

**Initiation of
Red Squirrel (*Tamiasciurus hudsonicus*)
Monitoring on
Carson National Forest, New Mexico**

A Final Contract R3-02-03-12 Completion Report

Submitted by:

Jennifer K. Frey, PhD

*Frey Biological Research
438 Diaz Rd.
Las Cruces, New Mexico 88007*

and

*Department of Fishery and Wildlife Sciences and
Department of Biology
New Mexico State University
P.O. Box 30003, MSC 4901
Las Cruces, New Mexico 88003-8003*

Submitted to:

**Carson National Forest
208 Cruz Alta Road
Taos, New Mexico 87571**

31 December 2003

Table of Contents

Executive Summary	3
Background	5
Purpose	6
Methods	
Field methods	7
Statistical methods	9
Results	
Sampling	10
Stand structure	11
Forest-wide patterns	
Red squirrel density	12
Red squirrel presence/absence	18
Density patterns by cover type	19
Inactive middens	26
Discussion	
Forest-wide patterns	27
Patterns within specific cover types	29
Conclusions	31
Recommendations	32
Acknowledgments	32
References	33
Appendix I	35
Appendix II	36

Executive Summary

Purpose

- The purpose of this study was to initiate monitoring of red squirrels on Carson National Forest in order to establish long-term trends in populations and habitat.

Method

- An index of red squirrel density was determined by counting active, primary middens (food caches) on each of two belt transects in a forest stand. One squirrel normally maintains and defends one primary midden. Thus, the density of active primary middens is a conservative estimate of squirrel density.
- Habitat data were collected at two random plots along each belt transect. Habitat variables included: slope, aspect, canopy cover, ground cover (of forbs, grasses, litter, bare, and other), woody understory species and cover, number, size and species of each tree, number and size of snags, and number and size of downed logs.
- Red squirrel midden and habitat data were collected in 58 forest stands. Forest stands were identified and mapped by Carson National Forest using geographic information system (GIS). These included 32 Douglas fir stands, 23 white fir stands, 16 blue spruce stands, 14 Engelmann spruce stands, 30 spruce-fir stands, and 1 aspen stand.

Results

- Red squirrel density ranged from 0 – 3.37 per acre with an overall mean of 0.47 per acre.
- Red squirrel densities were lowest in white fir and Douglas fir stands, intermediate in Engelmann spruce stands, and highest in blue spruce and spruce-fir stands.
- Based on univariate statistics, red squirrel density exhibited a significant positive correlation with stand cover type, Engelmann spruce, and large (12-16 inch DBH) subalpine fir. In contrast, red squirrel density exhibited a significant negative correlation with the presence of Douglas fir, white fir, small (4-8 inch DBH) aspen, and small diameter (< 8 inch diameter) downed logs. Small diameter downed logs usually appeared to be slash from recent thinning.
- Based on multivariate statistics, the single best predictor of red squirrel density was the density of large (12-16 inch DBH) Engelmann spruce.
- In comparison of stands where red squirrels were present, red squirrels were absent in stands with greater numbers of small (< 4 inch DBH) white fir, greater total density of white fir, greater proportion of white fir in a stand,

greater total density of all species of trees, and greater numbers of small diameter (< 8 inch diameter) downed logs. Further, red squirrels were absent in stands with a smaller proportion of Engelmann spruce and fewer numbers of large (12-16 inch DBH) Engelmann spruce.

- The relationship between habitat characteristics and red squirrel densities within each GIS stand cover type are presented in this report. However, because sample sizes are small within each cover type, these results should be considered preliminary and used only for directing future research.
- The density of inactive primary middens varied from 0 – 1.35 per acre with a mean of 0.07 per acre. The density of inactive primary middens did not vary significantly by GIS stand cover type.

