the frequency of nest sharing during autumn and winter (Koprowski, 1991a). Nest sharing in aggregate groups of small rodents has been shown to decrease the amount of energy expended to stay warm (Grodzinski, 1985). Southern flying squirrels (*Glaucomys volans*) reduce energy expenditure by as much as 36% when huddling in groups of three to six individuals (Stapp, et. al. 1991).

During the summer, winter nests may become too hot for arboreal squirrels, and they may build special open dreys in which they nest (Gurnell, 1987). Dreys were not found on Enchanted Mesa during any time of the year. However, nest maintenance does occur year round, and squirrels presumably may add or subtract nesting material and twigs to increase or decrease the amount of insulation provided by the nest. The

tendency of Abert squirrels on Enchanted Mesa to use nests with different compass orientations that vary seasonally needs to be looked at in further detail. This trend should be compared with studies on Abert squirrels at other study sites, and with studies on other arboreal squirrel species.

Structural stability. One advantage to building nests on the south or southeast side of trees may be increased structural stability. On Enchanted Mesa, powerful wind strikes the tops of Green Mountain and Bear Peak to the west; these winds are deflected downward. There may be local gusts with speeds as high as 225 kilometers per hour, which are considerably greater than that of the upper wind stream (Lanham, 1974). Prevailing west winds can cause a flagging effect in Ponderosa pines; the branches on the west side of the trees are broken, and the majority of the remaining crown is located on the eastern side. While flagging effects are obvious at tree line, they are also present at this altitude (M. Snyder, pers. comm.) Studies on located nests on other study sites in Arizona report similar wind conditions (Keith, 1965; Snyder and Linhart, 1993).

South and southeast oriented nests on Enchanted Mesa endure only slightly longer than other nests. Seventy-five percent of south to southeast facing nests survive 1.9 years, compared with 1.7 years for nests with other compass orientations. Therefore it would seem that Abert squirrels select the most stable position within a tree to build their nest, which usually, but not always, coincide with a south or southeast compass direction.

The tendency of Abert squirrels to show seasonal differences in nest use patterns does not refute the idea that Abert squirrels build nests on the south to southeast side of the tree to increase structural stability. Individual nests last an average of two years, and therefore all nests are subject to various climatic stresses, such as wind, rain and snow, regardless of whether they are inhabited.

Abert squirrels in this study typically built their nests at an average nest height to tree height ratio of 0.72. Farentinos (1972b) speculated that certain features of ponderosa pine trees may influence the vertical level at which Abert squirrels build their nests. Towards the lower part of the crown, side branches are sparse and at the top of the crown,

branches that would contain the nests are smaller, presumably less stable and more prone to wind. Abert squirrels may have an upper limit of nest height in which they prefer to build nests regardless of tree height. Patton (1974) found that nest height to tree height ratios decreased from 0.89 to 0.37 as the height of the tree increased from 12 to 36 meters. In general, arboreal squirrel nests are built at least halfway up the tree, but seldom lower than 3 meters or higher than eight to ten meters off of the ground, depending on the height of the tree (Brown and Twigg, 1965; Gurnell, 1987; Harestad, 1990; Rothwell, 1979; Tittensor, 1970; Vahle and Patton, 1983).

Another variable that may influence the structural stability of a nest is its placement in relationship to the trunk of the tree. Ninety-eight percent of all bolus nests located on this study site were built next to tree trunks at branch junctions. Reports in the literature of nest sightings agree with this finding (Farentinos, 1972b; Keith, 1965, Patton, 1974). In a similar study completed on 65 pine squirrel (Tamiasciurus hudsonicus) nests, 63% (n = 41) of those nests were located next to the trunk, whereas the remaining 37% (n = 24) were located within 0.5

meters from the trunk of the tree (Rothwell, 1979). Building nests next to trunks when combined with southeast exposure may provide additional protection from wind and rain.

Characteristics of nest trees and non-nest trees

Abert squirrels built nests in trees which were different from non-nest trees in the same area with respect to both intrinsic and extrinsic variables. These data suggest that Abert squirrels do select or choose tree types in which to build their nests, rather than building nests in randomly chosen trees.

All of the intrinsic tree variables that were significantly different in comparisons of nest trees and non-nest trees indicate that nest trees are larger than non-nest trees. This is consistent with the hypothesis that the placement of nests within trees maximizes structural stability. Trees with thicker trunks would be more resistant to wind and provide more protection from the rain when nests are placed against the trunk (Rothwell, 1979).

Abert squirrels select trees in plots with more Ponderosa pines greater than seven meters tall than non-nest plots. Nest trees are also on the interior of

a stand and have more access routes than non-nest trees. In addition to providing protection from weather, the close proximity of the nest tree to other trees increases the options squirrels have for approaching and leaving the nest, which may decrease predation risk (Hall, 1981; Rothwell, 1979). The two most common predators of Abert squirrels on Enchanted Mesa are goshawks (Accipiter gentilis) and coyotes (Canis latrans). Squirrels may avoid both of these predators by positioning themselves on the trunk of a tree, but are at risk when they try to locomote through the trees or on the ground. Increasing access to nests would decrease the travel time to nests and therefore decrease predation risk.

Only 80.5% of non-nest trees were correctly classified on the basis of tree height, access routes or crown dominance. This indicates that either more potential nest trees exist than are used by Abert squirrels on Enchanted Mesa, or that squirrels are also making selection choices based on other variables in addition to the variables measured as part of this study. Snyder and Linhart (1993) have recently completed a study on the secondary compounds found in trees utilized by squirrels for building nests. Their

results indicate that the phloem of nest trees have lower concentrations of copper, iron, and silicon than non-nest trees, and higher concentrations of sodium and non-structural carbohydrates. Discriminant function analysis on phloem characteristics correctly classified 90.6% of all nest trees, suggesting that tree chemistry may play a role in nest site selection. Although there was no difference in calcium concentrations between control and nest trees, the calcium content is higher in nest trees than target trees (those trees that squirrels utilize for food; Snyder and Linhart, 1993). In Abert squirrels, only pregnant and lactating females have been observed building nests (this study, Farentinos, 1972b; Keith, 1965), and reproductive females have a greater dietary calcium need than males (Havera, 1979).

Nest use by Abert squirrels

Pregnant and lactating females build an average of 6.3 nests each year that they initially inhabit with their litters. Females will move their litters every few days among their various nests, as a possible anti-predatory mechanism (Lair, 1985). However, Abert squirrels females whose nests were

monitored by radio signals given off by collared squirrels showed no difference in the number of times that they shifted nests when compared with females monitored visually (pers. obs.). Nest shifting may have evolved as a relatively inflexible anti-predatory mechanism that is used regardless of whether the animal was being actively watched by a predator.

Another reason that squirrels may shift nest sites is to decrease the number of skin parasites, mainly fleas, to which a squirrel may be exposed (Gurnell, 1987). Fleas are closely associated with nests because the egg, larval and pupal stages in the life cycle of the flea are not spent on the squirrel, but in the nest (Gurnell, 1987). That red squirrels (Sciurus vulgaris) shift nests more often during the spring and summer when squirrels suffer most from fleas is consistent with this idea (Wauters and Dhondt, 1990a).

After the juveniles are weaned, they stop sharing nests with their mother, and will take over a separate nest of their own. Although male and female juveniles inhabit both kinds of nests, female juveniles tend to inhabit a nest built by their

mothers, whereas males show a trend towards inhabiting nests built by other females (pers. obs.).

The number of nests Abert squirrels maintain are independent of their home range size, but not independent of the number of months the squirrels were watched in the field. This suggests that squirrels maintain a relatively equal number of nests from year to year, and replace them one for one as nests deteriorate.

Nest sharing. Abert squirrels have large overlapping home ranges and are considered to be solitary mammals. Only four percent of their time is spent in social interactions (this study; Chapter IV). Therefore, little or no nest sharing would be expected. Published accounts of nest sharing by Abert squirrels are rare. It has been assumed that shared nests consist of females and one or more of their young of the year congregating during the winter months (Keith, 1965). Koprowski (1991a) found that eastern grey squirrels (S. carolinensis) nested in groups ranging from two to nine squirrels per den and that the sexes tended to nest separately; the most common assemblage was all female kin groups. In contrast, in fox squirrels

almost all (35/48; 73%) communal nesting groups consisted of adult males (Koprowski, 1991a).

Communal nesting on Enchanted Mesa by adult Abert squirrels was rare, but of the 24 observed nest sharing encounters only three were young of the year who had returned to their natal nest during winter. The majority (88%) of the observed nest sharings involved unrelated individuals; either female (3/24; 12%) or male-female pairs (16/24; 67%). A similar pattern is exhibited by solitary non-territorial red squirrels where simultaneous nest use among adults was only observed between a male and a female, never between squirrels of the same sex. Nest sharing occurred during the mating season, or outside the mating season among squirrels who had mated previously (Wauters and Dhondt, 1990a). Female Abert squirrels are in estrus for one day every year and mate with several males sequentially during a mating bout. Nest sharing did occur between unrelated males and females who had mated previously, or with whom she later mated (pers. obs.).

Conclusion

The differences between nest trees and non-nest trees indicates that Abert squirrels are selecting nest trees that are taller than non-nest trees, have more access routes, and are in closed stands. Seasonal difference in nest use indicates that Abert squirrels do not choose nest locations on the south east sides of trees to facilitate behavioral thermoregulation. Therefore, Abert squirrels may be selecting nest site locations to 1) maximize the number of entry and escape routes; 2) inhibit detection by predators; and 3) maximize structural stability which may provide protection from wind and rain.

CHAPTER III
SEASONAL HOME RANGE VARIATION BY ABERT SQUIRRELS,
(Sciurus aberti)

ABSTRACT

Many of the characteristics of a home range may vary seasonally. The size of home range may fluctuate during the mating season, or when different food items are available. In the present study home ranges (95% minimum convex polygons) were calculated for thirteen adult Abert squirrels (Sciurus aberti). There was no significant difference in annual home range size among males and females, but males had significantly larger home ranges than females during the mating season. Home range sizes did not significantly change with seasonal fluctuations in diet. Total (100%) home ranges were also compared to data obtained on this study site 20 years ago. At that time the density of adult Abert squirrels was higher than during this study. No significant difference was found among males living in populations of different densities, but females showed a significant increase in home range size when the population density decreased.

INTRODUCTION

Space use, like other patterns of behavior, may vary as a function of proximate conditions. Resources such as food, shelter, and mates are distributed in space, so space itself is an important resource. How animals use space is closely linked to how they organize themselves socially; species are commonly characterized by observed spacing patterns. Studies have shown that the size of a home range may be influenced by age, sex, season, population density, food distribution, and other habitat variables (Heany, 1984; Layne, 1954; Schoener, 1981; Simon, 1975). In the present study, "home range" was defined as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943; page 351).

Home range size for arboreal squirrels ranges from 0.15 hectares for non-territorial pine squirrels (Tamiasciurus hudsonicus) to greater than 18 hectares for fox squirrels (Sciurus niger; Gurnell, 1987; Layne, 1954; Wiegl et. al., 1989). However, caution must be used when comparing home range sizes across species and across studies, because the methods used

to obtain information on home ranges differ, as do the habitats of the individual populations. It is often best, for comparative purposes, to look at the variation and trends within a population, rather than exact home range size (Gurnell, 1987).

Most studies of home range size of arboreal sciurids have concentrated on determining the overall home range of the species, often on the basis of data from single seasons or from radiotracking a few individuals. Previous studies of this type have been completed on grey squirrels (Sciurus carolinensis; Doebel and McGinnes, 1974), fox squirrels (Adams, 1976; Baumgartner, 1943; Benson, 1980; Bernard, 1972; Havera and Nixon, 1978; Kantola and Humphrey, 1990), pine squirrels (Gurnell, 1984), and Abert squirrels (Sciurus aberti; Hall, 1981; Keith, 1965),

Many of the trends found in home range size variation in arboreal squirrels have been summarized by Don (1983) and Heany (1984). Adult males tend to have larger home ranges than adult females, which may be attributed to the males' tendency to increase their home ranges during the spring and summer mating season (Benson, 1980; Ortega, 1988; Wiegl et. al., 1989). This period also coincides with the time that females

are lactating and remaining close to their nests (Kenward, 1984).

Food supply is also closely linked to home range size. Across species, home range sizes of arboreal squirrels are positively correlated with seasonal precipitation, and negatively correlated with the number of plant species that an animal consumes (Heany, 1984). Thompson (1978a) found little change in the home range size for grey squirrels during summer, fall and winter, but did notice an increase in home range size during spring for both sexes when food was scarce. Fox squirrels did not alter their home range size during periods of food scarcity, but decreased their activity levels and used all areas of their home ranges equally, possibly looking for food (Wiegl et al., 1989).

Kenward (1984) suggests that population density, and not food supply, is the main factor affecting home range size. Grey squirrels had smaller home ranges when population density increased, even when this increase was followed by a food shortage. However, as Don (1983) pointed out, food supply is closely related to population density, and therefore it may be impossible to separate the influence of these two

variables. Most of the data on population density and home range size in arboreal squirrels come from different populations of the same species (Don, 1983), and therefore it is difficult to separate out different factors that may influence home range size.

Home range size of Abert squirrels

Farentinos (1979) found that Abert squirrels have larger winter home ranges than summer home ranges. The mean winter home range for males was 5.3 hectares and the mean summer home range was 2.6 hectares. Winter home ranges for females were 4.9 hectares, as opposed to 1.3 hectares during the summer. Farentinos attributed the increase in home ranges during the winter to a shift in the food supply from Ponderosa pine cones to inner bark. Although inner bark is readily available, it is poor in nutritional quality, and Abert squirrels are highly selective about the trees from which they obtain inner bark (Capretta and Farentinos, 1979; Capretta et. al. 1980; Snyder, 1990). In contrast, data from a study completed in Arizona showed that home ranges were three times as large in summer (18 acres) than during winter (5 acres; Keith, 1965). In both of these

studies, home range size was analyzed according to calendar seasons, not according to the seasonal availability of different food types.

Farentinos (1979) also found that home ranges for males increased to an average of 20.8 hectares during the breeding season, whereas females did not increase their home ranges. He attributed the larger home ranges of males during the breeding season to increased activity when males searched for estrous females. However, Farentinos defined the breeding season as including only the months of April and May, and Abert squirrels have been observed to mate as early as February and as late as June on this same study site (this study, Chapter 6).

Using the same study site as Farentinos gave me the unique opportunity to make comparisons between his data and data obtained on a population inhabiting the same area 20 years later. The purpose of this portion of the study was to 1) evaluate home range sizes for adult Abert squirrels when different food items were consumed; 2) compare home range sizes during the mating season (February to June) and during the non-mating season; and 3) compare these home range data to

data published for this study site by Farentinos (1979).

MATERIALS AND METHODS

This study was conducted in a 72 hectare region of Ponderosa pine forest located in Boulder, Colorado which is commonly called Enchanted Mesa (elevation 1940 meters above sea level). A grid system of x and y coordinates was mapped onto the study area with markers placed approximately every 30 meters. Aluminum tags were placed on all 4 sides of selected trees and lettered sequentially A - Z from north to south, and numbered 1 - 30 from east to west. Quadrats within the study site were 30 x 30 meters; the four corners were defined by sequential grid markers. A map was created of the area by plotting the grid system onto a reduced aerial photograph of the study site.

Squirrels were trapped using Tomahawk #202 live traps baited with peanut butter and sunflower seeds. After being caught, squirrels were permanently marked with an ear tattoo and a freeze brand using "quik-freeze" brand liquid cryogenic. Dye marks were also

used as temporary visible identifiers. The squirrels' age, weight, and sex were recorded.

Between May 1989 and October 1991, 13 adult (seven male and six female) squirrels were observed year round from sunrise until one half hour before sunset, or when it was determined that all squirrels had entered their nests for the evening. Days were normally divided into two sampling periods; 1/2 the number of daylight hours in duration. Dawn to dusk observations were attempted at least one day per week.

Once marked squirrels were found, they were followed and their behavior patterns were recorded using focal animal sampling (Altmann, 1974). Their location on the study site was recorded using grid markers as reference points. Marked squirrels were observed with 10 x 50 binoculars using trees as natural blinds. Squirrels habituated to observers' presence and did not appear to alter their activities when followed. Behavioral data were spoken into a microcassette recorder and later transcribed into notebooks. Data were then subsequently entered into a computer for analyses. Only those squirrels that were sampled a minimum of ten days were included in the analyses.

In the winter and spring of 1991, four female squirrels were fitted with radio transmitter collars. Individual collars weighed between 15 and 20 grams. A collar was placed on an individual while she was held in a cloth handling bag. Signals were transmitted at various rates at 164 MHz, and were received using a model CE12 receiver with a three element Yagi antenna. All radio components were built by Custom Electronics, Urbana, Illinois. Radio telemetry was used only to locate individuals. All of the data on these squirrels were collected using the same methods as those used on non-radio collared individuals. Radio transmitter collars were removed from these squirrels in the summer of 1991.

An individual "sighting" was defined as the location of the first observation of a marked squirrel on a given day, and any subsequent observations of that individual on the same day that were separated by more than 10 meters. While foraging, squirrels would often make short movements (1 - 2 meters) until the next edible food item was found. In order not to bias the results, these were not counted as individual sightings. Given the size of published records of Abert squirrel home ranges, the criterion of 10 meters

separation and the accuracy in determining the locations of individual squirrels are well within acceptable limits (Farentinos, 1979).

Abert squirrels mated on Enchanted Mesa between February 15 and June 5 of each year. Assuming that males altered their home range patterns to search for estrous females, it is possible that males began to increase their home ranges before the first female went into estrous each year, and continued to increase their home ranges until after the last female had completed estrous. Therefore, the mating season was defined as February 1 to June 15 of each year, and the non-mating season was defined as June 16 to January 31 of each year.

To compare home range size as a function of food items consumed, sampling periods were divided into months, and months were assigned to one of four categories dependent upon the dominant food item consumed. Dominant food items were determined by summing the total number of all items consumed in a month; the food item that was consumed at least twice as often as any other food item consumed was determined to be dominant. Dominant food item categories were 1) Ponderosa pine inner bark; 2)

Pondersosa pine cones (male and/or female); 3) Other tree items including Douglas fir (Pseudoseuga menziesii) shoots or cones, and 4) Ground items including mushrooms and other ground items including fallen cones and hypogeous fungi.

Home range calculations

Although a variety of methods have been devised to calculate home ranges (Bekoff and Mech, 1984; Hayne, 1949; Jennrich and Turner, 1969; Koepl et al., 1977; Mohr, 1947; Mohr and Stumpf, 1966; Schoener, 1981) the minimum convex polygon method was used for home range calculations because this method can be used to compare many different studies and gives results that are comparable to those obtained with grid trapping and telemetry (Harris et al, 1990). Overall home ranges were calculated using both the 100% and the 95% minimum convex polygon (MCP) method (Bekoff and Mech, 1984; Michener, 1979; Mohr and Stumpf, 1966). The geometric center of activity for each home range was calculated by averaging separately all locations along the vertical axis and all locations along the horizontal axis (Hayne, 1949). The 95% minimum convex polygons were calculated by

omitting the five percent of those observations that were farthest from the geometric center (Bekoff and Mech, 1984; Mohr and Stumpf, 1966). The 95% MCP were used for most of the analyses because they are less sensitive to excursions outside the home range by an individual animal (Harris et. al., 1990), but 100% MCP home ranges were used for comparison purposes with Farentinos' (1979) data because he presented only these data.

The area of the polygons was calculated using a digitizing tablet and the computer program JAVATM (Jandel Corp, 1991). Home ranges were measured three times and the average of these measurements was recorded. When making comparisons between the sexes and mating seasons, the sample sizes were often small. Therefore two-tailed non parametric Mann-Whitney U tests or Wilcoxon paired sample tests were used to test for the differences between groups (Minitab, 1991). A non-parametric Friedman test for within subjects was used to compare home range sizes for different dominant food categories (Linton and Gallo, 1975). Data are expressed as mean \pm standard deviation except where noted.

RESULTS

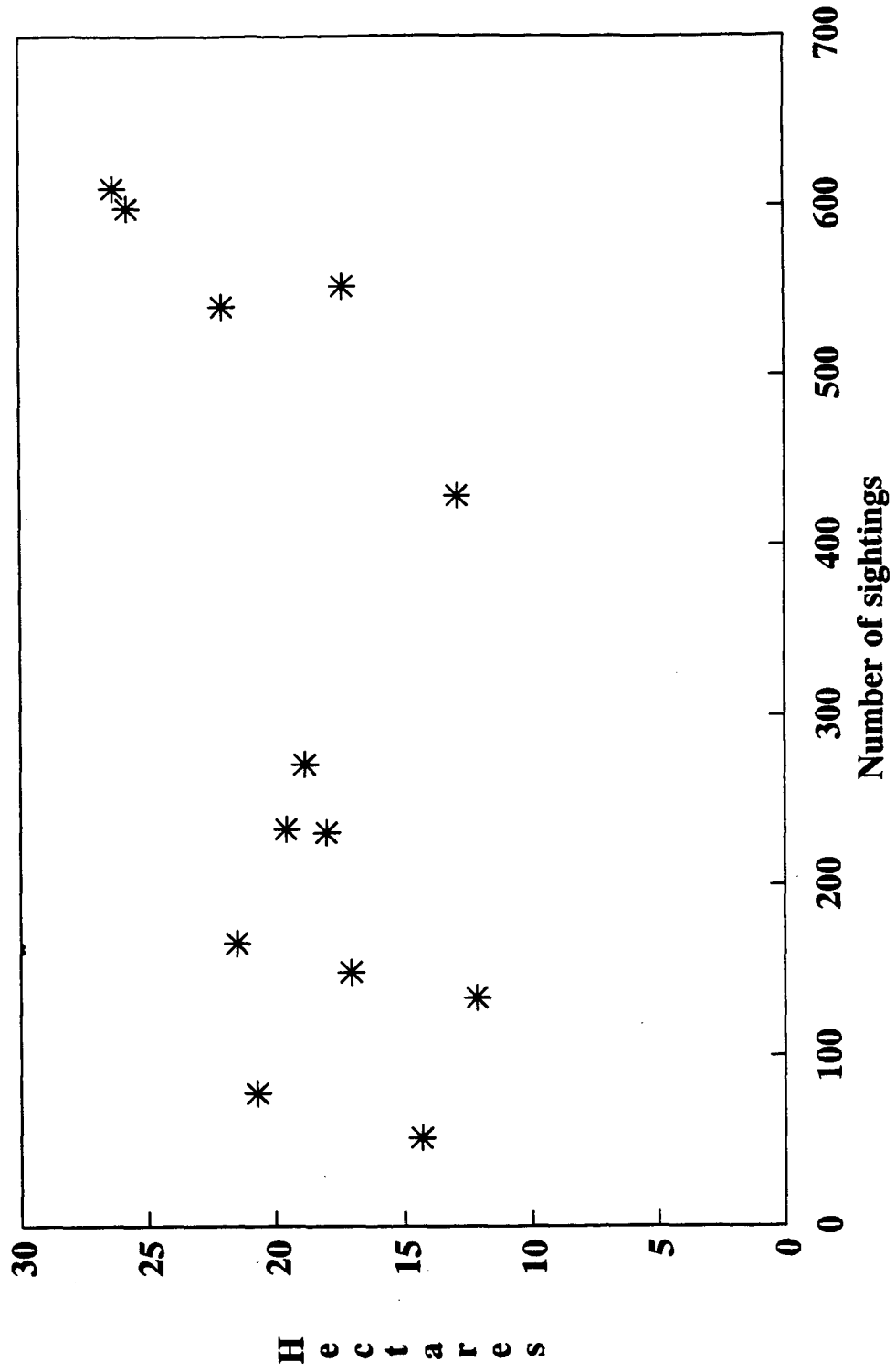
Seventeen (nine female and eight male) adult Abert squirrels inhabited Enchanted Mesa during this study (from May 1989 to October, 1991). A total of 4139 sightings was obtained on 13 (seven female and six male) squirrels that met the 10 day minimum sampling criteria during 2097 hours of data collection.

There was no significant difference in the mean number of home range sightings between males (mean = 321 ± 94.4 SE) and females (mean = 302 ± 75.9 SE; $U = 58.0$, $p > 0.05$; Table 3.1). Overall 95% MCP home range sizes were independent of the number of sightings used in the calculation ($r_s = 0.52$, $n = 13$, $p > 0.05$; Figure 3.1). Seasonal 95% MCP home range size and the 95% MCP home range size calculated as a function of the dominant food item consumed were also independent of the number of sightings used in the calculations ($r_s = 0.22$, $p > 0.05$ and $r_s = 0.31$, $p > 0.05$, respectively). However, total (100%) MCP home ranges were correlated with the number of sightings ($r_s = 0.63$, $n = 13$, $p < 0.05$).

Table 3.1. The sizes (hectares) of total home ranges (100%) minimum convex polygons and 95% minimum convex polygons for Abert squirrels (Sciurus aberti) on Enchanted Mesa from May 1989 to October 1991. (N = 13 squirrels).

Squirrel	Sex	100%	95%	Percentage of area
BBH	F	23.50	19.55	83.2
BBMH	F	15.70	12.16	77.4
BLH	F	17.85	17.04	95.5
BRH	F	33.20	22.02	66.3
BRMH	F	22.37	17.32	77.4
GBH	F	22.10	20.71	93.7
GRH	F	24.70	12.89	52.2
BBF	M	35.52	25.77	72.6
BLF	M	15.08	14.35	95.2
BLFM	M	26.38	21.50	81.5
BRF	M	24.27	17.99	74.1
BRFM	M	28.10	26.31	93.6
GRF	M	35.88	18.83	52.5
Mean	F	22.77	17.38	77.96
Std. Dev.	F	5.60	3.76	15.18
Mean	M	27.54	20.79	76.58
Std. Dev.	M	7.76	4.67	14.07

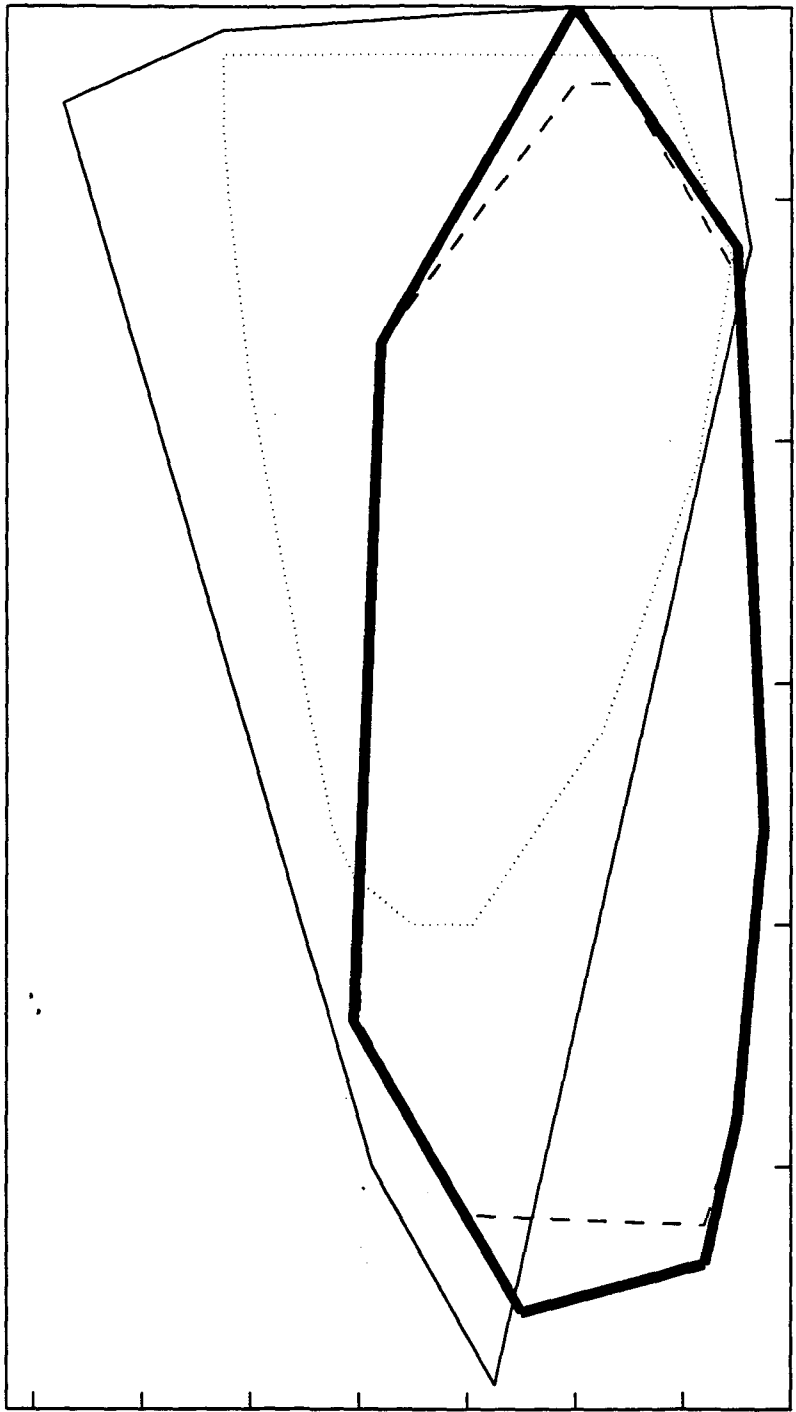
Figure 3.1. The number of sightings used in the calculations and the size of the resulting 95% minimum convex polygon home ranges, for Abert adult squirrels (Sciurus aberti) on Enchanted Mesa. (N = 13).



There was no significant difference in overall size between male (mean = 27.5 ± 7.8) and female (17.4 ± 3.7) 100% MCP home ranges ($U = 34, p > 0.05$) or between male (20.8 ± 4.7) and female (17.4 ± 3.4) 95% MCP home ranges ($U = 40, p > 0.05$). The 95% MCP home ranges enclosed an average of 78.1% (± 14.2) of the area of the 100% polygons (Table 3.1 and Figure 3.2). The home range of an individual squirrel overlapped extensively with the other squirrels on the study site. There was no significant difference in the amount of same sex home range overlap between males (mean = $87.8 \pm 16.0\%$) and females (mean = $91.2 \pm 10.0\%$; $U = 48.5, p > 0.05$), nor was there any significant difference in the amount of total home range overlap between males (mean = 99.2 ± 1.5) and females (mean = 97.2 ± 2.4 ; $W = 39.0, p > 0.05$; Table 3.2).

Males had significantly larger 95% MCP home ranges (mean = 18.7 ± 2.9) than females (mean = 12.01 ± 5.4) during the mating season ($U = 17.0, p < 0.05$), but there was no statistically significant difference between 95% MCP home ranges between males (mean = 13.6 ± 4.7) and females (mean = 15.6 ± 4.5) during the non-mating season. Four of the five males (80%) had larger

Figure 3.2. Total home range (100%) and 95% minimum convex polygon home ranges for representative male (BRFM) and female (BRH) adult Abert squirrels (Sciurus aberti) on Enchanted Mesa from May 1989 to October, 1991.



..... BRH 95% - - - BRFM 95% — BRH 100% ——— BRFM 100%

Table 3.2. The mean percentages of overlap among home ranges for Abert squirrels (*Sciurus aberti*) on Enchanted Mesa. Data are given for size of the area individuals shared with members of the same sex, and for size of the area shared with all squirrels. (N = 13 squirrels).

Squirrel	Sex	Same sex	Total ^a
BBH	F	97.3	98.1
BBMH	F	91.9	95.4
BLH	F	100.0	100.0
BRH	F	67.7	96.3
BRMH	F	94.2	99.8
GBH	F	96.7	98.3
GRH	F	90.7	92.6
BBF	M	82.2	95.8
BLF	M	54.6	99.7
BLFM	M	93.4	99.9
BRF	M	99.6	100.0
BRFM	M	97.1	99.5
GRF	M	100.0	100.0
Mean	F	91.2	97.2
Std. Dev.	F	10.0	2.4
Mean	M	87.8	99.2
Std. Dev.	M	16.0	4.3

^a The home range for any individual overlapped with all of the home ranges for other individuals within the population.

home ranges during the mating season than during the non-mating season, but these results were not statistically significant ($W = 12, p > 0.05$; Figure 3.3).

Home range size and feeding patterns

Abert squirrels typically ate the same foods during the same month of each year, when they were available. Ground items were the dominant food items consumed in June of 1989, 1990, and 1991. Male Ponderosa pine cones were also consumed during May of all three years. Female cones were consumed during 1989 and 1991, but were unavailable during 1990 due to a poor mast year. A shift in the dominant food item consumed was observed between winters. During fall and winter of 1989-90 Abert squirrels foraged mainly on the ground, but during this same season the following year they primarily ate Pondersosa pine inner bark (Figure 3.4).

There was no significant difference among male and female 95% MCP home range sizes when any of the four dominant food items were available, so the data were pooled across sexes. Adult Abert squirrels did not alter their home range size depending upon which

Figure 3.3. The mean home ranges sizes for adult Abert squirrels (Sciurus aberti), during the mating and non-mating season, on Enchanted Mesa from May, 1989 to October, 1991. (N = 6 males and 7 females).

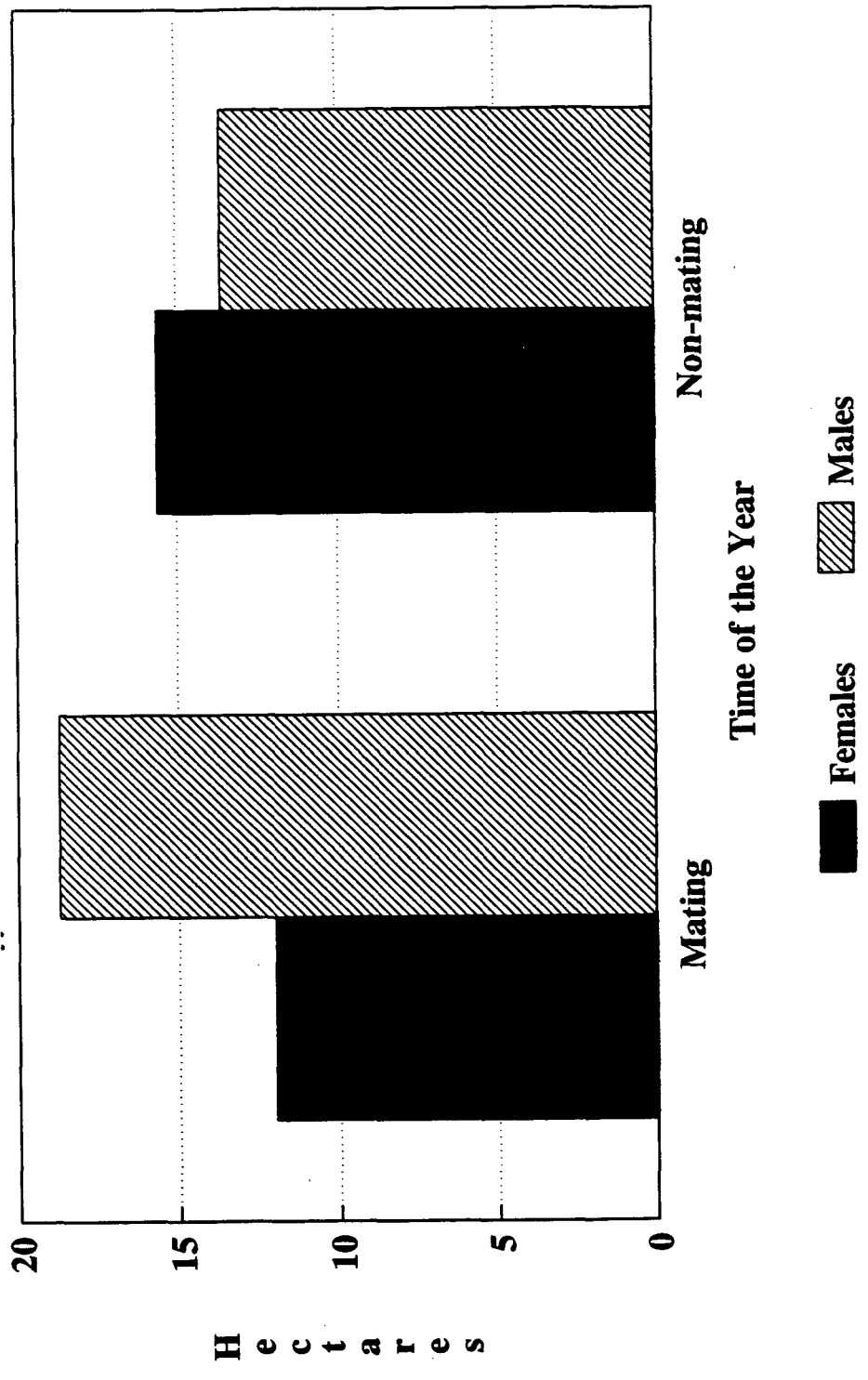


Figure 3.4. Dominant food types consumed by Abert squirrels (Sciurus aberti) from May 1989 to July 1991. (PCones = Ponderosa pine (Pinus ponderosa) cones, both male and female, IB = Ponderosa pine inner bark (phloem), Other = Other trees, such as Douglas fir, and Ground = mushrooms and other items eaten off the ground)

food items they were consuming (Friedman's $X^2 = 4.2$, $df = 3$, $p > 0.05$; Table 3.3).

The influence of population density on home range size

The data from this study were compared with a similar study performed at this location from December 1969 to May 1971 by Farentinos (1979). From 1971 to 1991 the annual population of adult Abert squirrels dropped 46%, from 24 adults to 13 adults. There was no significant difference between 100% MCP home range sizes for males between 1991 (mean = 27.5 ± 7.8) and 1971 (mean = 18.21 ± 8.7 ; $U = 47$, $p > 0.05$), but home ranges for females (mean = 17.4 ± 3.7) in 1991 were significantly larger than home ranges for females in 1971 (mean = 9.26 ± 2.9 , $U = 36$, $p < 0.01$; Table 3.4).

The home range sizes during the mating season were not directly compared to the non-mating season between the two populations because of differences in methods. Farentinos (1979) limited the mating season to April and May, and used the 100% MCP method for all home ranges. However, Farentinos showed a statistically significant increase in home range size for males during the mating season and no significant

Table 3.3. Seasonal differences in 95% minimum convex polygon home range sizes when Abert squirrels (Sciurus aberti) were consuming food items from different food categories. (IB = Ponderosa pine inner bark, C = Ponderosa pine cones; both male and female, OT = trees other than ponderosa pines, G = mushrooms and other items on the ground).

Squirrel	Sex	IB	C	OT	G
BBH	F	7.84	... ^a	...	6.38
BLH	F	5.94	11.53
BRH	F	17.61	10.00	7.79	12.59
BRMH	F	10.33	6.91	9.35	11.29
GBH	F	17.52	...
GRH	F	8.27	2.59	8.55	6.12
BBF	M	7.60	17.83	19.52	5.46
BLF	M	6.39
BLFM	M	11.57	10.54	...	16.46
BRF	M	14.65	8.44	7.62	15.14
BRFM	M	10.86	15.55	7.06	18.61
GBF	M	9.40	13.40
GRF	M	16.78	12.09	5.57	14.84
Mean		10.71	10.61	10.26	12.03
Std. Dev.		3.89	4.25	4.57	4.40

^aHome ranges for these columns were not calculated for these individuals because they did not meet the minimum sampling criteria of 10 days.

^bThere was no significant difference among home range sizes when squirrels were predominantly eating food items from different categories. Only those individuals that had data in all columns were used in the analysis.

Table 3.4. Total (100%) minimum convex polygon home range sizes for adult Abert squirrels (Sciurus aberti) inhabiting Enchanted Mesa during two studies that ended in 1971 (Farentinos, 1979) and 1991 (this study). The number of sightings used in home range size calculations are shown in parentheses. (N = total number of squirrels used in the analysis of home range sizes for each study).

Year	Residents per Year	Density	N	Home Range Size ^a	
				Male	Female
1971	24	0.33/ha	16	18.2 (118)	9.3 (63)
1991	13	0.18/ha	13	20.8 (321)	17.4 (302)

^a There was no significant difference in the number of sightings among males and females for 1991.

differences in home range size for females. The data from this study show a similar trend.

DISCUSSION

The home range sizes reported here are among the largest ever reported for any North American arboreal squirrel (Heany, 1984). Abert squirrels are classified as a solitary species (Farentinos, 1972a; Hall, 1981; Keith, 1965; pers. obs.) that do not defend territories. An average of 98% of the space used by an individual Abert squirrel on Enchanted Mesa overlapped with home ranges of other individuals. There was some degree of overlap with all other individuals within the population. The amount of home range overlap has not been published for many species, but Wauters and Dhondt (1985) found 70% overlap among individual grey squirrels within a population.

Home range size expansion by males during the mating season

Farentinos (1979) reported that males increase the size of their home range during the mating season. The data from this study show the same trend, although

seasonal variations were not significantly different. Furthermore, there was no significant difference in home range size due to a change in diet during this time of the year. These findings support the hypothesis that males increase their home range size during the time of year when females are in estrous.