Discussion and Conclusions

- Red squirrel densities on Carson National Forest were within the range of variation found in other geographic regions and habitat types.
- Most previous studies were conducted in regions with little topographic and habitat variation. Consequently, this study was somewhat unique in establishing habitat preferences for this species.
- Red squirrel densities were highest in stands where spruce (*Picea* spp.) was a major component. Spruce cones are a highly nutritious food source that can be stored in middens for a long period of time. In addition, the higher available moisture in these habitat types might promote the production of fungi, another important food resource for red squirrels.
- The best predictor of red squirrel density was the density of large (12-16 inch DBH) Engelmann spruce. Large trees may be associated with greater food production (cones, seeds, fungi) for red squirrels.
- Lower mixed conifer forest stands (i.e., Douglas fir, and especially white fir) were associated with low densities of red squirrel.

Recommendations

- Continue red squirrel monitoring using methods developed in this study.
- Develop additional studies to more fully establish the relationships between habitat characteristics and red squirrel densities within each forest stand cover type and to address the impacts of specific forest management strategies.
- Long-term data on conifer cone/seed and fungal production should be conducted in conjunction with red squirrel monitoring.

Background

The red squirrel (*Tamiasciurus hudsonicus*; also called pine squirrel, spruce squirrel or chickaree) occurs broadly throughout the boreal forest zones of North America with peninsular extensions southward in the Appalachian and Rocky mountains (Hall 1981). It reaches southern range limits in the American Southwest (Hall 1981). Recently, Arbogast et al. (2001) found that populations of red squirrel in the southwestern USA were distinct from other populations and could be recognized as a separate phylogenetic species, *T. fremonti*. This assessment was based on specimens collected from Sandoval Co. (i.e., probably the Jemez Mountains) New Mexico, and Apache Co., Arizona (Arbogast et al. 2001). In contrast, a single specimen from the Southern Rocky Mountains in Colorado was included within the wide-ranging northeastern subspecies *T. h. hudsonicus* (Arbogast et al. 2001). Carson National Forest is located in the southern portion of the San Juan and Sangre de Cristo mountain ranges. These are southern extensions of the large contiguous mountain region known as the Southern Rocky Mountains, which is centered in Colorado. Although it remains unknown to which group animals from the Carson National Forest belong, on a biogeographic basis it seem plausible that they belong to the *T. hudsonicus* group. However, it remains a possibility that extrapolation of results from other geographic areas may not be appropriate.

Red squirrels are primarily associated with various types of conifer forests, although in some areas of eastern North America they also inhabit hardwood and mixed hardwood-evergreen forests (Flyger and Gates 1982). In the Southern Rocky Mountains and Southwest, adiabatic cooling results in distinctive vegetation zones at different elevations. The lowest elevation conifer forests (= lower montane conifer forest) are dominated by ponderosa pine (*Pinus ponderosa*), mid-elevation mixed conifer forests (= upper montane conifer forests) are typically dominated by Douglas fir (*Pseudotsuga menzeisii*), white fir (*Abies concolor*), or blue spruce (*Picea pungens*), while the highest elevation boreal forests (= subalpine forests) are typically co-dominated by Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* variety *arizonica*; Dick-Peddie 1993). In Colorado and New Mexico, red squirrels are primarily associated with mixed conifer and boreal forests (Bailey 1931, Hatt 1943, Findley 1961, Findley et al. 1975, Fitzgerald et al. 1994). Interlocking canopy within these forests is important for foraging efficiency and escape from predators (Steele 1998). Abert's squirrel (*Sciurus aberti*), rather than red squirrel, typically occupy lower elevation ponderosa pine forests. However, both species can co-occur in the lower portions of the mixed conifer zone (Ferner 1974). Although large stands of mixed conifer or boreal forest seem necessary for red squirrel to maintain populations, red squirrel occasionally occupy ponderosa pine forests, especially in areas adjacent to mixed conifer forest (Finley 1969, Findley et al. 1975). Findley et al. (1975:138) thought that New Mexico red squirrel were especially partial to riparian groves of blue spruce, "to the exclusion of the surrounding conifers". Armstrong (1972) reported them in riparian cottonwood forests. Aspen (*Populus*) is considered a suboptimal habitat type (Steele 1998).

In general, there are very few data available on habitat selection by this species in the Southwest.