During the mating season, males were observed to enter and exit several nests in succession as they travelled around the study site during the early part of the day. These nests consisted of nests in which the male squirrels slept at night and nests used by known females. Males seldom entered nests for periods longer than two minutes in length, or visited nests during the non-mating season (this study; Chapter II).

Females did not show a change in home range size during the mating season, but the mating season as defined here is more applicable to males than to females. There may be no reason why females should alter their space use patterns because other females are in estrous. The time frame that would be more applicable for females would be the date of estrous through the weaning of young. These data were not collected for this study because once a female had mated, I concentrated on locating other females to

obtain information about their reproductive condition. When the juvenile squirrels were old enough to locomote around the study site, I spent my efforts trying to capture and mark the juveniles before they left the maternal nest.

Home range size and feeding patterns

There was no significant difference in home range sizes on the study site when different food items were being consumed. Trees in which Abert squirrels feed are dispersed throughout the study site. Food items that the squirrels would pick up and eat off the ground were also dispersed throughout the study site.

Although no significant differences in home range sizes were obtained when squirrels were eating diets from different dominant food categories, the home range sizes when ponderosa pine cones were not available (Other; July, September and October, 1989) are an underestimate of the total ranges that the squirrels used. These data represent only the area used within study site. During these months, squirrels would often leave the study site during the day and travel west at least one-half of a kilometer to feed

in Douglas fir (pers. obs.) I was unable to follow the squirrels on these journeys because they would cross a very steep ravine.

The lack of a ponderosa pine crop not only resulted in a shift in diet during the summer of 1990, but also may have influenced the winter diet. In a year with an abundant mast crop, squirrels rely on cones into the fall and winter. Even after cones have fallen to the ground, squirrels will retrieve them. Abert squirrels bury individual cones in shallow pits (Bailey, 1932; Keith, 1965; pers. obs.), but are the only arboreal squirrel species for which caching is considered to be moderately, rather than extremely, important (Heany, 1984). From October 1989 to April 1990, Abert squirrels foraged primarily on the ground, but during this same time period the following winter the dominant food item consumed was inner bark from Ponderosa pines. Ponderosa pine phloem is inferior to cones in nutritional quality and is less preferred by squirrels (Capretta and Farentinos, 1979; Capretta et. al., 1980; Keith, 1965; Snyder, 1990).

The present findings are not consistent with Farentinos' (1979) results. One possible reason for this discrepancy could be attributed to differences in

methods. Farentinos used 100% MCP home range calculations, which are more sensitive to sample size than the 95% MCP used here (Harris et. al., 1990; this study). Contrary to Farentinos' findings, Keith (1965) found summer home ranges to be larger than winter home ranges. However, his findings were based on a small sample size (n = 4 squirrels) and he did not report the number of sightings used in his calculations.

The influence of population density on home range size

Female 100% MCP home range size significantly increased between 1971 and 1991 from 9.3 hectares to 17.4 hectares. Male 100% MCP home ranges increased from 18.2 hectares to 27.5 hectares, but this increase was not statistically significant at the 0.05 level. One reason that male home range size may not have differed between years is that male home ranges already include the major portion of the study site during the breeding season. These data support the hypothesis that as population density decreases, home range size will increase (Heany, 1984; Kenward, 1984). However, these data must be interpreted with caution as the 1991 data are based on a larger number of observations than the 1971 data. Also, as previously

indicated 100% MCP home range calculations sizes are more sensitive to sample size than are 95% MCP home range calculations.

Home range size may be associated with squirrel density and food availability in three ways. The first is that abundant food could result in small squirrel ranges which reduce social pressures, energy expenditure, or predation risks, and therefore allow a high density of squirrels to live in a small area. This idea causally links home range size to an increase in food supply.

A second way in which home range size may be associated with population density and food availability, is that small home range size could result from increased social pressure at higher density levels, when abundant food leads to higher population densities. This idea causally links home range size to population density. A third way in which home range size may be associated with population density and food availability, is that increased food supply results in both small range size and high population density; small range size and high population density are correlated, but not causally related (Kenward, 1984).

Data obtained over several years on grey squirrels indicates that they did not alter their home ranges with a decrease in their food supply, but did decrease their home range size when the population increased. No change in home range size was observed when squirrels were given supplemental food, so Kenward (1984) concluded that home range size was linked to population density rather than to food availability.

In this study Abert squirrels did not alter their home range size on the study site when different foods were available, but did forage in areas outside of the study site during a poor mast year. If Abert squirrels decrease their home ranges when population densities are high because of social pressures, then they must avoid each other temporally, rather than spatially, since their home ranges overlap so extensively.

CHAPTER IV
SEASONAL CHANGES IN ACTIVITY BUDGETS OF ABERT
SQUIRRELS (Sciurus aberti)

ABSTRACT

The effects of seasonal changes in photoperiod, ambient temperature, and food availability on the activity patterns of Abert squirrels (Sciurus aberti) were studied in the foothills of the Rocky Mountains in Boulder County, Colorado. As photoperiod and ambient temperatures increased from winter to summer, the number of hours and percentage of available daylight hours during which squirrels were active outside of their nests also increased. Seasonal changes in activity budgets were also observed. Squirrels spent a larger percentage of time performing nesting behaviors in the summer and a smaller percentage of time performing nesting behaviors in winter. Squirrels spent a larger percentage of time performing social behaviors in the spring, which coincides with their mating season. In autumn, squirrels spent a larger percentage of time traveling, and a smaller percentage of time resting. The increase

in traveling may be due to the squirrels' tendency to forage on the ground during autumn, and this trend probably results in a decrease in the amount of time spent resting.

INTRODUCTION

Arboreal squirrels in temperate regions must adjust to fluctuating temperatures and changing food conditions because they are active year round. One way to adjust to these changes is to vary the amount of time spent outside of the nest. Another way in which squirrels may adjust to seasonal differences is to alter their activity budgets--how time is spent out of the nest--during different periods of the year.

The activity rhythms of arboreal squirrels are usually measured in terms of the number of total daylight hours during which squirrels are active. Studies on grey squirrels (Sciurus carolinensis; Thompson, 1977b), fox squirrels (Sciurus niger; Weigl et. al., 1989), red squirrels (Sciurus vulgaris; Wauters and Dhondt, 1992), and pine squirrels (Tamiasciurus hudsonicus; Ferron, et. al. 1986; Gurnell, 1984; Pauls, 1977) have shown that arboreal

squirrels alter their activity rhythms from season to season. During winter months squirrels typically exhibit a unimodal pattern; the greatest number of squirrels are active in the middle of the day. During summer, a bimodal pattern of activity is common, with one peak in the morning and a second peak during the late afternoon.

Most arboreal squirrels cache food in late summer and autumn, which they use during the winter months. Storing food in caches may decrease the amount of time these individuals need to search for food during winter, a consequence of which would be a change in the amount of time squirrels spend in activities, such as feeding and resting (Ferron, et al, 1986; Wauters and Dhondt, 1992).

Abert squirrel activity patterns

Abert squirrels (Sciurus aberti) are active year round; even during the coldest winter weather they will leave their nests for a portion of the day (Farentinos, 1977; Hall, 1981; Keith, 1965). They bury individual cones in shallow pits (Baily, 1932; Keith, 1965; pers. obs.), but are the only arboreal squirrels for which caching is considered to be moderately,

rather than extremely, important (Heany, 1984). The absence of a winter cache may have an impact on both the activity rhythms and budgets of this species, and Abert squirrels may show patterns different from those of other arboreal squirrels.

Golightly and Ohmart (1978) discovered that the body temperature of Abert squirrels rises during periods of locomotion and drops significantly during periods of rest (from 41 to 35 °C). Abert squirrels must also triple their metabolic rate when the ambient temperature drops from 20 to -20 °C. These thermoregulatory constraints may make it difficult for individuals to spend time outside of the nest resting on cold winter days, and may limit moving about on warm days. Therefore, the need to regulate body temperature may also cause Abert squirrels to alter their daily activity patterns from season to season.

Although Abert squirrels rely on Ponderosa pine (Pinus ponderosa) for their main food supply (Farentinos, Hall, 1981; Keith, 1965; Snyder, 1990), they eat different parts of the tree at different times of the year. Abert squirrels eat inner bark in the winter, male cones in the spring, and female cones in the summer. In addition to Ponderosa pine, they

also eat Douglas-fir (Pseudotsuga menziesii), seasonal mushrooms that appear after summer rains, and hypogeous fungi (Stephenson, 1974; 1975). The amount of nutrition and the handling time will also change when squirrels are eating different food items. Therefore activity budgets may differ seasonally because of the type of available food.

The purposes of this study were to describe the behavior and activity patterns of Abert squirrels and to describe how activity rhythms and budgets may change due to seasonal differences in day length, ambient temperature, and food supply.

MATERIALS AND METHODS

This study was conducted in a 72 hectare region of Ponderosa pine forest commonly called Enchanted Mesa which is located in Boulder, Colorado (elevation 1940 meters above sea level). A grid system of x and y coordinates was mapped onto the study area with markers placed approximately every 30 meters. Aluminum tags were placed on all 4 sides of selected trees and lettered sequentially A - Z from north to south, and numbered 1 - 30 from east to west. Quadrats within the

study site were 30 x 30 meters; the four corners were defined by sequential grid markers. A map was created of the area by plotting the grid system on to a reduced aerial photograph of the study site.

Squirrels were trapped using Tomahawk #202 live traps baited with peanut butter and sunflower seeds. After being caught, squirrels were permanently marked with an ear tattoo and a freeze brand using "quik-freeze" brand liquid cryogenic. Dye marks were also used as temporary visible identifiers. The squirrels' age, weight, and sex were recorded.

From May to November 1989 and from January 1990 to October 1991, squirrels were observed year round from sunrise until one half hour before sunset, or when it was determined that all squirrels had entered their nests for the evening. Days were normally divided into two sampling periods; 1/2 the number of daylight hours in duration. Dawn to dusk observations were attempted at least one day per week.

In the winter and spring of 1991, four female squirrels were fitted with radio transmitter collars. Individual collars weighed between 15 and 20 grams. A collar was placed on an individual while they were held in a cloth handling bag. Signals were transmitted

at various rates at 164 MHz, and were received using a model CE12 receiver with a three element Yagi antenna. All radio components were built by Custom Electronics, Urbana, Illinois. Radio telemetry was used only to locate individuals. All of the data on these squirrels were collected using the same methods as those used on non-radio collared individuals. Radio transmitter collars were removed from these squirrels in the summer of 1991.

~~The mean monthly maximum temperature (°C), the mean monthly minimum temperature (°C), and the total amount of precipitation (centimeters) for each month were obtained from the WEB reports (Weather Enthusiasts of Boulder, 1989-1991). Sunrise and sunset data were obtained from the Boulder Daily Camera Newspaper (1989 - 1991).~~

Activity rhythm analysis

The time at which squirrels were seen leaving their nests in the morning, and the time at which squirrels were seen entering their nests in the evening, were recorded (Mountain Standard Time). These data were averaged for two week intervals. The number of hours between the mean time leaving the nest and

the mean time entering the nest was considered to be the mean amount of time squirrels were active for that two week interval. The percentage of daylight hours that squirrels were active was calculated by dividing the mean active time by the average number of daylight hours available for that two week period. Kruskal-Wallis tests were performed to test for seasonal differences in daytime activity (number and percentage of hours).

Activity budget analysis

Once marked squirrels were found, they were followed and their behavior patterns were recorded using focal animal sampling (Altmann, 1974). Their location on the study site was recorded using grid markers as reference points. Marked squirrels were observed with 10 x 50 binoculars using trees as natural blinds. Squirrels habituated the observer's presence and squirrels did not appear to alter their activities when followed. Behavioral data were spoken into a microcassette recorder, transcribed into notebooks, and entered into a computer for analyses. Squirrels were more visible when performing some behaviors such as locomotion, than when engaging in

other behaviors such as resting, so only data obtained from continuous observation periods longer than one hour were used for activity budget analysis.

Each observed behavior pattern was given a unique numeric code (see Appendix 1). Data were recorded continuously; the starting times and durations of each behavior pattern was recorded. Behavior patterns were also grouped into categories and the duration of behavior patterns in each category was summed for all squirrels each season. Seasons were classified as Winter (December 21 thru March 20); Spring (March 21 thru June 20); Summer (June 21 thru September 20); and Autumn (September 21 thru December 20).

A similar method was used to analyze activity budget data when squirrels were eating different types of foods. Food item categories were Ponderosa pine cones (May, July, August and September, 1989; May, 1990; May and July, 1991), Ponderosa pine inner bark (November and December, 1990; January, February and March, 1991), Ground items (June, October, and November, 1989; February, March, April, June, and August, 1990; June, 1991), and Other (July, September, and October, 1990). For a description of the

derivation of food categories see Chapter III, this study.

Chi-square analyses were used to determine if squirrels altered their activity budgets among seasons, or at different times of year based on food items consumed. The categories "food-related behaviors" and "other solitary behaviors" were combined, decreasing the number of cells within the contingency table that had small frequencies. Data are expressed as means \pm standard deviations, unless specified. Significant cells within the contingency tables were identified using a simple approximation derived from Castellan's (1965) method of partitioning contingency tables (Lefebvre, 1981).

Categories of behavior

The behavior patterns observed were placed into one of eight categories.

I. Feeding: The location of the squirrel (ground or tree) was recorded in addition to the item consumed. Common items eaten in trees were Ponderosa pine and Douglas fir cones and apical buds, and Ponderosa pine inner bark. Common items eaten on the ground were

epigeous fungi (mushrooms), hypogeous fungi, and fallen or cached Ponderosa pine cones.

II. Food related behaviors: This category included caching food items and traveling while carrying food items. Digging in the ground was also included, though digging did not always result in the procurement of a food item.

III. Resting: When squirrels rested, their abdomens touched the substrate and their limbs were stretched away from their body. Quite often they would lay their chins on the substrate. Their tails would either hang down alongside their bodies, or else curl over their backs. When squirrels rested, they usually kept their eyes open. Squirrels usually rested on tree limbs, but also rested on fallen logs, rocks, stumps, and the ground.

IV. Traveling: Behaviors such as walking, running, jumping, and climbing were included in this category. However, if the squirrel was carrying an item in its mouth, such as nesting material or food, it was not included in this category because these behaviors

would be nest related or food related. The location of the activity (ground or tree) was recorded.

V. Grooming: Licking or mouthing the fur, scratching with hind feet, and brushing the fur with the forepaws were all considered to be grooming behaviors. The part of the body groomed was recorded when possible.

VI. Nest related behaviors: This category included leaving and entering of nests, and other behaviors associated with the nests such as building, maintaining (either adding bedding material to the nest cavity, or adding twigs to the nest structure), and moving a litter from one nest to the next.

VII. Other solitary behaviors: The behavior patterns included in this category were urinating, defecating, drinking water from streams and rock pools, cheek rubbing, and displaying aggressively (tail flicking, forefoot thumping, and vocalizing) that occurred in the absence of observable conspecifics. Sitting alert was also included in this category and was differentiated from resting by the squirrels' posture. The weight of an alert squirrel was supported by the

limbs, their heads were up, and the squirrels appeared to be scanning their environment.

VIII. Social behaviors: Behavior patterns that involved two or more conspecifics were included in this category. The most common social behaviors were agonistic behaviors (chasing, displacing, attacking, and fleeing). Mating behaviors (approaching, mounting, copulating) and amicable acts (following and allogrooming) were rare but also included in this category.

RESULTS

From May 1989 to October 1991, the average high temperature on Enchanted Mesa ranged from 29.0 °C during July to 5.7 °C during December. The average low temperature ranged between 14.3 °C in July to -7.6 °C in December (Table 4.1). The climate in Boulder County, Colorado is semi-arid and the highest average precipitation was during May (monthly averages ranged from 1.8 to 6.6 cm), although August had the highest average number of days (14) with precipitation. Snow can be found on the study site from the middle of

Table 4.1. Average temperatures ($^{\circ}\text{C}$) and precipitation (cm) recorded in Boulder County, Colorado from May 1989 to October 1991. (Total = the total amount of precipitation, Days = the number of days per month that precipitation fell, Snow = the total amount of snowfall, and Cover = the number of days of snow cover on the ground).

Month	Temperature ($^{\circ}\text{C}$)			Total	Precipitation		
	High	Low	Mean		Days	Snow	Cover
January	7.8	-4.9	1.5	2.5	7.5	38.1	17.5
February	9.4	-3.3	3.0	1.8	4.5	20.3	9.0
March	11.7	-1.3	5.2	6.4	8.5	33.0	10.5
April	15.0	2.4	8.8	5.8	11.0	37.1	5.0
May	21.5	6.6	14.0	6.6	14.0	0.0	0.0
June	26.9	11.7	19.3	4.8	10.7	0.0	0.0
July	29.0	14.3	21.7	6.6	13.7	0.0	0.0
August	28.4	14.0	21.4	4.8	16.0	0.0	0.0
September	24.4	11.1	17.7	5.3	14.0	0.5	0.3
October	18.6	4.5	11.5	2.8	11.0	24.4	4.0
November	11.8	-0.7	5.6	4.1	9.0	39.4	12.3
December	5.7	-7.6	-0.9	2.0	2.0	29.0	15.7

September to late April. March usually has the highest average snowfall, but from 1989 to 1991 the month with the highest average snowfall was November (mean = 98.4 cm.). This was due to a record snowfall during November 1991 (71.1 cm), which inflated the average for that month (Figures 4.1 and 4.2).

Activity rhythms

There were 92 observations of squirrels leaving their nest in the morning, and 93 observations of individuals entering their nest for the night. Five of the two week intervals were missing either morning or evening data, so the duration of squirrel activity was not calculated for those weeks.

Abert squirrels generally left their nest an average of 0.8 (\pm 0.5) hours after sunrise and returned to their nest an average of 3.2 (\pm 0.9) hours before sunset (Figure 4.3). Squirrels spent significantly more time out of their nests in summer (mean = 10.65 \pm 2.2) and spring (mean = 9.8 \pm 1.4), than in autumn (mean = 7.1 \pm 1.3), or winter (mean = 6.3 \pm 0.5; $H = 16.61$, $df = 3$, $p < 0.01$). They also used a significantly greater percentage of the total daylight hours available in summer (mean = 75.6 \pm

Figure 4.1. The average high and low temperatures ($^{\circ}\text{C}$) recorded for Boulder County, Colorado from May 1989 to October, 1991.

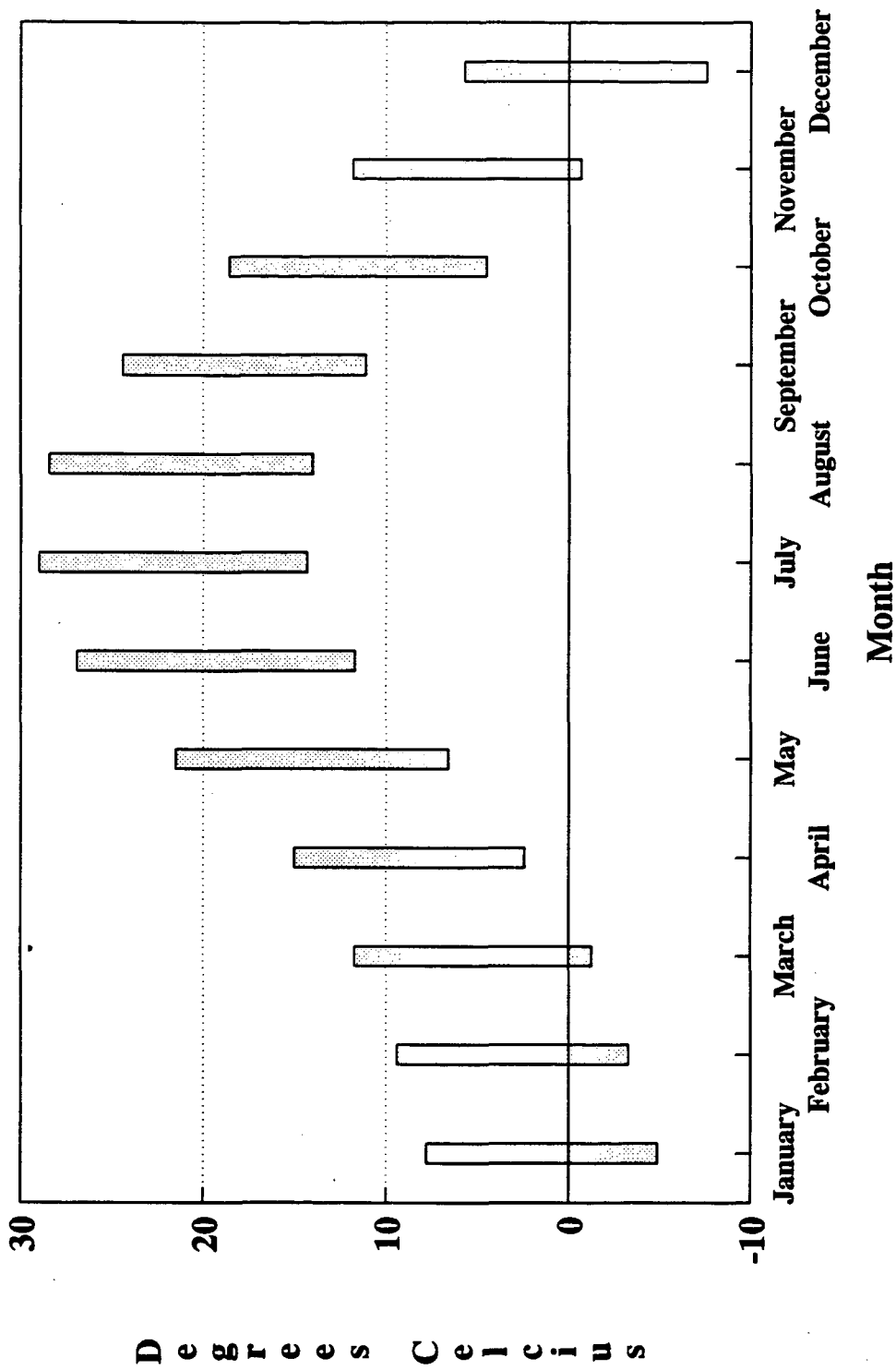


Figure 4.2. The average amount of precipitation (cm) that fell in Boulder County, Colorado from May 1989 to October, 1991.

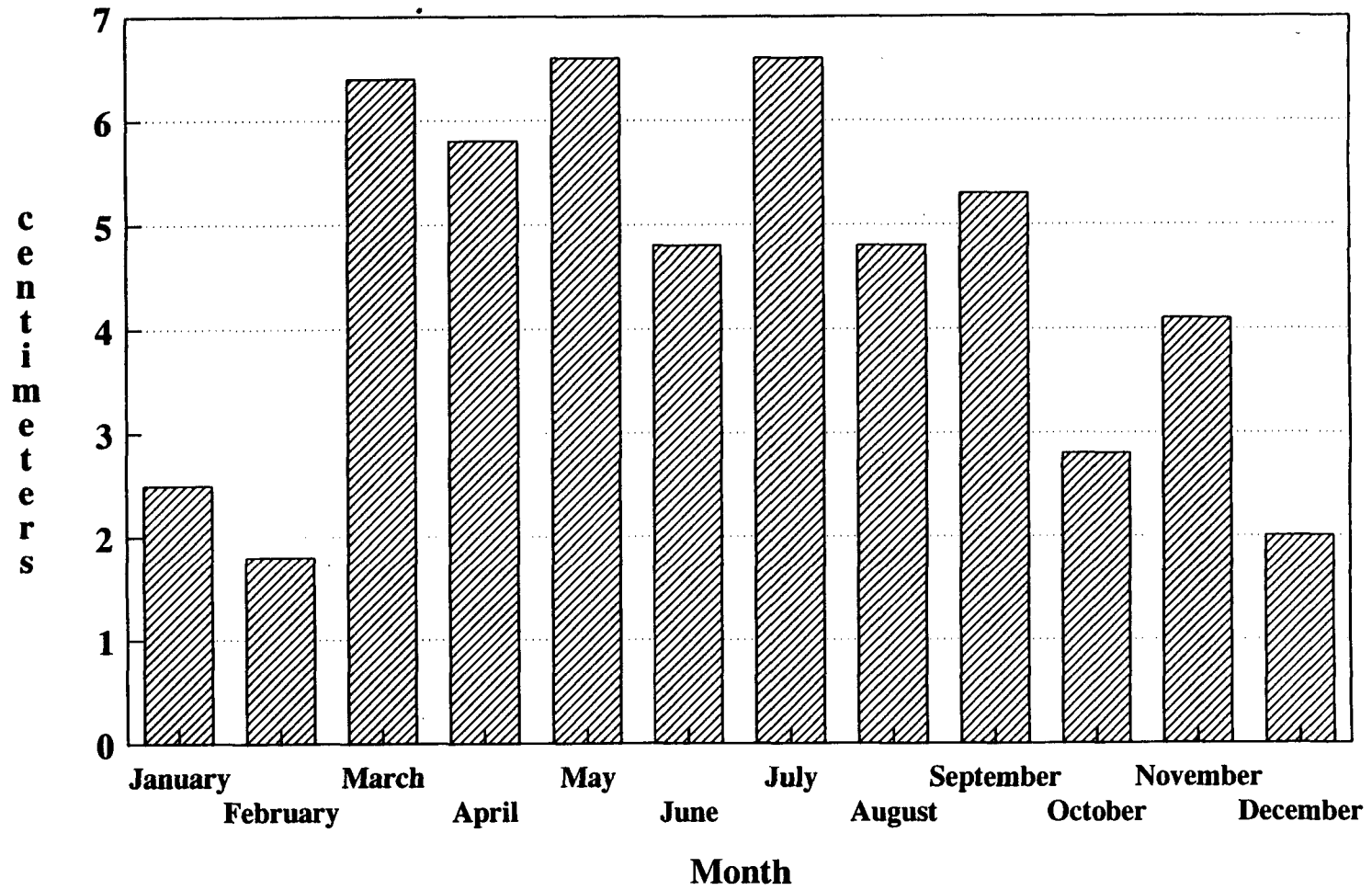
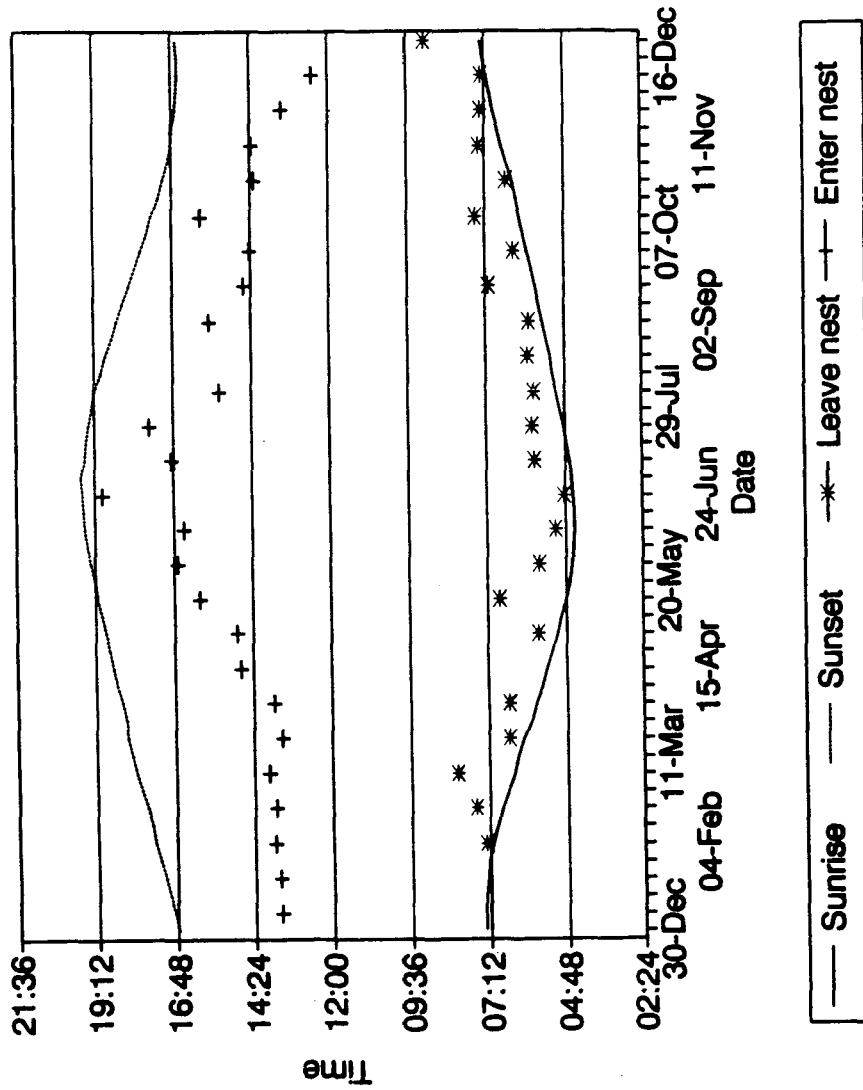


Figure 4.3. The average time adult Abert squirrels (Sciurus aberti) left their nests in the morning and entered their nests in the evening, compared with published sunrise and sunset times on Enchanted Mesa from May 1989 to October 1991.



11.4%) than during autumn (mean = $67.0 \pm 7.3\%$), winter (mean = $56.6 \pm 5.3\%$) or spring (mean = $69.3 \pm 5.8\%$; $H = 11.86$, $df = 3$, $p < 0.01$; Figure 4.4).

Activity budgets

A total of 843 hours of observation was obtained for 17 adult squirrels on 249 days. Although there were more days sampled in the spring (78) and summer (70) than the autumn (61) and winter (40; $X^2 = 12.91$, $df = 3$, $p < 0.05$) the length of time that an individual was watched per sampling period was independent of season (Chi-square = 15.06, $df = 9$, $p > 0.05$; Table 4.2). The time of day that observations were recorded were evenly distributed among all daylight hours, however, there were no early morning or late day sampling periods for winter, and no early morning sampling periods for autumn, because squirrels were not active at those times during those seasons (Table 4.3).

There was no significant difference between the number of days sampled among males (mean = 14.9 ± 13.2) and females (mean = 14.4 ± 12.5 ; $W = 79.5$, $p > 0.05$). There was also no significant difference between the average number of hours sampled among

Figure 4.4. The number of daylight hours and the percentage of total daylight hours during which Abert squirrels (Sciurus aberti) were active on Enchanted Mesa, from May 1989 to October, 1991.

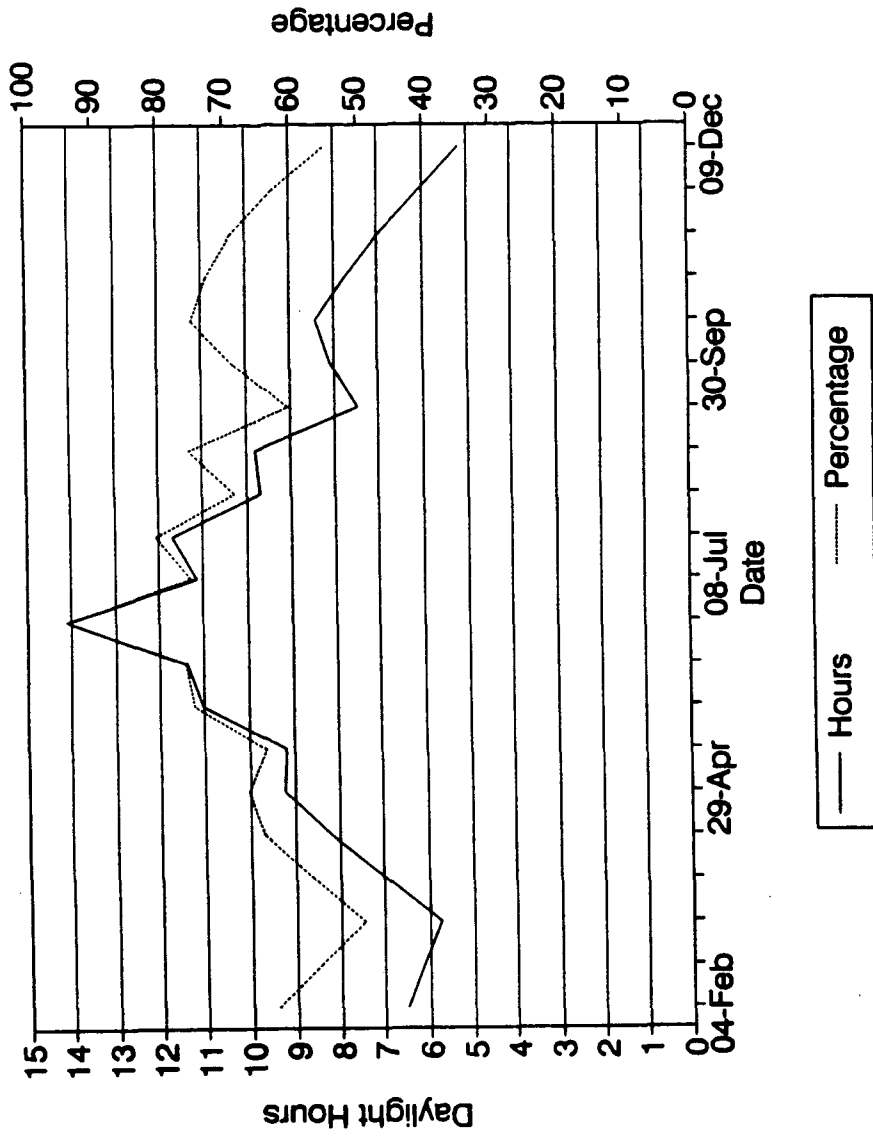


Table 4.2. The number of observation periods, of varying lengths of time, adult Abert squirrels (Sciurus aberti) were watched on Enchanted Mesa from May 1989 to October 1991.

Number of hours	Number of observation periods			
	Winter	Summer	Spring	Autumn
1-2 hours	23	41	39	33
3-4 hours	11	17	20	11
5-6 hours	4	9	7	15
7-8 hours	2	11	4	2
Total	40	78	70	61

Table 4.3. The distribution of observation periods for four seasons on Enchanted Mesa from May 1989 to October, 1991.

Time Started	Number of Observation Periods			
	Winter	Summer	Spring	Autumn
5:00	0	9	10	0
8:00	21	38	42	53
11:00	19	18	9	5
14:00	0	13	9	2
Total	40	78	70	61

males (mean = 50.1 ± 45.5) and females (mean = 49.0 ± 12.5 ; $W = 80.0$, $p > 0.05$), or the average number of hours per day sampled for males (mean = 3.0 ± 0.9) and females (mean = 3.3 ± 72.5 , $p > 0.05$). There were no significant differences among males and females for the amount of time they performed behaviors in any of the behavioral categories, so the data for males and females were pooled (Table 4.4).

The total amount of time that behaviors from different categories were performed varied seasonally (Chi-square = 51.3, $df = 18$, $p < 0.01$). In the autumn, squirrels were observed resting less often and travelling more often than would be expected. In the spring, squirrels spent more time engaged in social behaviors than would be expected. Nesting behaviors were performed for a significantly longer time in summer and a significantly shorter time in winter (Table 4.5, Figure 4.5). A theoretical daily activity budget is presented in Table 4.6. This was calculated by multiplying the percentage time spent in each behavior category by the number of hours that the squirrels were active each season.

The total amount of time spent performing behaviors from different categories also depended on

Table 4.4. The mean amount of time spent performing behaviors in each behavior category by adult Abert squirrels (*Sciurus aberti*) on Enchanted Mesa from May 1989 to October, 1991.

	Females	Males	W	p
Number of days	14.9 ± 13.2	14.4 ± 12.5	79.5	> 0.05
Hours/day	3.0 ± 0.9	3.3 ± 0.7	72.5	> 0.05
Feeding	11.5 ± 13.7	13.7 ± 14.3	80.0	> 0.05
Food-related	1.0 ± 1.1	4.6 ± 11.0	78.5	> 0.05
Resting	10.8 ± 10.8	13.2 ± 13.1	74.0	> 0.05
Traveling	12.1 ± 12.1	16.1 ± 13.1	76.0	> 0.05
Grooming	2.8 ± 2.8	3.6 ± 13.3	86.0	> 0.05
Nesting	3.5 ± 3.5	1.5 ± 2.8	79.0	> 0.05
Other solitary	0.4 ± 0.4	1.5 ± 1.7	74.5	> 0.05
Social	1.8 ± 1.8	2.4 ± 2.9	78.0	> 0.05
All Behaviors	50.1 ± 45.5	54.7 ± 43.4	78.0	> 0.05

Table 4.5. The total number of hours and the relative percent of time during which adult Abert squirrels (*Sciurus aberti*) were observed performing behaviors in seven different behavior categories on Enchanted Mesa from May 1989 to October 1991; partitioned by seasons of the year. Analysis was performed on raw data.

Category	Winter		Spring		Summer		Autumn	
	Hours	%	Hours	%	Hours	%	Hours	%
Feeding	43.1	36.8	109.5	36.6	54.2	25.0	63.1	30.2
Tree	31.8	27.2	78.1	26.1	32.8	15.1	33.8	16.1
Ground	11.3	9.6	31.4	10.5	21.4	9.9	39.3	14.1
Resting	23.2	19.9	72.7	24.3	56.2	25.9	32.7	5.6 ^a
Traveling	32.3	27.6	62.9	21.0	59.2	27.2	76.9	36.7 ^b
Grooming	7.7	6.6	17.6	5.9	8.9	4.1	15.3	7.3
Nesting	1.4	1.2 ^a	7.5	2.5	22.9	10.6 ^b	6.8	3.2
Other	6.5	4.7	9.1	8.9	8.6	4.0	10.1	4.8
Food	1.6	1.3	4.1	1.3	5.7	2.6	2.6	1.2
Social	3.8	3.3	20.0	6.7 ^b	7.1	3.2	4.5	2.2
Total	116.9	100	299.1	100	217.6	100	209.4	100

^aThese behaviors occur less often than would be expected ($p < 0.05$).

^bThese behaviors occur more often than would be expected ($p < 0.05$).

Figure 4.5. The relative percentage of time during which adult Abert squirrels (Sciurus aberti) were observed performing behaviors in seven different behavior categories on Enchanted Mesa from May 1989 to October 1991; partitioned by seasons of the year.

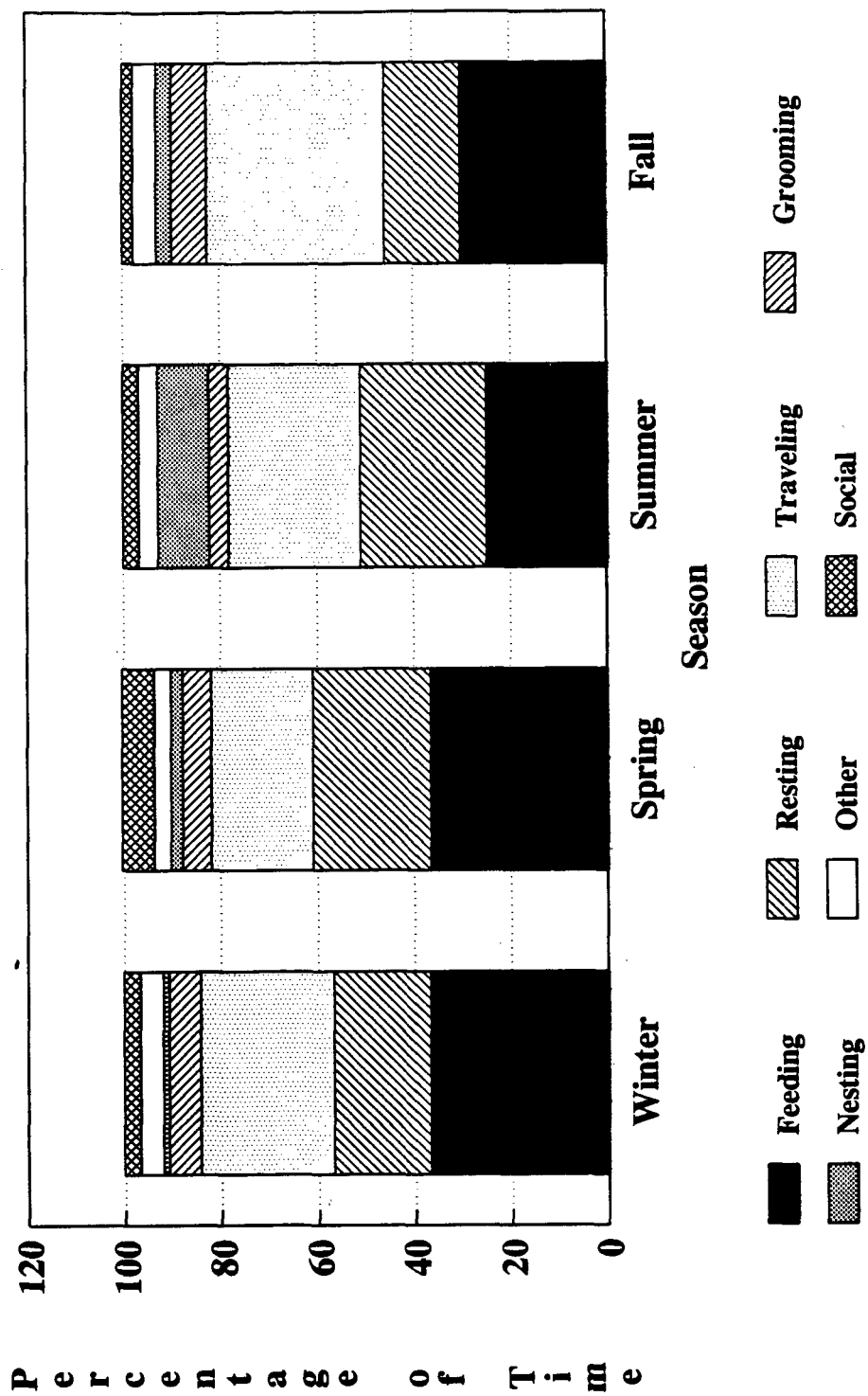


Table 4.6. The mean number of hours Abert squirrels (*Sciurus aberti*) spent performing behaviors in each category per day. This table is based on the mean number of hours per day squirrels were active, and the mean percentage of time squirrels were observed performing behaviors in each category.