Red squirrel eat a wide variety of food including winter terminal buds of evergreens, seeds, bark, fruits, sap, berries, various kinds of fungi, insects, and other animal material (Flyger and Gates 1982, Steele 1998). However, their dietary staple consists of the cones of conifer trees with which they have coevolved (Smith 1970). In New Mexico, all of the dominant conifer trees have cones that mature in the fall and release their seeds. Consequently, red squirrels are larder-hoarders that must harvest the immature "green" cones before they release their seeds and then store them in caches (Smith and Reichman 1984). Cones are usually cached in a single, centrally located midden, typically situated at the base of a large feeding tree (Yeager 1937, Finley 1969, Smith 1970). In some situations, squirrels will also construct smaller, satellite middens and feeding sites. Middens consist of cone scales, cores of eaten cones, and stored uneaten cones. Typically a midden contains enough food to last one or two seasons (Gurnell 1984, M.C. Smith 1968). Middens may be used by many generations of squirrels. This results in very large middens (e.g., 9 m across, 0.5 m deep; Fitzgerald et al. 1994) that endure on the landscape for many years. Midden characteristics, including its location and size, contribute to a cool, moist midden environment; this environment prevents the conifer cones from opening (Smith 1968). Red squirrels are capable of consuming the seeds within the cone by biting through the cone like an ear of corn. Other small mammals may not be able to access the seeds within a closed cone. Thus, by storing the cones in the cool, moist midden environment, the red squirrel is able to prevent its stored seeds from being used by other competitive small mammals (Smith 1968).

In part due to the need to defend cached food supplies, both male and female red squirrels defend exclusive territories centered on the midden (Smith 1968, Kemp and Keith 1970, Rusch and Reeder 1978, Gurnell 1984). Territory size and aggressiveness are related to food availability (Flyger and Gates 1982, Steele 1998). Territorial defense occurs year-round but is most intense in fall when cones are harvested. Regions with conifer species that have serotinous cones (i.e., cones remain closed on trees for several years after they mature), such as lodgepole pine, provide a more consistent cone crop, which results in lowered territorial aggressiveness (Rusch and Reeder 1978, Smith 1968). In addition, it is possible that a more consistently available cone crop might result in more stable populations. In contrast, in regions such as New Mexico that lack serotinous conifers, red squirrel populations are likely to fluctuate in relation to cone crop (Fitzgerald et al. 1994). However, there are very few data on factors influencing red squirrel distribution and abundance and none are available for northern New Mexico..

Purpose

The red squirrel was designated a management indicator species (MIS) by the Carson National Forest. Consequently, information is needed on their distribution and abundance on the forest, habitat associations, population trends,

and how they are impacted by forest management practices. The main purpose of this study was to initiate a monitoring study for this species on the Carson National Forest that will provide information on habitat and population trends. More specifically, the objectives were to develop and implement monitoring protocols, to determine occurrence and density of red squirrel, to determine the relationship between red squirrel density and habitat characteristics, and to provide the baseline data for a long-term monitoring program.

Methods

Currently, no standard technique has been developed to monitor red squirrel populations over large areas of forest. Most studies of red squirrels have concerned their population ecology on relatively small study areas. Consequently, many techniques used in ecological studies (e.g. radio telemetry, trap-mark-resight, etc) are not appropriate for the objectives of this study, which is geared at monitoring the species over a broad geographic area. One notable monitoring program concerns the federally endangered Mount Graham red squirrel (*T. h. grahamensis*). This squirrel occurs in a highly isolated, relatively small area of forest habitat. Because each squirrel maintains and defends one primary midden and because middens are obvious landscape features (e.g., Kilham 1954), Mount Graham red squirrel monitoring has focused on midden activity (Frederick et al. 2003). Currently, this monitoring study involves mapping middens and evaluating changes in midden activity (Frederick et al. 2003). This technique is not possible for monitoring red squirrels on Carson National Forest because it involves identifying the locations of all middens. This method is not feasible in a study area of the extremely large size of Carson National Forest. However, midden activity can provide a means for monitoring red squirrels in larger areas. In the method here developed for monitoring red squirrels on the Carson National Forest, active midden density in belt transects is used as an estimate of population size. Similar methodology was used to survey Mount Graham red squirrels prior to the development of the more intensive methods based on the specific mapping of middens (Spicer et al. 1985). Similar studies using midden counts have been used for other studies of small areas (e.g., Wolff and Zasada 1975).