Category	Winter	Spring	Summer	Autumn
Feeding	2.3	3.6	2.7	2.2
Resting	1.3	2.3	2.8	1.1
Traveling	1.7	2.0	2.7	2.6
Grooming	0.4	0.5	0.4	0.5
Nesting	0.1	0.2	1.1	0.2
Other Solitary	0.3	0.8	0.4	0.4
Social	0.2	0.6	0.3	0.1
Total	6.3	9.8	10.6	7.1

the food items that squirrels were eating (Chi-square = 77.6, $df = 18$, $p < 0.01$). During the time of year that squirrels predominantly ate cones, they spent more time nesting than would be expected. During the time period that squirrels were predominantly eating inner bark, they spent more time eating and less time nesting. During the time period that squirrels were eating ground items, they spent less time feeding and more time resting than would be expected due to chance. During the time period that squirrels were eating other items, they spent less time eating, more time locomoting, more time nesting, and more time performing other behaviors than would be expected due to chance (Figure 4.6 and Table 4.7).

DISCUSSION

Seasonal changes in activity rhythms

Previous studies that documented activity rhythms of arboreal squirrels usually counted the number of squirrels active during various time periods throughout the day. This was accomplished by direct observation, trapping or hunting (Ferron, et. al. 1986; Gurnell, 1984; Pauls, 1977; Smith, 1968;

Figure 4.6. The relative percentage of time during which adult Abert squirrels (Sciurus aberti) were observed performing behaviors in seven different behavior categories on Enchanted Mesa from May 1989 to October 1991; when squirrels were eating different types of food.

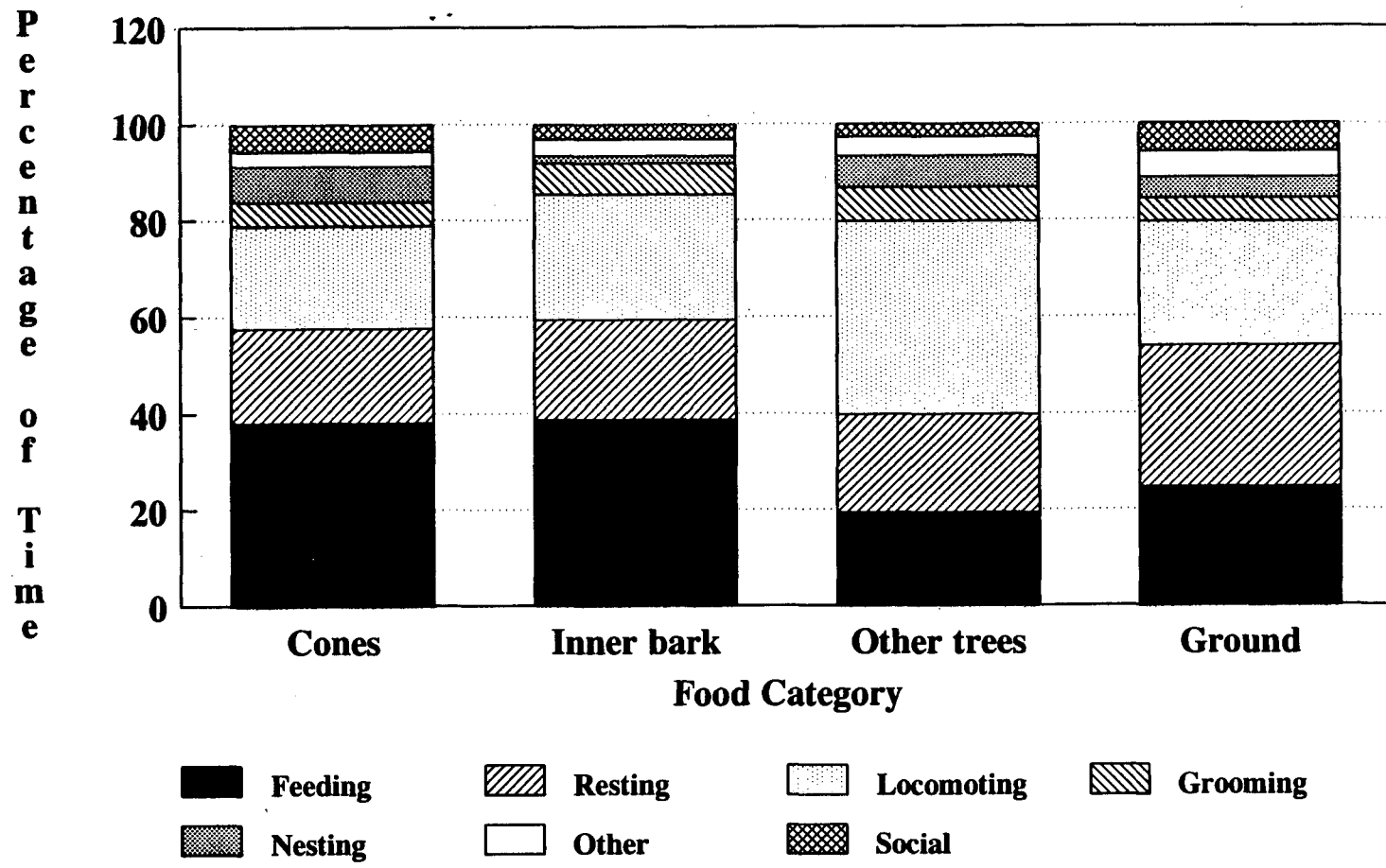


Table 4.7. The total number of hours, and the relative percentage of time during which adult Abert squirrels (*Sciurus aberti*) were observed performing behaviors in seven different behavior categories on Enchanted Mesa from May 1989 to October 1991; partitioned by dominant food item groups. Analysis was performed on raw data.

Category	Cones		Inner bark		Other		Ground	
	Hours	%	Hours	%	Hours	%	Hours	%
Feeding	77.7	38.1	120.4	38.6 ^b	29.2	19.3 ^a	39.9	24.6 ^a
Tree	62.0	30.4	84.7	28.3	11.6	7.7	16.8	10.4
Ground	15.7	7.7	35.7	11.9	17.6	11.6	23.1	14.2
Resting	39.7	19.4	64.6	20.7	31.0	20.4	47.4	29.2 ^b
Traveling	43.5	21.3	81.2	26.0	60.1	39.9 ^b	42.0	25.7
Grooming	10.1	5.0	20.4	6.5	10.5	7.0	8.0	4.9
Nesting	15.1	7.4 ^b	4.6	1.5 ^a	10.0	6.6 ^b	7.0	4.3
Other	6.4	3.1	11.2	3.5	9.2	4.0 ^b	8.9	5.4
Social	11.4	5.6	9.2	3.0	4.1	2.7	9.6	5.9
Total	203.9	100	311.6	100	150.7	100	162.3	100

^aThese behaviors occur less often than would be expected ($p < 0.05$).

^bThese behaviors occur more often than would be expected ($p < 0.05$).

Thompson, 1977b; Wauters and Dhondt, 1992, Weigl et. al., 1989). Squirrels that are traveling or foraging on the ground are more visible than squirrels that are resting or foraging in trees. Therefore, the bivariate activity patterns of summer may be a result of squirrels traveling to and from nests during the morning and late afternoon, and spending the middle part of the day foraging or resting in trees (Layne, 1954). Using these methods, resting would not be considered activity.

It is difficult to separate changes in activity rhythms due to seasonal changes in ambient temperature and photoperiod for temperate regions, because these two factors are highly correlated. One laboratory study on pine squirrels demonstrated that the photoperiod is the single controlling factor for activity onset time, but environmental temperature can have an overriding influence (Bahnak and Kramm, 1977). However, another study on pine squirrels demonstrated that temperature, rather than photoperiod, had a greater influence on the amount of time spent out of the nest (Pauls, 1978).

Because temperature and photoperiod are correlated, it is difficult to account for their

independent effects on activity. The relative importance of these two factors in influencing activity rhythms of squirrels may vary depending on the microhabitats in which individuals and populations live. Attempts at isolating these variables in a laboratory setting may produce artificial conditions resulting in activity patterns that differ from those found in natural populations. In laboratory studies, the relative importance of these two variables may be dependent on experimental methods.

In this study, Abert squirrels showed a decrease in the number and percentage of daylight hours during which they were active from summer to winter. They generally left their nests within an hour after sunrise and remained outside of their nest until three hours before sunset. One reason Abert squirrels on Enchanted Mesa may skew their activity rhythms towards the beginning of day is that the mountains to the direct west of the study site cause the sun to set up to two hours earlier than the published time for the city of Boulder (Lanham, 1974; pers. obs.). The sun sets earlier in the western region of Enchanted Mesa, and later in the eastern regions. Although it remains light for approximately one and one half hours after

the sun sets, there is a noticeable drop in temperature once the sun is behind the mountains, especially in winter (pers. obs.).

Abert squirrels usually were active even during periods of inclement weather. They were active in the winter when the ambient temperature was as low as -13.3°C , and they were active in the summer when the ambient temperature was as high as 40°C . They remained out of their nests during summer thundershowers and winter snow showers. The only times squirrels were predictably absent were the days following heavy snow storms. It is believed squirrels avoid these days because it is difficult to locomote in tree branches that are laden with snow (Farentinos, 1972; Hall, 1981; Keith, 1965).

Seasonal changes in activity budgets

The increase in the amount of time spent performing nesting behaviors in the summer coincides with the time of year during which females are building nests to accommodate their litters (this study, Chapter 2). The decrease in nesting behaviors during the winter is probably due to a decrease in nest maintenance. The most common form of nest

maintenance is the addition of bedding material (dry grass clippings) to the nest. Although nest maintenance occurs year round, new bedding material is scarce during winter months and often under snow cover. Twice, squirrels were observed removing bedding material from a neighboring squirrel's nest within minutes after the resident squirrel left the nest for the day. Both times this behavior occurred during winter when there was at least 15 cm of snow on the ground.

A third factor that plays an important role in the way squirrels alter their activity patterns is the seasonal availability of different food items. Squirrels eat cones in late spring and summer, and inner bark predominantly in autumn and winter. Therefore the changes in activity budget show the same trends for time spent in nesting behaviors whether partitioned according to dominant food items eaten or seasons. However, Abert squirrels show an increased amount of time feeding when they are predominantly eating Ponderosa pine inner bark. Abert squirrels do not lay down fat deposits (Golightly and Ohmart, 1978), and because they are active for a fewer number of hours during the winter they must spend a larger

proportion of their time feeding. Inner bark is also poorer in nutritional quality than other items such as Ponderosa pine cones (Snyder, 1990).

The increase in social behaviors during spring coincides with the mating season. In addition to the mating bouts themselves, male Abert squirrels spend increased amounts of time following and remaining within close proximity to females. Following occurs most often on days preceding a mating bout as females are coming into estrous.

In the autumn squirrels spent more time traveling than would be expected. This pattern of behavior coincides with one of the time periods during which squirrels eat scattered and cached cones on the ground in addition to hypogeous fungi. Patches of food on the ground are less clumped than patches of food located in trees, therefore squirrels may travel further to obtain new food items. Squirrels also show a decrease in the amount of time resting, which may be due to a decrease in the number of daylight hours or a response to an increase in time spent traveling.

Food habits also influenced activity patterns. When activity budgets are partitioned according to food items eaten, squirrels spent more time resting

when feeding on ground items, than would be expected due to random variation. In addition to feeding on the ground in autumn, Abert squirrels also eat seasonal mushrooms during June and August when the days are longer and the temperature is warmer. The increase in resting during these time periods is greater than the decrease in resting during the autumn. Squirrels also spent less time eating than would be predicted by chance alone when eating items on the ground. This reduced time spent eating may also be due to the effects of the warmer summer months. Abert squirrels decrease their metabolic rates when resting and when ambient temperatures rise (Golightly and Ohmart, 1978). Similar findings were obtained by Ferron et.al. (1986), who observed that when daylight hours were relatively constant (observations took place from May to August), pine squirrels spent an increasing amount of time resting outside of their nest and a decreasing amount of time handling food as the temperature increased from 0 to 30 °C.

During the time period when squirrels were feeding on other trees, they would leave the study site during the day and forage on Douglas fir (Pseudotsuga menziesii) in an area west of Enchanted

Mesa. This period of time coincides with a poor mast year of Ponderosa pine cones. The observed increase in the amount of time spent traveling, and the observed decrease in the amount of time spent feeding, are due to the fact that these data represent observations conducted primarily on the study site. Therefore, they are not a true representation of the activity budgets for those months.

Activity budget data presented for other arboreal squirrels differ from the data presented in this study. Two studies on European red squirrels (Tonkin, 1983; Wauters et. al., 1992) and one study on grey squirrels (Hougert and Flyger, 1981) indicate that these arboreal squirrels spend between 67 and 85% of their time in foraging activities. These data are not strictly comparable to those collected in this study, because the amount of time spent caching food items was included in the category called foraging, as was the amount of time spent searching for food. Abert squirrels do not store large quantities of food and these behaviors were not included in the category of feeding. In this study searching for food was included in the category of locomotion. The categories were organized in this manner because without knowing the

intentions of an individual, it is impossible to know whether the squirrel was searching for food while traveling, or traveling through the woods before happening upon some food that was subsequently eaten. Only the actual time spent eating was included in the category of feeding.

Abert squirrels, when compared to other species for which there are similar data, spend a larger percentage of time grooming (4.1% to 7.3%). Hougert and Flyger (1981), Tonkin (1983), and Wauters, et. al. (1992) found that eastern grey and European red squirrels spent less than 2.8% of the time grooming. Abert squirrels also spent between 15.6% and 25.9% of the time resting, whereas eastern grey and European red squirrels spent less than 1% of the time resting in winter, and less than 7% of their time resting in summer (Hougert and Flyger, 1981; Tonkin, 1983; Wauters et. al., 1992). These observed differences may be due to variations in methods rather than to actual differences among arboreal squirrel time budgets. As stated earlier, resting squirrels are less visible than squirrels performing other behaviors. Although other studies were aided by radiotracking, the

durations of observation periods and sampling methods were not reported.

CHAPTER V
CHEEK RUBBING BY ABERT SQUIRRELS

ABSTRACT

Cheek rubbing may be a form of scent marking in many terrestrial and arboreal sciurids. However, several studies on arboreal sciurids suggest that cheek rubbing may also be a form of self-grooming. The purpose of this study was to examine possible functions of cheek rubbing by Abert squirrels (Sciurus aberti). When the frequencies of behaviors that occurred within a cheek rubbing sequence were compared to the frequencies of behaviors that occurred at other times, grooming and alert behaviors had a higher probability of occurring during cheek rubbing, whereas traveling, nesting, and various other social behaviors (such as chasing) had a significantly lower probability of occurring during cheek rubbing sequences. Food related behaviors or grooming usually preceded cheek rubbing. Cheek rubbing did not predominantly occur at home range boundaries or at nest sites. These results suggest that cheek rubbing

by Abert squirrels is a form of self-grooming to remove food residue, and not active scent marking.

INTRODUCTION

Olfactory communication by means of chemical deposition (frequently called scent marking) is common in sciurids; many squirrels (both terrestrial and arboreal) leave chemical signs throughout their home range. These signs may result from urination, defecation, anal dragging, dorsal rubbing (twist marking), cheek rubbing, or pedal gland secretions deposited during scratching (Gurnell, 1987; Halpin, 1984). Chemical deposits may be used by squirrels as social signals during greeting and agonistic encounters, to indicate territory or home range boundaries, or to advertise 1) occupancy of a burrow or nest; 2) reproductive status; or 3) social position. To date, chemical communication has not been investigated in Abert squirrels (Sciurus aberti). The objective of this study was to investigate cheek rubbing, one possible form of chemical communication in Abert squirrels.

Cheek rubbing as scent marking in Sciurids

Cheek rubbing is considered to be a form of scent marking in many terrestrial and arboreal sciurids. When cheek rubbing, squirrels twist the head to one side and drag the side of their face across an object (Steiner, 1974). This behavior pattern is easy to recognize and the squirrel acts as if it is deliberately orienting its face toward the object. Histological examination of the oral angle has not been performed on Abert squirrels, but in many sciurids the oral angle has glands that produce a chemical substance that can be transferred to a substrate during cheek rubbing (Benson, 1980; Quay, 1965; Steiner, 1974; Walro et. al., 1983). The substrate used for marking by arboreal squirrels is usually a tree branch (Ferron and Ouellet, 1989), whereas terrestrial squirrels perform cheek rubbing on stumps, stones, roots, sides of dirt mounds, and den entrances (Betts, 1976; Halpin, 1984; Kivett et. al., 1976; Steiner, 1974).

Scent marking by cheek rubbing has been well documented for terrestrial squirrels of all ages (Kivett, et. al., 1976). Cheek rubbing is also exhibited with equal frequency by males and females

(Steiner, 1974). In some species of ground squirrels, both sides of the face are usually rubbed, while in others such as the golden-mantled ground squirrel (Spermophilus lateralis; Halpin, 1984) only one side of the face is rubbed. Once the behavior is completed, the animal usually sniffs where it has marked (Halpin, 1984). Cheek rubbing may be used to advertise the occupation of a burrow by woodchucks (Marmota monax; Ouellet and Ferron, 1988) and is associated with agonistic encounters between conspecifics in yellow-bellied marmots (Marmota flaviventris; Armitage, 1976) and California ground squirrels (Spermophilus beechyi; Owings et. al., 1977).

Cheek rubbing by arboreal pine squirrels (Tamiasciurus hudsonicus) and northern flying squirrels (Glaucomys sabrinus) has been observed at grooming and resting sites of the marking squirrel and is thought to be used to maintain the animal's familiarity within its home range (Ferron, 1983; Ferron and Ouellet, 1989). Fox squirrels older than two years have been observed to perform cheek rubbing more often than younger squirrels. Cheek rubbing also occurs frequently during agonistic encounters in fox squirrels. Benson (1980) concluded that cheek rubbing

in fox squirrels may serve to maintain the dominance hierarchy among males, because males greater than two years tend to be dominant. However it should be noted that there were no differences in the frequencies of cheek rubbing by male and female fox squirrels, and females are not part of the dominance hierarchy.

Cheek rubbing as self grooming in Sciurids

Abert squirrels eat inner pine bark and actually prefer to eat trees that have a lower oleoresin flow rate (Snyder, 1990). However, resin appears to get on their muzzle when eating in pine trees. I have also frequently observed cheek rubbing by squirrels after they have consumed peanut butter, another sticky substance. When Abert squirrels perform cheek rubbing following feeding, it may be to remove food residue from the muzzle. Therefore, a second possible function of cheek rubbing, that has been given little attention in the literature, is self grooming.

Several studies of arboreal squirrels in which the behavioral context of cheek rubbing has been investigated include data that suggest that cheek rubbing may be a form of self grooming. In red squirrels, cheek rubbing is associated with self

grooming 44% of the time (Ferron, 1976). Cheek rubbing is also commonly performed at grooming, resting, or feeding sites by northern flying squirrels (Ferron, 1983). Although the context in which this behavior usually occurs may be self grooming rather than scent marking, this does not rule out the possibility of a scent being deposited during this behavior. This scent could be used by an individual to orient to its nest sites, feeding trees, or home range boundaries. Abert squirrels have large home ranges with extensive overlap and they utilize several nests within their home range (this study; Chapters 2 and 3). It is not known what cues they may be using to navigate within their home range or to discriminate their nests from the other nests on the study site.

The purpose of this portion of my study was to examine possible functions of cheek rubbing by Abert squirrels. The specific objectives were 1) to determine if cheek rubbing occurs as self grooming after ingestion of food, or at key locations within their home range such as nest sites; and 2) to make predictions as to whether Abert squirrels use information that may be deposited as a result of cheek rubbing.

MATERIALS AND METHODS

This study was conducted on a 72 hectare region of a Ponderosa pine (Pinus ponderosa) forest commonly called Enchanted Mesa, which is located in Boulder County, Colorado (elevation: 1940 meters above sea level). A grid system of x and y coordinates was mapped onto the study area with markers placed approximately every 30 meters. Aluminum tags were placed on all 4 sides of selected trees and lettered sequentially A - Z from north to south, and numbered 1 - 30 from east to west. Quadrats within the study site were 30 x 30 meters; the four corners were defined by sequential grid markers.

Between May 1989 and October 1991 squirrels were observed year round from sunrise until one half hour before sunset, or when it was determined that all squirrels had entered their nests for the evening. Days were normally divided into two sampling periods, one half the number of daylight hours in duration, and dawn to dusk observations were attempted at least one day per week.

Squirrels were trapped using Tomahawk #202 live traps baited with peanut butter and sunflower seeds.

After being caught, squirrels were permanently marked with an ear tattoo and a freeze brand using "Quik-freeze" brand liquid cryogenic. Dye marks were also used as temporary visible identifiers. The squirrels' age, weight, and sex were recorded.

To census the population of squirrels, transects were walked along the grid markers until a marked squirrel was found. At this time the marked squirrel was followed, their behavioral patterns were recorded using focal animal sampling (Altmann, 1974), and their location on the study site was recorded using grid markers as reference points. Marked squirrels were observed with 10 x 50 binoculars using trees as natural blinds. The squirrels habituated to the observers' presence and did not appear to alter their activities when followed. Behavioral data were spoken into a microcassette recorder, transcribed into notebooks, and subsequently entered into a computer for analysis.

Behavior patterns were placed into one of several categories. A brief description of these categories is: 1) FEEDING - ingestion of food objects, 2) CACHING AND CARRYING - behaviors involving the handling, but not the ingesting of food; 3) RESTING -

squirrel relaxing with its abdomen pressed against a substrate; 4) TRAVELING - all acts of locomoting with the exception of carrying food or nest material; 5) GROOMING - all maintenance behaviors such as scratching, or mouthing fur; 6) NESTING - all behaviors associated with nests such as nest building, maintaining, and using the nest.; 7) ALERT - all behaviors performed when the animal appeared to be actively scanning the environment, including solitary aggressive displays; 8) SOCIAL - all interactions with other Abert squirrels; and 9) OTHER - any solitary behavior not previously mentioned such as urinating or defecating.

Definition of cheek rubbing and sequence analysis

A cheek rubbing was defined as an event during which the animal twisted its head to the side and dragged the side of its face across an object (rock, tree, branch) or across the ground. The dragging of one or both sides of the head in succession constituted a single act (Figure 5.1). The frequencies with which different behavior patterns were performed within a cheek rubbing sequence were compared to the frequencies with which behaviors were performed

outside of cheek rubbing. A behavior pattern was considered to be part of a cheek rubbing sequence if it occurred within 5 behavioral acts or within 2 minutes before or after cheek rubbing. These arbitrary criteria were established to insure that only those behaviors associated with cheek rubbing were included in the analysis.

Contextual analysis of cheek rubbing within a behavioral sequence was performed following the methods outlined by Oullet and Ferron (1988) in their study of woodchucks (Marmota monax) and by Ferron and Oullet (1989) in their study of red squirrels (Tamiasciurus hudsonicus). This allowed for a direct comparison of my results on Abert squirrels with studies of other sciurid species.

Sequence data (transitions between two actions) are presented in the form of a transition matrix. After the frequencies of occurrence of all acts were tabulated, significant transitions were identified by using a simple approximation derived from Castellán's (1965) method of partitioning contingency tables. Using this method, any cell in the transition matrix with a transformed frequency greater than $\sqrt{X^2_{.05}(1-1/r)}$ (df = 1; r = the number of categories) was

Figure 5.1. Line drawing of cheek rubbing by an adult
Abert squirrel (Sciurus aberti).



considered significant below the 0.05 level (Lefebvre, 1981). The transformed frequency is equal to the observed frequency minus the expected frequency divided by the square root of the expected frequency. The expected frequency of each cell is calculated by dividing the product of the corresponding column and row by the total number of acts. Significant positive transitions (those transitions that occurred more often than would be expected by chance) were illustrated in a transition diagram along with their corresponding frequencies.

An analysis of the spatial distribution of cheek rubbing was performed by plotting the location of each cheek rub on the 95% minimum convex polygon home range of an individual squirrel (see Chapter III). The number of cheek rubbing sequences that occurred in perimeter quadrats was compared with the number of sequences that occurred within interior quadrats. A Wilcoxon paired test was used to analyze these data (Minitab, 1991). This analysis was performed for eight of the 15 individuals for whom greater than ten cheek rubbings were recorded.

RESULTS

A total of 959 hours was spent in the field observing adult Abert squirrels perform a total of 203 cheek rubbing sequences. Of the 203 cheek rubbing sequences observed, the two minute criteria was used 195 times (96%) to indicate the beginning of a sequence and 186 times (92%) to indicate the end of a sequence. To minimize the number of cells that would have an expected frequency of zero, some categories with low frequencies were pooled with other categories for the purposes of performing the transition matrix analysis. The category CACHING AND CARRYING was combined with the category FEEDING into a category labelled "FOOD" indicating food-related behaviors. The categories of NESTING and SOCIAL were pooled with the group OTHER.

Of the 17 marked squirrels (9 females and 8 males) observed during this study, 15 (8 females and 7 males) were observed to cheek rub. Cheek rubbings were evenly distributed throughout the day, and throughout the year (Chi-square = 5.42, $p > 0.05$) when adjusted for time spent in the field. There were no significant differences in the number of hours that males and

females were observed in the field ($t = 0.20$, $p > 0.05$), or in the frequencies of cheek rubbing by males and females ($t = 0.44$, $p > 0.05$), so these data were pooled (Table 5.1).

Eighty two percent (166/203) of the cheek rubbing sequences consisted of a single act whereas 18% (37/204) consisted of 2-4 cheek rubs within a single sequence (Table 5.2). The majority of cheek rubbing sequences observed were performed in trees (171/203; 84%), whereas 16% (32) were performed on the ground. Of those sequences observed in trees, only 17 were observed to take place in a tree that also contained a nest (10% of those observed in trees; 8% of total).

When the frequencies of behaviors that occurred within a cheek rubbing sequence were compared to the frequencies of behaviors that occurred at other times, grooming and behaviors associated with being alert had a higher probability of occurring during cheek rubbing sequences (Table 5.3). This analysis also points out that traveling, social, nesting, and other behaviors had a significantly lower probability of occurring during cheek rubbing sequences than at other times. Cheek rubbing was not associated with all food

Table 5.1. Frequency of cheek rubbing by female (F) and male (M) Abert squirrels (*Sciurus aberti*). A sequence consists of one or more cheek rubbing behaviors performed within a single cheek rubbing bout.

Squirrel	Sex	Hours Observed	Sequence Total	per Hour	Cheek Rubbings Total	per Hour
BBH	F	51.8	16	0.31	19	0.37
BBMH	F	25.9	7	0.27	12	0.46
BLH	F	40.0	9	0.23	9	0.23
BRH	F	136.3	22	0.16	33	0.24
BRMH	F	138.6	27	0.19	33	0.24
GBH	F	31.7	9	0.28	13	0.41
GLH	F	2.2	1	0.45	1	0.45
GRH	F	103.9	15	0.14	19	0.18
BBF	M	120.7	29	0.24	33	0.27
BLF	M	12.5	3	0.24	3	0.24
BLFM	M	34.9	3	0.08	4	0.11
BRF	M	59.1	7	0.12	7	0.12
BRFM	M	127.3	35	0.27	50	0.39
GLF	M	8.4	3	0.35	3	0.36
GRF	M	65.4	17	0.26	17	0.26
MEAN	F	66.3	13.3	0.25	17.4	0.32
SE	F	18.6		0.03		0.04
MEAN	M	61.2	13.8	0.23	16.7	0.25
SE	M	18.1		0.03		0.04

There was no significant difference between males and females for the number of sequences or the number of cheek rubbings performed ($p > 0.05$).

Table 5.2. Number of cheek rubbings per sequence by Abert squirrels (Sciurus aberti) on Enchanted Mesa from May 1989 to October 1991.

Number of cheek rubbings	Number of sequences
1	166
2	29
3	5
4	3
	<hr/>
	203

Table 5.3. The number (N) and percentage (%) of behavior patterns performed by adult Abert squirrels (*Sciurus aberti*), based on all observations (total minus those related to cheek rubbing) and on behavior patterns occurring within five acts of cheek rubbing. Data for both sexes are combined.

Behavior Patterns	All observations		Cheek Rubbing		p
	N	%	N	%	
Feeding	2435	19.8	196	19.0	n.s.
Cache/Carry	452	3.8	27	2.6	n.s.
Resting	738	6.0	54	5.2	n.s.
Locomotion	6197	50.4	420	40.7	p < .001
Grooming	989	8.0	263	25.4	p < .001
Alert	150	1.2	36	3.5	p < .001
Nesting	394	3.2	8	0.8	p < .001
Social	581	4.7	21	2.0	p < .001
Other	350	2.9	8	0.8	p < .001
Total	12296	100	1033	100	

handling, and food handling was performed at similar frequencies regardless of whether the animal was involved in a cheek rubbing sequence.

An analysis of the two-act transition matrix indicates that food related behaviors or grooming usually preceded cheek rubbing, while grooming, traveling, or resting usually followed cheek rubbing (Table 5.4 and Figure 5.2). Thus, cheek rubbing is closely associated with feeding, grooming, traveling, or resting behaviors.

The analysis of the spatial distribution of cheek rubs indicates that cheek rubbing does not occur at the edges of home ranges, and that Abert squirrels are not using cheek rubbings to mark home range boundaries. There was no significant difference in the number of cheek rubbings per quadrat for the perimeter ($X = 0.04 \pm 0.04$) or the interior ($X = 0.08 \pm 0.02$) of an individual's home range ($W = 24.5$, $n = 7$, $p > 0.05$; Figure 5.3).

DISCUSSION

The contextual analysis of cheek rubbing by Abert squirrels indicated that this behavior was

Figure 5.2. Significant ($p < .05$) positive transitions between behavioral patterns performed within 5 acts or 2 minutes of cheek rubbing by Abert squirrels. Each number indicates the transition probability between 2 acts that were executed in a cheek rubbing context.

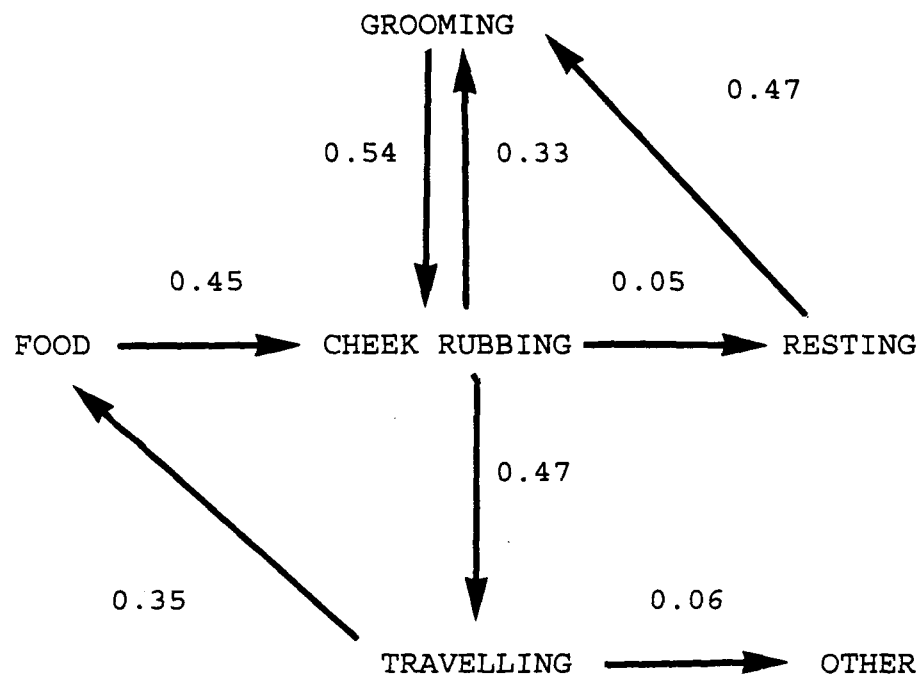
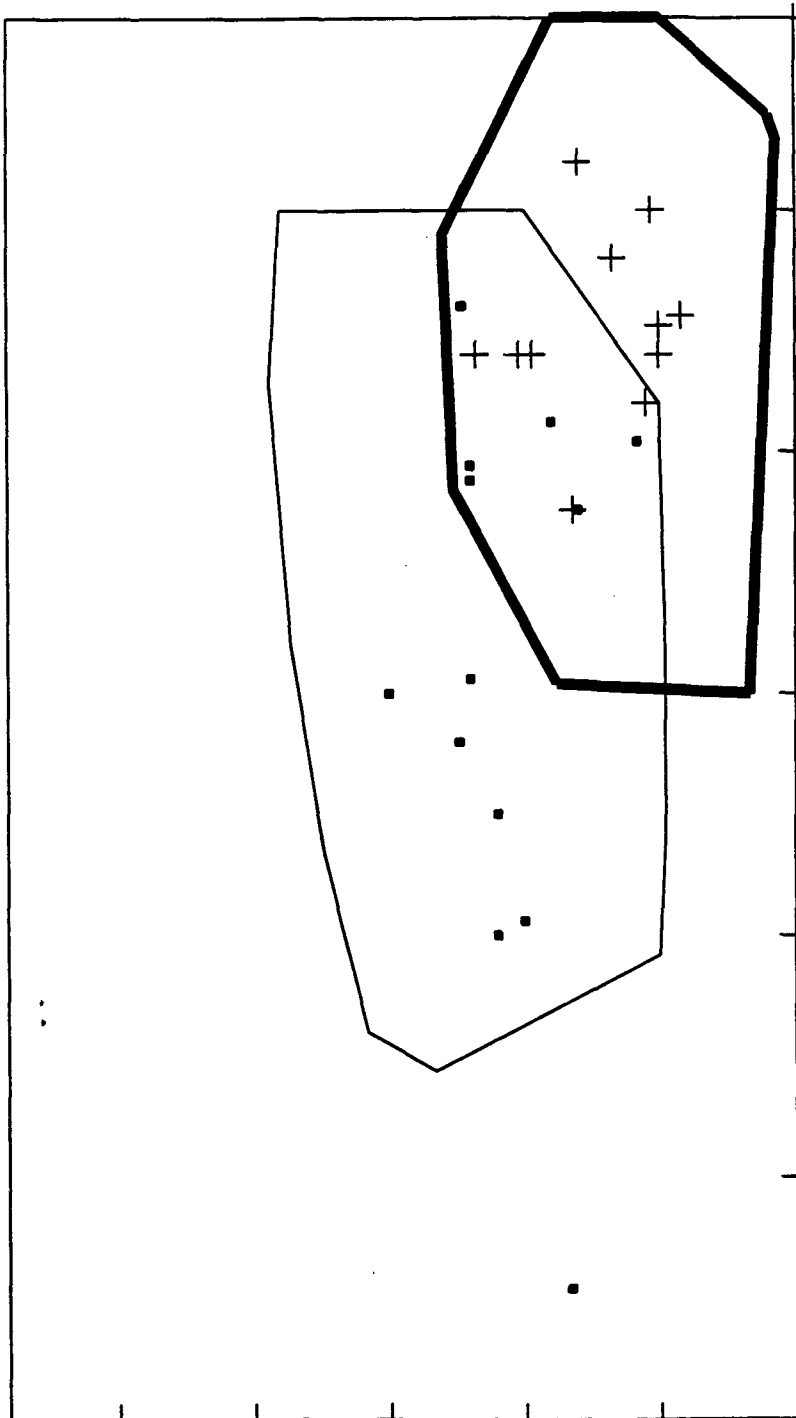


Figure 5.3. Representative 95% minimum convex polygon home ranges of male (GRF) and female (GRH) Abert squirrels with cheek rubbing locations marked within them.



— GRF 95% • GRF CR — GRH 95% + GRH CR

Table 5.4. A two-act transition matrix for cheek rubbing sequences performed by 16 adult Abert squirrels (*Sciurus aberti*). Data are presented as the probability of a transition from the row behavior to the column behavior within 5 acts or 2 minutes of cheek rubbing by Abert squirrels. These values were obtained by dividing the cell total of the raw data by the row totals. Data were pooled for both males and females. Significant positive transitions are underlined. (FD = food related behaviors, RST = resting, TR = traveling, GR = grooming, AL = Alert, CR = Cheek rub, OTH = other).

	FD	RST	TR	GR	AL	CR	OTH
FD	0.10	0.01	0.28	0.09	0.02	<u>0.45</u>	0.04
RST	0.03	0.00	0.24	<u>0.47</u>	0.08	0.13	0.05
TR	<u>0.35</u>	0.03	0.00	0.21	0.04	0.31	<u>0.07</u>
GR	0.03	0.05	0.32	0.00	0.04	<u>0.54</u>	0.02
AL	0.06	0.03	0.20	0.31	0.11	0.26	0.03
CR	0.90	<u>0.05</u>	<u>0.47</u>	<u>0.34</u>	0.01	0.02	0.01
OTH	0.19	0.00	0.43	0.05	0.05	0.23	0.05

closely associated with squirrels being alert and grooming, and less of an association with travelling, social, and nesting behaviors. The handling of food items and grooming generally preceded the act of cheek rubbing, while grooming, traveling, or resting generally followed cheek rubbing. Traveling often preceded feeding, and resting often preceded grooming. Thus, cheek rubbing appears to be performed most often in the behavioral contexts of grooming and feeding, and may be considered a form of self-grooming.

The majority (84%) of cheek rubbing sequences were performed in trees, while only 16% were performed on the ground. When in trees, squirrels primarily eat Ponderosa pine cones and inner bark. These food items contain oleoresins (Snyder, 1990) and may leave more residue on squirrels' muzzles than mushrooms and other items squirrels eat while on the ground. A second possible reason why Abert squirrels may have been observed performing cheek rubbing more often in trees is that it is more difficult to observe this behavior when squirrels are on the ground.

Ferron (1983) hypothesized that cheek rubbing in arboreal squirrels is a self-oriented behavior that maintains the animal's familiarity with its home

range. He based his theory on his analysis of the locations of cheek rubbing. Ferron found that cheek rubbing was most likely to occur at grooming, resting, and feeding sites, and during traveling along the paths used by marking squirrels. Abert squirrels spend between 82% and 91% of their time performing feeding, resting, grooming, and traveling behaviors (this study; Chapter 4). Therefore arboreal squirrels may perform cheek rubbing at specific locations within their home ranges simply because that is where they spend most of their time.

Abert squirrels do not perform cheek rubbing behaviors at home range boundaries or at nest sites more often than they perform these behaviors at other locations. Therefore, it appears squirrels are not actively laying down scent marks that are used for navigating within their home ranges. The role of cheek rubbing as a form of passive scent marking cannot be ruled out. During cheek rubbing, saliva or other chemicals from the oral angle may be transferred to the substrate. Information from these deposits may be used by an individual or by conspecifics. However, subsequent investigation of markings by Abert squirrels has not been observed.

Many studies in which the behavioral context of cheek rubbing by arboreal squirrels has been investigated (Benson, 1980; Ferron, 1983; Ferron and Ouellet, 1989; Ferron, et. al., 1986) have started with the assumption that cheek rubbing is a form of scent marking. The focus of the resulting investigation is centered on explaining observed patterns of cheek rubbing within the behavioral context of scent marking, rather than exploring the context of cheek rubbing itself.

One reason that cheek rubbing is considered to be a form of scent marking in arboreal squirrels is that cheek rubbing is widely accepted as a form of scent marking in terrestrial squirrels (Armitage, 1976; Kivett, et. al., 1976; Ouellet and Ferron, 1988; Owings, et. al., 1977; Steiner, 1974). Cheek rubbing by terrestrial squirrels is generally observed within the context of various social behaviors (Halpin, 1984); including agonistic (Armitage, 1976; Steiner, 1974) or amicable encounters (Kivett, et. al., 1976). Cheek rubbing appears to be performed similarly by all terrestrial squirrel species, and is generally preceded and followed by sniffing the object on which the deposit is placed. Sniffing before or after cheek

rubbing was not observed for Abert squirrels nor has it been reported for other arboreal squirrel species.

Cheek rubbing is generally not associated with social behaviors in arboreal squirrels (Ferron, 1983; Ferron and Ouellet, 1989; this study). However, there is some evidence suggesting that cheek rubbing may be associated with agonistic encounters in fox squirrels (Benson, 1980). Of the 118 cheek rubbing sequences Benson observed, agonistic encounters were associated with 40 (33%). However, data for the association of cheek rubbing with other behaviors such as feeding or grooming were not presented.