Field Methods

Geographic information system (GIS) vegetation cover maps were generated for conifer forest stands on the Carson National Forest. Forest Service GIS cover types included white fir, Douglas fir, blue spruce, Engelmann spruce, and Engelmann spruce-subalpine fir. Only stands within one mile of an established road were included on maps. Selection of stands for red squirrel monitoring was based on the following criteria: 1) stands were in geographic proximity in order to allow for the survey of an average of approximately 4 stands per day; 2) stands were distributed among the five Carson National Forest

Districts (Canjilon, El Rito, Questa, Tres Piedras, Camino Real) with relatively more stands surveyed in districts with more red squirrel habitat; 3) survey effort was distributed amongst the stand types; 4) large stands were preferentially selected (minimally, they had to be large enough to contain two 1968 x 33 ft. (= 600 m X 10 m) belt transects; 5) stands were selected to reflect various geographic regions and physiographies; and 6) stands were selected so as to minimize drive time to ensure timely project completion.

Surveys were completed between 1 August and 13 August 2003. A total of 58 forest stands were surveyed including 6 on the Canjilon, 10 on the El Rito, 15 on the Questa, 7 on the Tres Piedras, and 20 on the Camino Real districts. The Jicarilla District was not included in this study because red squirrels do not occur there (Stace Walker personal communication). We confirmed the absence of red squirrels on the Jicarilla District by surveying the three largest patches of mixed conifer forest on the district; no evidence of red squirrels was observed. Once a stand was selected, maps and stand center coordinates were used to determine the general location and direction of two belt transects. Belt transects were 1968 x 33 ft. (= 600 m X 10 m; = 0.6 ha, 1.5 acres). The date, name(s) of persons collecting data, stand location (including district and coordinates of stand center), and cover type as reported by Carson NF were recorded. A transect starting point and bearing was haphazardly selected in such a way to insure that the transect was fully contained within the stand and well away from forest edges (where possible). Coordinates of the starting point was determined with a GPS unit and a compass was used to determine the transect bearing; these data were recorded.

The observer slowly walked the transect, maintaining the bearing, and carefully looked for red squirrel middens. A wire flag was used to mark the observer's position on the transect if the observer had to leave the transect in order to search behind any visual obstructions. Only middens within 16 ft (5 m) on either side of the transect were recorded. The 16 ft was measured with the aid of a retractable "golf ball retriever" pole. For each midden observed on the transect, data on its size, age, activity, and location were recorded. This included any midden that was at least partially within the belt. Midden size included an assessment of whether the midden was a large primary midden or a smaller satellite midden. In the case of a satellite midden, the associated primary midden had to be found in order to verify the satellite status of the observed midden. Age of the midden was assessed by observing the relative state of decay of the midden material. In newly constructed middens, the midden material is fluffy and not compacted or decayed (Fluffy stage). As a midden ages, the midden material becomes compacted (Compacted stage) and eventually begins to decay (Composted stage). Compaction and decay begin at the bottom of the midden. Activity of the midden was assessed by observations of squirrel or sign. An active midden was determined by the presence of a squirrel at the midden or by the presence of fresh cones or feeding remains at the midden. Fresh cone remains have bright coloration. The midden location was the approximate meter location along the transect. Further, a midden could

be fully contained within the belt or partially on the belt. Middens only partially in the belt were recorded as < 50% or > 50% within the belt.

Habitat data were collected at two random points along each transect. Random points were selected by using 1-600 random number tables. Habitat data were collected within a 16.4 ft (= 5 m) radius plot (= 78.5 m², = 0.019 acres, = 845 ft²) at the two random points. Habitat variables were averaged for a transect. All tree densities in this report are reported as the mean number within an 845 ft² (= 78.5 m²) area. To calculate the mean density of trees per acre, use the following formula: density = mean number of trees per plot / 0.0194. At each point, location was determined using a GPS unit. Slope and aspect of the surrounding terrain were visually estimated. Canopy cover was assessed by using a convex spherical densiometer and taking readings in the four cardinal directions at the point. Percent ground cover was visually estimated on the plot. Ground cover classes included forbs, grasses, litter, bare ground, and other. Percent cover classes included 0-5, 5-25, 25-50, 50-75, 75-95, and 95-100%. Using the same percent cover classes, understory cover of woody shrubs and saplings < 39 in (= 1 m) tall were visually estimated. Dominant understory species were recorded. All trees on the plot were identified and classed into seven size classes based on diameter at breast height including: < 4 in (= 10 cm), 4-8 in (= 10-20 cm), 8-12 in (= 20-30 cm), 12-16 in (= 30-40 cm), 14-20 in (= 40-50 cm), 20-24 in (= 50-60 cm), and > 24 in (= 60 cm). The number of standing dead trees (snags) was counted for two size classes including < 8 in (= 20 cm) and > 8 in (= 20 cm) DBH. The number of downed trunks (logs) was counted for two size classes including < 8 in (= 20 cm) and > 8 in (= 20 cm) diameter. After completion of the transect, observers sketched a map of the transect location, made notes on the general condition of the stand, and recorded observations of any mammal sign observed.

Statistical Methods

All variables were checked for normality using a one-sample Kolmogorov-Smirnov test. All variables other than canopy cover were non-normal. Thus, where possible, nonparametric tests were performed for non-normal variables. Because of high habitat variation within a stand, both transects within a stand were analyzed separately. In addition to the GIS forest cover types provided by Carson National Forest, transect habitat was also classified into four general vegetation types based on plot data. These vegetation types included 1) lower mixed conifer forest (included ponderosa pine, Douglas fir, white fir), 2) upper mixed conifer forest (included Douglas fir, white fir, and Engelmann spruce), 3) boreal forest (included Engelmann spruce and subalpine fir), and 4) blue spruce (blue spruce dominant). These classifications were based on tree composition of the habitat plots. Unless otherwise indicated, all statistics were based on the density of active primary middens on a transect. All statistical analyses were run using SPSS for Windows version 10.0.

Forest-wide analyses.—Kruskal-Wallis test was used to test whether red squirrel midden density significantly differed by cover type and vegetation type. Wilcoxon signed rank tests were used to test whether midden density and the percent of middens in each Forest Service GIS cover type was significantly different from the proportion of each cover type sampled. Simple correlations were assessed between red squirrel midden density estimates and each independent variable. Multiple regression including all independent variables was used to assess the power with which all variables together predicted red squirrel midden density. Stepwise multiple regression were used to assess the significance of each independent variable for predicting red squirrel midden density.

Based on all available evidence, stands were classified as red squirrels present or absent. Univariate Kolmogorov-Smirnov tests were used to test whether each variable significantly differed in stands where red squirrels were present versus stands where red squirrels were absent. Discriminant function analysis was used to develop statistical models for red squirrel presence or absence in a stand. This model was used to statistically classify stands as either red squirrel present or red squirrel absent. This provides an indication of how well the model works.

Cover-type analyses.—Stands within each Forest Service GIS cover type were also analyzed separately in order to evaluate habitat factors that influence red squirrel distribution and abundance in each major cover type. Simple correlations were assessed between red squirrel midden density estimates and each independent variable. Stepwise multiple regression were used to assess the significance of each independent variable for predicting red squirrel midden density. Discriminant function analyses were calculated to model habitat characteristics that differed between stands classified as red squirrel present or absent. However, results of these analyses were deemed unreliable due to small sample sizes. Univariate Kolmogorov-Smirnov tests were used to test whether each variable significantly differed in stands where red squirrels were present versus stands where red squirrels were absent.