The majority of data obtained on the role of cheek rubbing by arboreal squirrels have been collected on pine squirrels (Tamiasciurus hudsonicus), a territorial and solitary species, and flying squirrels (Glaucomys sabrinus), a relatively social species (Ferron, 1983). Further studies on the role of cheek rubbing by arboreal squirrels, especially by solitary non-territorial species of the genus Sciurus, still need to be done. The possibility that cheek rubbing is a form of self-grooming behavior when performed by Abert squirrels, and is a form of scent

marking when performed by other arboreal squirrels, cannot be ruled out.

Abert squirrels do not perform cheek rubbing at home range boundaries or at nest sites which indicates that squirrels are probably not using these marks for navigating within their home range. Furthermore, cheek rubbing is not associated with social behaviors, and sniffing of the cheek rub locations has not been observed. These results suggests that cheek rubbing is not a form of active scent marking. However, cheek rubbing is associated with feeding and grooming, and cheek rubbing follows feeding and carrying food. These data support the idea that cheek rubbing by Abert squirrels is a form of self-grooming to remove food residue from the muzzle.

CHAPTER VI
THE TIMING OF ESTRUS AS A REPRODUCTIVE PATTERN IN
FEMALE ABERT SQUIRRELS
(Sciurus aberti)

ABSTRACT

The relationship between the date of mating and litter size was documented in twelve cases for Abert squirrels (Sciurus aberti). Although the breeding season lasted from mid-February to early June, females were observed to mate on only one day a year. Litter size ranged from one to five offspring, with an average of 2.9 young per litter. Litter size was related to the date on which a female mated; litters born to females that mated early were smaller than litters born to females that mated later in the year. Litter size may vary with food availability at the time of estrus, whereas juvenile survival may depend on food availability at the time of emergence from the nest. The timing of estrus may be a reproductive pattern that is dependent on these two factors.

INTRODUCTION

Variation in reproductive success can be due to many factors, but is commonly attributed to four variables: survival to breeding age, reproductive life span, average fecundity per year of the reproductive lifespan, and offspring survival to reproductive age (Brown, 1988; Clutton-Brock, 1988). Producing larger litters can also increase mean fecundity, but may not increase reproductive success if young do not survive. Investments associated with parental care, including lactation, may restrict the number of offspring a female can successfully rear to reproductive age.

In the Sciuridae, litter size is negatively correlated with a number of variables including adult weight, the number of litters a female produces, longevity, mean precipitation, and the length of the growing season (Armitage, 1981 Eisenberg, 1981, Heany, 1984). Litter size is positively correlated with food availability (Smith, 1968; Thompson, 1977a; Wauters and Dhondt, 1990b; Wiegler et. al., 1989).

The purpose of this study was to formulate a hypothesis about possible relationships among the date on which a female mated, litter size, and food

availability, and how these three factors might influence the reproductive success of female Abert squirrels.

MATERIALS AND METHODS

The study was conducted in a 72 hectare region of Ponderosa pine forest commonly called Enchanted Mesa, which is located in Boulder, Colorado (elevation 1940 meters above sea level). A grid system of x and y coordinates was mapped onto the study area with markers placed approximately every 30 meters. Aluminum tags were placed on all 4 sides of selected trees and lettered sequentially A - Z from north to south, and numbered 1 - 30 from east to west. Quadrats within the study site were 30 x 30 meters; the four corners were defined by sequential grid markers. A map was created of the area by plotting the grid system on to a reduced aerial photograph of the study site.

Squirrels were trapped using Tomahawk #202 live traps baited with peanut butter and sunflower seeds. After being caught, squirrels were permanently marked with an ear tattoo and a freeze brand using "quik-freeze" brand liquid cryogenic. Dye marks were also

used as temporary visible identifiers. The squirrels' age, weight, and sex were recorded.

In the winter and spring of 1991, four female squirrels were fitted with radio transmitter collars. Individual collars weighed between 15 and 20 grams. A collar was placed on a squirrel while she was held in a cloth handling bag. Signals were transmitted at 164 MHz and received using a model CE12 receiver with a three element Yagi antenna. All radio components were built by Custom Electronics, Urbana, Illinois. Radio telemetry was used only to locate individuals. All of the data on radio collared squirrels were collected using the same methods as those used on non-radio collared individuals. Radio transmitter collars were removed from these squirrels in the summer of 1991.

Females went into estrus and were observed to mate one day each year between mid-February and early June. The average gestation period of female Abert squirrels is 40 days (Keith, 1965; Nash and Seaman, 1977). Nests of known lactating squirrels were monitored from the ground several times during the day to look for litters. The date on which a litter was first observed outside of the nest (date of emergence) and litter size were recorded. The number of weeks

between the mating date of the female and the date of first emergence by the litter was calculated in eight cases. For four females, the mating date was estimated based on the emergence date of the litter. Spearman's rank correlation was used to determine if the number of offspring that emerged from the nest was related to the date on which a female mated.

Twenty four offspring (70%) were trapped and marked before they left the maternal nest. All juveniles who were not successfully trapped and marked disappeared from the population prior to the first winter following their birth. The number of offspring who remained in the population and participated in mating activities was determined by direct observation.

RESULTS

Female Abert squirrels mated from mid-February to the beginning of June. Twelve litters were born on the study site from 1989 through 1991. The average time between the mating date and the date on which a litter first emerged was 15 weeks. Litter size at emergence ranged from one to five offspring (mean =

2.9 \pm 1.2; Table 6.1). Litter size at emergence was significantly correlated with the date that the mother mated ($r_s = 0.78$, $n = 12$, $p < 0.01$; Figure 6.1).

The maximum number of offspring from each litter that remained in the population until reproductive age was one. All yearlings (2 females and 3 males) who remained in the population were reproductively active. All squirrels trapped and marked on the study site after July of 1989 were juveniles born on the study site.

DISCUSSION

The date on which a female Abert squirrel mated was significantly correlated with the size of the litter that she subsequently produced. Females who mated early in the year (February through April) produced smaller litters than females who mated later in the year (May and June). The time of the year during which females mate may depend on a trade off between the food available to the female when she goes into estrus and the food available to the litter upon emergence.

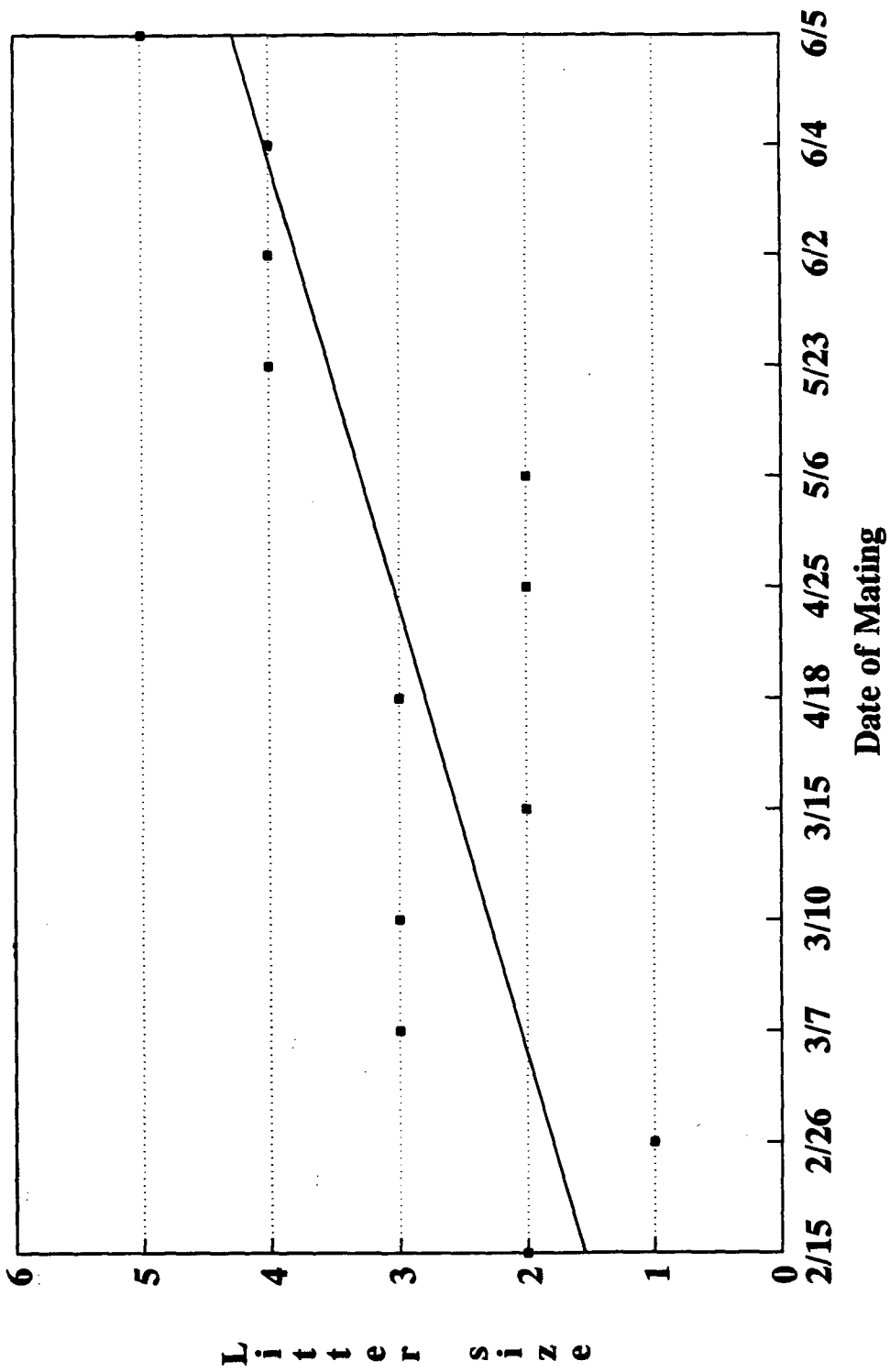
Table 6.1. The date on which female Abert squirrels (*Sciurus aberti*) mated and litter size at emergence for each of 12 litters on Enchanted Mesa from 1989 through 1991. The date on which the litter was first observed outside of the nest (date of emergence) and the number of offspring that remained in the population as yearlings is also presented.

Squirrel	Year	Date Mated	Litter Size	Date of Emergence	Number of Yearlings
BRMH	1990	02/15 ^b	2	05/30	0
GRH	1990	02/26	1	06/13	1
BRH	1990	03/07	3	06/20	1
BRMH	1989	03/10 ^b	3	06/25	1
GLH	1989	03/15 ^b	2	06/30	0
GLFD	1989	04/18	3	08/01	1
BLH	1991	04/25	2	08/08	... ^a
GBH	1991	05/06	2	08/16	... ^a
BBMH	1990	05/23	4	09/21	0
GRH	1989	06/02	4	09/15	1
GRH	1991	06/04 ^b	4	09/19	... ^a
BRH	1989	06/05	5	09/20	0

^a The number of yearlings was not obtained for these litters due to termination of the study.

^b The date females mated for these litters was estimated as 15 weeks prior to the date of emergence. This was based on the average time lapse between mating and the date of emergence for the other eight litters.

Figure 6.1. The date on which female Abert squirrels (Sciurus aberti) mated and the size of the resulting litters on Enchanted Mesa from 1989 through 1991 (n = 12). Litter size at emergence was significantly correlated with the date a female mated ($r_s = 0.78$, $p < 0.05$).



Physiological and anatomical changes associated with reproductive condition and reproductive behavior require a considerable amount of energy above that needed for daily maintenance. Arboreal squirrels will generally not enter reproductive condition unless they are in a positive energy balance (Gurnell, 1987). Food availability is highly correlated with the onset of the breeding season in arboreal squirrels (Nixon and McClain, 1975; Rusch and Reeder, 1978; Sullivan and Sullivan, 1982). A correlation between food availability and litter size has also been observed in eastern grey squirrels (Sciurus carolinensis; Smith, 1968; Thompson, 1977a), European red squirrels (S. vulgaris; Wauters and Dhondt, 1990), and fox squirrels (S. niger; Wiegl, et. al., 1989). In fox squirrels, Wiegl, et. al., (1989) found that 90% of the females did not produce litters during a year of limited food availability, as compared with 12% during a year when food was abundant. Furthermore, in the same year during which females had the most litters, they also had the largest litters. For arboreal squirrel species that produce two litters, spring litters are usually smaller than summer litters (Gurnell, 1983; Thompson, 1978a).

Adult female Abert squirrels on Enchanted Mesa may use different reproductive patterns which maximize offspring survival. During the early part of the breeding season, February and March, Abert squirrels generally eat inner bark from Ponderosa pine trees (Farentinos, 1972a; Hall, 1981; Keith, 1965; Stephenson, 1974; 1975, this study). Inner bark is poorer in nutritional quality than Ponderosa pine staminate cones that squirrels eat later in the breeding season (Capretta and Farentinos, 1979; Capretta et. al., 1980). The relatively poor quality of food may reduce the number of offspring a female can produce if she mates early in the breeding season. The offspring of females who mate early emerge from the nest during summer when Ponderosa pine ovulate cones are generally abundant. These juveniles have a longer period of time to develop before the onset of winter when compared to juveniles who are born to females who mate later in the breeding season. Therefore, the timing of emergence from the nest may affect overwinter survival of juvenile squirrels.

A second pattern that female Abert squirrels may use which maximizes offspring survival is to mate later in the breeding season. During May and early

June, Abert squirrels commonly eat staminate cones (Farentinos, 1972a; Hall, 1981; Keith, 1965; Stephenson, 1974; 1975, this study) that are generally abundant and of higher nutritional quality than inner bark (Capretta and Farentinos, 1979; Capretta et. al., 1980). Increased food availability and quality may increase the number of offspring a female can produce. These offspring emerge from the nest in late August and September and have a shorter period of time to grow before the onset of winter, when compared to juveniles who emerge during the summer. In addition, inner bark which is available at the time of fall emergence is of lower quality than Ponderosa pine ovulate cones available to young who emerge during the summer.

Although the average sizes of the litters that emerge in the fall are larger than litters that emerge during summer, the maximum number of young who survived to reproductive age from any litter born during this study was only one. There was no recruitment into the population of individuals born off the study site. If the number of juveniles who survived to reproductive age is equal to the number of individuals recruited into the population, then

breeding early and producing smaller litters would be a better reproductive strategy. Less reproductive effort devoted to raising young, would achieve the same level of fitness as breeding late and producing larger litters.

Breeding early may not be an advantageous strategy during years when there is a failure of the mast crop, because there is a limited amount of available food during summer; in some species the survival of juveniles is directly correlated with food availability (Barkalow et. al., 1970; Glanz et. al., 1982; Heany, 1984; Koprowski, 1991b; Wauters and Dhondt, 1990). In this study, there appeared to be no difference in survival to one year among juveniles born in a good mast year (1989), when compared to juveniles born in a poor mast year (1990). However, juvenile survival to weaning in fox and grey squirrels was found to decrease from 94% during a year with relatively good food abundance to 39% during a year with a failed seed crop (Koprowski, 1991b). One reason that juvenile survival may have been less affected by food supply in the present study was that during the poor mast year, squirrels on Enchanted Mesa left the study site during the day and fed in Douglas fir trees

less than one half of a kilometer away. In other geographical areas this may not be a practical alternative.

Juvenile mortality prior to emergence from the nest was not examined in this study, but it is assumed that it was not a significant factor because the average number of placental scars in other necropsied Abert squirrels is the same as the average litter size for the squirrels in the present study (2.9; range equals 2 - 4; Stephenson, 1975). In pine squirrels, juvenile mortality prior to emergence from the nest is rare (K. Larson, pers. comm.).

Therefore if juvenile mortality prior to emergence in Abert squirrels is low, then females who mate early in the year have smaller litters than females that mate later in the year. Because litter size may vary with food availability at the time of estrus, whereas juvenile survival may depend on food availability at the time of emergence from the nest, the timing of estrus may be a reproductive strategy dependent upon these two factors.

CHAPTER VII

LITERATURE CITED

- Adams, C.E. 1976. Measurements and characteristics of fox squirrel Sciurus niger rufiventer home ranges. American Midland Naturalist 95:211-215.
- Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49:227-267.
- Armitage, K.B. 1976. Scent marking by yellow-bellied marmots. Journal of Mammalogy 57:583-584.
- Armitage, K.B. 1981. Sociality as a life-history tactic of ground squirrels. Oecologia 48:36-49.
- Armitage, K.B. 1984. Recruitment in yellow-bellied marmot populations: Kinship, philopatry and individual variability. In J.O. Murie and G.R. Michener (Eds.) The Biology of Ground-Dwelling Squirrels, University of Nebraska Press, Lincoln. pp375-403.
- Bahnak, B.R. and K.R. Kramm, 1977. The influence of environmental temperature and photoperiod on activity in the red squirrel (Tamiasciurus hudsonicus), International Journal of Biometeorology 21:348-356.
- Baily, F.M. 1932. Abert squirrel burying pine cones. Journal of Mammalogy 13:156-166.
- Barkalow, F.S., R.B. Hamilton, and R.F. Soots. 1970. The vital statistics of an unexploited gray squirrel population. Journal of Wildlife Management 34:489-500.
- Baumgartner, L.L. 1943. Fox squirrels in Ohio. The Journal of Wildlife Management, 7:193-202.
- Bekoff, M. and L.D. Mech. 1984. Simulation analyses of space use: Home range estimates, variability, and sample size. Behavior Research Methods, Instruments, and Computers 16:32-37.

- Bekoff, M. A.C. Scott, and D.A. Conner. 1989. Ecological analyses of nesting success in evening grosbeaks. *Oecologia* 81:67-74.
- Benson, B.N. 1980. Dominance relationships, mating behavior, and scent marking in fox squirrels (Sciurus niger). *Mammalia* 44:143-160.
- Bernard, R.J. 1972. Social organization of the western fox squirrel. Unpublished Master's Thesis. University of Michigan, East Lansing. 41 pp.
- Betts, B.J. 1976. Behavior in a population of Columbian ground squirrels, Spermophilus columbianus columbianus. *Animal Behavior* 24:652-680.
- BMDP Statistical Software Inc. 1990. BMDP Statistical Software Manual: to Accompany the 1990 Software Release. Dixon, W.J., M.B. Brown, L. Engelman, and R.I. Jennrich (Eds). University of California Press, Berkeley, CA. 1385 pp.
- Boag, D.A. and J.O. Murie. 1981. Population ecology of Columbian ground squirrels in southwestern Alberta. *Canadian Journal of Zoology*. 59:2230-2240.
- Brown, D. 1988. Components of lifetime reproductive success. In T.H. Clutton-Brock (Ed) *Reproductive Success*. The University of Chicago Press, Chicago, IL. pp 439-453.
- Brown, L.N. 1965. Abert's squirrel in southern Wyoming. *Journal of Mammalogy* 46:516.
- Brown, L.N., and R.J. McGuire. 1975. Field ecology of the exotic Mexican red-bellied squirrel in Florida. *Journal of Mammalogy*, 56:405-419.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 346-352
- Capretta, P.J. and R.C. Farentinos 1979. Determinants of selective herbivory in tassel-eared squirrels

- (Sciurus aberti). In J.H.A. Kroeze, (Ed) Preference Behavior and Chemoreception. Information Retrieval Limited, London, UK. pp 205-218.
- Capretta, P.J., R.C. Farentinos, V.M. Littlefield, and R.M. Potter. 1980. Feeding preferences of captive tassel-eared squirrels (Sciurus aberti) for ponderosa pine twigs. Journal of Mammalogy 61:734-737.
- Castellan, N.J. 1965. On the partitioning of contingency tables. Psychological Bulletin. 64:330-338.
- Clutton-Brock, T.H. 1988. Reproductive Success. In T.H. Clutton-Brock (Ed) Reproductive Success. The University of Chicago Press, Chicago, pp 472-485.
- Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour 30:1183-1192.
- Doebel, J.H. and B.S. McGinnes. 1974. Home range and activity of a gray squirrel population. Journal of Wildlife Management 38:860-867.
- Don, B.A. 1983. Home range characteristics and correlates in tree squirrels. Mammal Review 13:123-132.
- Eisenberg, J.F. 1981. The Mammalian Radiations. Chicago University Press. Chicago
- Farentinos, R.C. 1972a. Social dominance and mating activity in the tassel-eared squirrel (Sciurus aberti). Animal Behaviour 20:316-326.
- Farentinos, R.C. 1972b. Nests of the tassel-eared squirrel. Journal of Mammalogy, 53:900-903.
- Farentinos, R.L. 1979. Seasonal changes in home range size of tassel-eared squirrels (Sciurus aberti). The Southwestern Naturalist 24:46-62.
- Farentinos, R.L. 1980. Sexual solicitation of subordinate males by female tassel-eared squirrels (Sciurus aberti). Journal of Mammalogy 61:337-341.