Results

Sampling

A total of 116 transects on 58 forest stands was surveyed for red squirrel middens; this was a total sampling area of 172 acres (= 69.6 ha). Appendix 1 provides a brief evaluation of the effort and logistics required to complete this inventory. Sampling effort by Forest District and forest cover type are presented in Table 1. Elevation of belt transects ranged from 8,197 ft. (= 2,499 m) to 11,083 ft. (= 3,379 m). A total of 197 middens were detected (Table 2). Of these, 41.1 % were considered active primary middens; these formed the basis for most statistical analyses.

Table 1. Red Squirrel sampling by Carson National Forest district and cover type during August 2003. The sampling unit consisted of a 1968 x 33 ft. (= 600 m X 10 m) belt transect.

Forest Cover	Camino Real	Canjilon	El Rito	Questa	Tres Piedras	Total
Douglas fir	8	4	6	8	6	32
White fir	8	3	6	4	2	23
Blue spruce	8		2	4	2	16
Engelmann spruce	8		2	2	2	14
Spruce-fir	8	4	4	12	2	30
Aspen	0	1	0	0	0	1
Total	40	12	20	30	14	116

Table 2. Number and type of middens detected on belt transects on Carson National Forest in August 2003.

Midden Activity	Primary	Satellite	Total
Active	81	78	159
Inactive	20	14	34
Uncertain	3	1	4
Total	104	93	197

Stand Structure

Across all stands, Engelmann spruce was the most abundant tree sampled (22.6 %). Other dominant trees sampled included aspen (19.9%), Douglas fir (19.1%), and white fir (14.6%). Less common trees included subalpine fir (10.9%), blue spruce (5.9%), ponderosa pine (3.3%), and others (3.6%). The size distribution for all species of trees was skewed toward smaller diameter trees (Table 3). More than half of all trees were < 8 in. DBH and trees over 16 in. DBH generally accounted for less than 5 % of all trees of a given species.

Table 3. Summary of stand size structure of dominant conifer tree species across all red squirrel sampling transects on Carson National Forest in August 2003. Values by size class are presented as percent of total trees of that species (top line) and cumulative percentage (bottom line).

Tree Species	Mean Tree Density (per acre)	Size Class (inches DBH)						
		< 4	4-8	8-12	12-16	16-20	20-24	> 24
Douglas fir	184.7 (= 456.3/ha)	32.4	23.9	21.7	14.1	3.8	2.6	1.4
		32.4	56.3	78.0	92.1	95.9	98.5	99.9
White fir	142.4 (=352.0/ha)	49.4	19.5	16.2	9.8	2.8	1.9	0.3
		49.4	68.9	85.1	94.9	97.7	99.6	99.9
Blue spruce	57.5 (=142.2/ha)	49.4	22.4	13.5	8.5	3.1	2.3	0.8
		49.4	71.8	85.3	93.8	96.9	99.2	100.0
Engelmann spruce	236.0 (= 583.1/ha)	45.2	19.6	16.4	13.4	4.3	0.9	0.2
		45.2	64.8	81.2	94.6	98.9	99.8	100.0
Subalpine fir	206.9 (= 511.2/ha)	69.7	15.0	9.8	3.5	1.3	0.6	0.0
		69.7	84.7	94.5	98.0	99.3	99.9	99.9

Forest-wide Patterns

Red squirrel density.—Density of active primary middens varied from 0 – 3.37 per acre (= 0 - 8.33 per hectare) with an overall mean of 0.47 per acre (SD = 0.81; = 1.16/ha, SD = 1.99). Density of active primary middens varied significantly by Forest Service GIS cover types (Kruskal-Wallis nonparametric test $\chi^2 = 16.407$, $df = 5$, $P = 0.006$; Table 4, Figure 1). Densities were lowest in Douglas fir and white fir, intermediate in Engelmann spruce, and highest in spruce-fir and blue spruce (Table 4). The percentage of each cover type sampled was not significantly correlated with either midden density ($r_s = 0.257$, $P = 0.623$) or the percentage of middens in each cover type ($r_s = 0.371$, $P = 0.468$). Similarly, the percentage of each cover type sampled exhibited a significantly different distribution than midden density (Wilcoxon signed rank test $Z = -2.201$, $P = 0.028$). However, the percentage of each cover type sampled did not exhibit a significantly different distribution than percent of middens in each cover type (Wilcoxon signed rank test $Z = -0.105$, $P = 0.917$). In comparison with the percent of each cover type sampled, there was a relatively higher percent of middens in blue spruce and spruce-fir forests and a relatively lower percent of middens in white fir and Douglas fir forests.