- Farentinos, R.L., P.J. Capretta, R.E. Kepner, and V.M. Littlefield. 1981. Selective herbivory on tassel-eared squirrels: role of monoterpenes in Ponderosa pines chosen as feeding trees. *Science* 213:1273-1275.
- Ferron, J.P. 1976. Comfort behavior of the red squirrel (Tamiasciurus hudsonicus) *Z. Tierpsychol.* 42:66-85.
- Ferron, J.P. 1983. Scent marking by cheek rubbing in the northern flying squirrel (Glaucomys sabrinus). *Canadian Journal of Zoology* 61:2377-2380.
- Ferron, J. and J.P. Ouellet, 1989. Behavioral context and possible function of scent marking by cheek rubbing in the red squirrel (Tamiasciurus hudsonicus). *Canadian Journal of Zoology* 67:1650-1653.
- Ferron, J., J.P. Ouellet, and Y. Lemay. 1986. Spring and summer time budgets and feeding behavior of the red squirrel (Tamiasciurus hudsonicus). *Canadian Journal of Zoology* 64: 385-391.
- Fitzwater, W.D., Jr., and W.J. Frank. 1944. Leaf nests of grey squirrel in Connecticut. *Journal of Mammalogy*, 25:160-170.
- Gaines, M.S. and L.R. McClenaghan. 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics* 11:163-196.
- Glanz, W.E., R.W. Thorington, J. Madden, and L.R. Heany. 1982. Seasonal food use and demographic trends in Sciurus gratanensis. in E. Leigh, A.S. Rand, and D.M. Windsor, eds *The Ecology of a Tropical Forest: Seasonal Rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C. 468 pp.
- Goldman, E.A. 1928. The Kaibab or white-tailed squirrel. *Journal of Mammalogy* 9:127-129.
- Golightly, R.T., and R.D. Ohmart, 1978. Heterothermy in free-ranging Abert's squirrels (Sciurus aberti). *Ecology* 59:897-909.

- Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140-1162.
- Grodzinski, W. 1985. Ecological energetics of bank voles and wood mice. *Symposium of the Zoological Society of London*. 55:169-192.
- Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. *Mammal Review* 13:133-148.
- Gurnell, J. 1984. Home range, territoriality, caching behavior and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. *Animal Behaviour* 32:1119-1131.
- Gurnell, J. 1987. *The Natural History of Squirrels*. Facts on File Publications, New York NY. 201 pp.
- Hall, J.G. 1981. A field study of the Kaibab squirrel in Grand Canyon National Park. *Wildlife Monographs* 75:1-54.
- Halliday, T. and S.J. Arnold. 1987. Multiple mating by females: a perspective from quantitative genetics. *Animal Behaviour* 35:939-942.
- Halpin, Z.T. 1984. The role of olfactory communication in the social systems of ground-dwelling sciurids. In J.O. Murie and G.R. Michener (Eds.) *The Biology of Ground-Dwelling Squirrels*, University of Nebraska Press, Lincoln. pp 201-225.
- Hanken, J. and P.W. Sherman. 1981. Multiple paternity in Belding's ground squirrel litters. *Science* 212:351-353.
- Harestad, A.S. 1990. Nest site selection by northern flying squirrels and Douglas squirrels. *Northwestern Naturalist* 71:43-45.
- Harris, S., W.J. Cresswell, P.G. Forde, W.J. Trewhella, T. Woollard and S.Wray. 1990. Home-range analysis using radio-tracking data- a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20:97-123.

- Hatt, R.T. 1943. The pine squirrel in Colorado. *Journal of Mammalogy*, 24:311-345.
- Havera, S.P. 1979. Energy and nutrient cost of lactation in fox squirrels. *Journal of Wildlife Management* 43:958-965.
- Havera, S.P. and C.M. Nixon. 1978. Interaction among adult female fox squirrels during the adult breeding season. *Transactions of the Illinois State Academy of Sciences* 71:24-38.
- Hayne, D.W. 1949. Calculation of home range. *Journal of Mammalogy* 30:1-18.
- Heaney, L.R. 1984. Climatic influences on life-history tactics and behavior of North American tree squirrels. In J.O. Murie and G.R. Michener (Eds.) *The Biology of Ground-Dwelling Squirrels*, University of Nebraska Press, Lincoln. pp 43-78.
- Hoffmeister, D.F. and V.E. Diersing. 1978. Review of the tassel-eared squirrels of the subgenus Otosciurus. *Journal of Mammalogy* 59:402-413.
- Holekamp, K.E. 1984. Dispersal in ground-dwelling sciurids. In J.O. Murie and G.R. Michener (Eds.) *The Biology of Ground-Dwelling Squirrels*, University of Nebraska Press, Lincoln. pp 295-320.
- Holekamp, K.E. and P.W. Sherman. 1989. Why male ground squirrels disperse. *American Scientist* 77:232-238.
- Hougart, B. and V. Flyger. 1981. Activity patterns of radio-tracked squirrels'. *New England Wildlife Society*. 38:11-16.
- Ingles, L.G. 1947. Ecology and life history of the California grey squirrel. *California Fish and Game*, 33:139-158.
- Jandel Corporation. 1991. *Jandel Video Analysis Software*. Jandel Scientific Publishers, Corte Madera, CA. 353 pp.

- Jennrich, R.I. and F.B. Turner. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology* 22:227-237.
- Juelson, T.C. 1970. A study of the ecology and ethology of the rock squirrel, Spermophilus variegatus (Erxleben), Unpublished Ph.D. Dissertation. University of Utah 192 pp.
- Kachigan, S.K. 1986. *Statistical Analysis*. Radius Press, New York.
- Kantola, A.T. and S.R. Humphrey. 1990. Habitat use by Sherman's fox squirrel (Sciurus niger shermani) in Florida. *Journal of Mammalogy* 71:411-419.
- Keith, J.O. 1965. The Abert squirrel and its dependence on ponderosa pine. *Ecology* 46:150-163.
- Kenward, R.E. 1984. Ranging behavior and population dynamics of grey squirrels. in R.M. Sibly and R.H. Smith (eds) *Behavioral Ecology*. Blackwell Scientific Publications, Oxford, pp.319-30.
- Kivett, V.K., J.O. Murie, and A.L. Steiner. 1976. A comparative study of scent-gland location and related behavior in some northwestern nearctic ground squirrel species (Sciuridae): an evolutionary approach. *Canadian Journal of Zoology* 54: 1294-1306.
- Koepl, J.W., N.A. Slade, K.S. Harris, and R.S. Hoffmann. 1977. A three dimensional home range model. *Journal of Mammalogy* 58:213-220.
- Koford, R. 1982. Mating System of a territorial tree squirrel (Tamiasciurus douglasii) in California. *Journal of Mammalogy* 63:274-283.
- Koprowski, J.L. 1991a. The evolution of sociality in tree squirrels: the comparative behavioral ecology of fox squirrels and eastern gray squirrels. Unpublished Ph.D. Thesis. University of Kansas 176 pp.
- Koprowski, J.L. 1991b. Response of fox squirrels and gray squirrels to a late spring-early summer food shortage. *Journal of Mammalogy* 72:367-372.

- Lair, H. 1985. Length of gestation in the red squirrel Tamiasciurus hudsonicus. Journal of Mammalogy 66:809-810.
- Lanham, U. 1974. The Enchanted Mesa: An Introduction to its Natural History. Pruett Press, USA. 141 pp.
- Layne, J.N. 1954. The biology of the red squirrel, Tamiasciurus hudsonicus loquax (Bangs), in central New York. Ecological Monographs, 24:227-267.
- Lefebvre, L. 1981. Grooming in crickets: Timing and hierarchical organization. Animal Behavior 29:973-984.
- Lidicker, W.Z. 1975. The role of dispersal in the demography of small mammals. In F.B. Golley, K. Petrusewicz, and L. Ryszkowski (Eds.) Small Mammals: Their Productivity and Population Dynamics. Cambridge University Press, London, pp 103-122.
- Linton, M. and P.S. Gallo. 1975. The Practical Statistician: Simplified Handbook of Statistics. Brooks Cole Publishing Company, Monterey, CA. 384 pp.
- Littlefield, V.M. 1984. Habitat interrelationships of Abert squirrels (Sciurus aberti) and fox squirrels (Sciurus niger) in Boulder County, Colorado. Unpublished PhD thesis. Miami University 93 pp.
- McKee, E.D. 1941. Distribution of the tassel-eared squirrels. Plateau 14:12-20.
- McClosky, R.J. and K.C. Shaw. 1977. Copulatory behavior of the fox squirrel. Journal of Mammalogy 58:663-665.
- Merriam, C.H. 1930. A nest of the California gray squirrel (Sciurus griseus). Journal of Mammalogy, 11:494-495.
- Michener, G.R. 1979. Spatial relationships and social organization of adult Richardson's ground squirrels. Canadian Journal of Zoology 59:1666-1676.

- Michener, G.R. 1981. Ontogeny of spatial relationships and social behavior in juvenile Richardson's ground squirrels. *Canadian Journal of Zoology* 59:1666-1676.
- Minitab, 1991. Minitab Reference Manual. Duxbury Press, Boston, MA. 154 pp.
- Mohr, C.O. 1947. Table ^{of} ~~if~~ equivalent populations of North American Small Mammals. *The American Midland Naturalist* 37:223-249.
- Mohr, C.O. and W.A. Stumpf. 1966. Comparison of methods for calculation areas of animal activity. *Journal of Wildlife Management* 30:293-304.
- Moore, J.C. 1957. The natural history of the fox squirrel, Sciurus niger shermani. *Bulletin of the American Museum of Natural History*, 113:1-72.
- Moore, J. and R. Ali, 1984. Are dispersal and inbreeding avoidance related? *Animal Behaviour* 32:94-112.
- Murie, O.J. 1927. The Alaska red squirrel providing for winter. *Journal of Mammalogy*, 8:37-41.
- Nash, D.J. and R.N. Seaman. 1977. Sciurus aberti, *Mammalian Species*. 80:1-5.
- Nixon, C.M. and M.W. McClain. 1975. Breeding season and fecundity of female gray squirrels in Ohio. *Journal of Wildlife Management* 39:426-438.
- Ortega, J.C. 1987. Den site selection by the rock squirrel (Spermophilus variegatus) in southeastern Arizona. *Journal of Mammalogy* 68:792-798.
- Ortega, J.C. 1988. The behavioral ecology and natural history of the rock squirrel (Spermophilus variegatus) in southeastern Arizona. Unpublished Ph.D. Thesis. University of Colorado 216 pp.
- Ouellet, J.P. and J. Ferron. 1988. Scent marking behavior by woodchucks (Marmota monax) *Journal of Mammalogy* 69:365-368.

- Owings, D.H., M. Borchert, and R. Virginia. 1977. The behavior of California ground squirrels. *Animal Behaviour* 25:221-230.
- Patton, D.R. 1974. Characteristics of Ponderosa Pine Stands Selected by Abert's Squirrel for cover. University of Arizona, PhD thesis.
- Pauls, R.W. 1978. Behavioral strategies relevant to the energy economy of the red squirrel (Tamiasciurus hudsonicus). *Canadian Journal of Zoology* 56:1519-1525.
- Pederson J.C. and B.L. Welch. 1985. Comparison of ponderosa pines (Pinus ponderosa) as feed and nonfeed trees for Abert squirrels (Sciurus aberti). *Journal of Chemical Ecology* 11:149-158.
- Pfeiffer, S.L.R. 1982. Disappearance and dispersal of Spermophilus elegans juveniles in relation to behavior. *Behavioral Ecology and Social Biology* 10:237-243.
- Quay, W.B. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angles in rodents. *Journal of Mammalogy* 46:23-37.
- Robinson, D.J. and I.M. Cowan. 1954. An introduced population of the grey squirrel (Sciurus carolinensis Gmelin) in British Columbia. *Canadian Journal of Zoology*, 32:261-282.
- Rothwell, R. 1979. Nest sites of Red Squirrels (Tamiasciurus hudsonicus) in the laramie range of southeastern Wyoming. *Journal of Mammalogy* 60:404-405.
- Rusch, D.A. and W.G. Reeder. 1978. Population ecology of Alberta red squirrels. *Ecology* 59:400-420.
- Sanderson, H.R., Healy, W.M., Pack, J.C., Gill, J.D. and J. Ward Thomas. 1976. Gray squirrel habitat and nest tree preference. *Proceedures of the Annual Conference of the Southeast Association of the Game and Fish Commission* 30:609-616.

- Schoener, T.W. 1981. An empirically based estimate of home range. *Theoretical Population Biology* 20:281-325.
- Schwagmeyer, P.L. 1984. Multiple mating and intersexual selection in thirteen-lined ground squirrels. In J.O. Murie and G.R. Michener (Eds.) The Biology of Ground-Dwelling Squirrels. University of Nebraska Press, Lincoln, pp 275-294.
- Setoguchi, M. 1991. Nest site selection and nest building behavior of red-bellied tree squirrels on Tomagashima Island, Japan. *Journal of Mammalogy*, 72:163-170.
- Shaw, W.T. 1925. The seasonal differences of north and south slopes in controlling the activities of the Columbian ground squirrel. *Ecology*, 6:157-162.
- Simon, C. 1975. The influence of food abundance on territory size in the iguanid lizard Sceloporus jarrovi. *Ecology* 56:993-998.
- Smith, C.C. 1968. The adaptive nature of social organization in the genus of tree squirrel Tamiasciurus. *Ecological Monographs* 38:30-63.
- Snyder, M. 1990. Interactions between Abert's squirrel (Sciurus aberti) and ponderosa pine (Pinus ponderosa): Selective herbivory and host plant fitness. Unpublished PhD dissertation 118 pp.
- Snyder, M. 1992. Selective herbivory by Abert's squirrel mediated by chemical variability in ponderosa pine. *Ecology* 73:1730-1741.
- Stapp, P., P.J. Pekins, and W.W. Mautz. 1991. Winter energy expenditure and the distribution of southern flying squirrels. *Canadian Journal of Zoology* 69:2548-2555.
- Steiner, A.L. 1974. Body-rubbing, marking, and other scent-related behavior in some ground squirrels (Sciuridae), a descriptive study. *Canadian Journal of Zoology* 52:889-906.

- Stephenson, R.L. 1974. Seasonal food habits of Abert's squirrels, Sciurus aberti. Journal of the Arizona Academy of Sciences, Proceedings Supplement 9:8.
- Stephenson, R.L. 1975. Reproductive biology and food habits of Abert's squirrels in central Arizona. Unpublished Master's Thesis. Arizona State University 66 pp.
- Stephenson, R.L. and D.E. Brown. 1977. Snow cover as a factor influencing mortality of Abert squirrels. Journal of Wildlife Management 44:951-955.
- Sullivan, T.P. and D.S. Sullivan. 1982. Population dynamics and regulation of the Douglas squirrel (Tamiasciurus douglasii) with supplemental food. Oecologia 53:264-270.
- Svendsen, G.E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. Ecology, 55:760-771.
- Thompson, D.C. 1977a. Reproductive behavior of the grey squirrel. Canadian Journal of Zoology 55:1176-1184.
- Thompson, D.C. 1977b. Diurnal and seasonal activity of the grey squirrel (Sciurus carolinensis). Canadian Journal of Zoology 55:1185-1189.
- Thompson, D.C. 1978a. Regulation of a northern grey squirrel (Sciurus carolinensis) population. Ecology 59:708-715.
- Thompson, D.C. 1978b. The social system of the grey squirrel. Behaviour 64:305-328.
- Tittensor, A.M. 1970. Red squirrel drey. Journal of Zoology (London), 162:528-533.
- Tonkin, J.M. 1983. Activity patterns of the red squirrel (Sciurus vulgaris). Mammalian Review 13:99-111.
- Uhlig, H.G. 1956. A theory on leaf nests built by grey squirrels on Seneca State Forest, West Virginia. The journal of Wildlife Management, 20:263-266.

- Vahle, J.R. and D.R. Patton. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. *Journal of Forestry* 81:14-22.
- Walro, J.M., P.T. Meier, and G.E. Svendsen. 1983. Anatomy and histology of scent glands associated with the oral angle in woodchucks. *Journal of Mammalogy* 64:701-730.
- Waser, P.M. and W.T. Jones. 1983. Natal philopatry among solitary mammals. *The Quarterly review of Biology* 58:355-390.
- Wauters, L.A. and A.A. Dhondt. 1985. Population dynamics and social behavior of red squirrel populations in different habitats. XVII Congress of the International Union of Game Biologists, Brussels 311-18.
- Wauters, L.A. and A.A. Dhondt. 1987. Activity budget and foraging behavior of the red squirrel (*Sciurus vulgaris* Linnaeus, 1758) in a coniferous habitat. *Z. Saugetierkunde* 52:341-353.
- Wauters, L.A. and A.A. Dhondt. 1990a. Nest-use by red squirrels (*Sciurus vulgaris* Linnaeus, 1758). *Mammalia* 54:377-389.
- Wauters, L.A. and A.A. Dhondt. 1990b. Red squirrel (*Sciurus vulgaris* Linnaeus, 1758) population dynamics in different habitats. *Z. Saugetierkunde* 55:161-175.
- Wauters, L.J., C. Swinnen, and A.A. Dhondt. 1992. Activity budget and foraging behavior of red squirrels (*Sciurus vulgaris*) in coniferous and deciduous habitats. *Journal of the Zoological Society of London* 227:71-86.
- Wettstein, P.J. and J.S. States. 1986. The major histocompatibility complex of tassel-eared squirrels. II. Genetic diversity associated with Abert squirrels. *Immunogenetics* 24:242-250.
- Wiegl, P.D., M.A. Steele, L.J. Sherman, and J.C. Ha. 1989. The ecology of the fox squirrel (*Sciurus*

niger) in North Carolina: Implications for survival in the southeast. Bulletin of Tall Timbers Research Station. 24:1-93.

Zar, J.H. 1984. Biostatistical Analysis. Second edition. Prentice Hall, Inc., Englewood Cliffs, New Jersey, 718 pp.

APPENDIX 1

List of Behavior Pattern Codes

FEEDING

- 10 Ponderosa pine bark
- 11 Ponderosa pine male cone
- 12 Ponderosa pine female cone
- 13 Douglas fir shoot
- 14 Douglas fir male cone
- 15 Douglas fir female cone
- 16 Other object in tree
- 17 Unknown object in tree
- 18 Ponderosa pine shoot
- 20 Mushroom
- 21 Truffle
- 22 Fallen cone
- 23 Shrub/leaves/berries
- 24 Other object on ground
- 25 Unknown object on ground

SEARCHING

- 33 Digging in ground
- 34 Caching food item in ground
- 35 Caching food item in tree
- 36 Carrying food while locomoting in tree
- 37 Carrying food while locomoting on the ground
- 38 Sniffing

RESTING

- 40 In tree; posture not specified
- 41 In tree; tail over body in shade
- 42 In tree; tail over body in sun
- 43 In tree; tail beside body in shade
- 44 In tree; tail beside body in sun
- 45 On ground; in shade
- 46 On ground; in sun
- 47 On fallen log
- 48 On rock
- 49 On stump

TRAVELING

- 50 On ground
- 51 Ascending tree
- 52 Descending tree
- 53 Crossing into adjacent tree

54 Scrambling/locomotor play
55 Within same tree
56 On fallen log

GROOMING

60 Unspecified
61 Face
62 Right side of body
63 Left side of body
64 Tail
65 Scratch
66 Ears
67 Back
68 Underside
69 Genitalia

NESTING

70 In nest
71 Entering nest PM
72 Entering nest AM
73 Maintenance
74 Building
75 Entering nest midday
76 Leaving nest midday
77 Moving litter
78 Other

ALERT

80 Sitting on ground
81 Sitting on tree
82 Sitting on rock
83 Sitting on stump

AGGRESSION

85 Vocalization
86 Foot Stomp
87 Tail fluff
88 Tail flick

OTHER

90 Cheek rubbing
92 Drinking from rock pool
93 Drinking from stream
94 Urinating
95 Defecating
96 Other solitary behavior
97 Eating snow

99 Out of view

SOCIAL

- 100 Other social interactions
- 101 Hesitant approach
- 102 Direct approach
- 103 Chase
- 104 Face threat
- 105 Displace
- 106 Attack
- 107 Flee
- 108 Mount
- 109 Copulate
- 110 Stop chase
- 111 Tolerate
- 112 Was displaced
- 113 Following
- 114 Investigate
- 115 Bite
- 116 Kick
- 117 Move away
- 118 Mom with juvenile