By broad vegetation type, densities of active primary middens were lowest in lower mixed conifer forest, intermediate in upper mixed conifer and boreal

forest, and highest in blue spruce forest (Table 5, Figure 2). Midden density was not significantly different by broad vegetation type (Kruskal-Wallis nonparametric test $\chi^2 = 6.249$, $df = 5$, $P = 0.100$).

Table 4. Density of active, primary red squirrel middens in different Forest Service GIS cover types on Carson National Forest in August 2003.

Forest Service cover type	Cover type		Active primary middens			
	No. Stands	Percent surveyed	Mean Density (middens/acre)	SE	Range	Percent of Middens
Douglas fir	32	27.6	0.17 (=0.42/ha)	0.053	0 – 0.67	9.9
White fir	23	19.8	0.15 (=0.36/ha)	0.059	0 - 0.67	6.2
Blue spruce	16	13.8	0.97(=2.40/ha)	0.254	0 – 3.37	28.4
Engelmann spruce	14	12.1	0.43(=1.07/ha)	0.182	0 - 2.02	11.1
Spruce-fir	30	25.9	0.81 (=2.00/ha)	0.203	0 - 3.37	44.4
Aspen	1	0.9	0	-	-	0

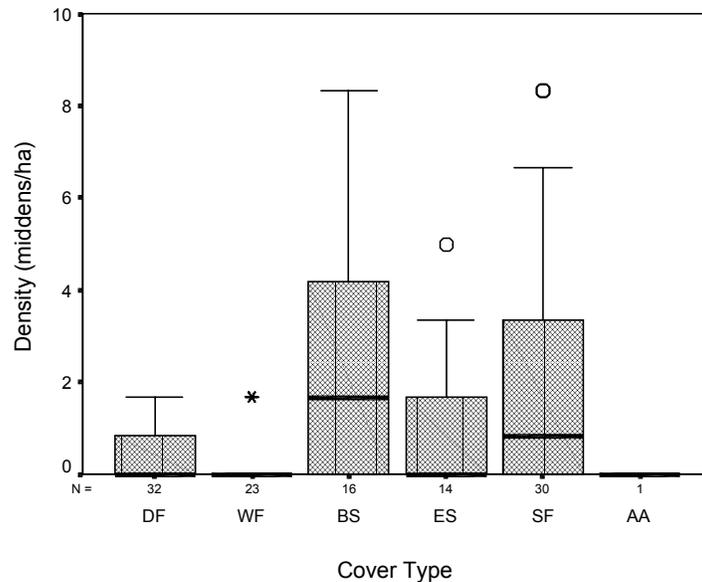


Figure 1. Density of active, primary red squirrel middens in six Forest Service GIS cover types on Carson National Forest in August 2003. Black bars represent medians, boxes represent quartiles, circles indicate outliers, and the asterisk represents a statistical extreme value. Cover types are Douglas fir (DF), white fir (WF), blue spruce (BS), Engelmann spruce (ES), spruce-fir (SF), and aspen (AA). To convert from middens per ha to middens per acre, divide displayed density by 2.471.

Table 5. Density of active, primary red squirrel middens in different vegetation types on Carson National Forest in August 2003.

Vegetation type	No. stands	Mean density (middens/acre)	SE	Range
Blue spruce	3	1.12 (=2.78/ha)	1.12	0 – 3.37
Lower mixed conifer	45	0.18 (=0.44/ha)	0.04	0 – 0.67
Upper mixed conifer	29	0.56 (=1.38/ha)	0.13	0 – 2.02
Spruce-fir	39	0.47 (=1.71/ha)	0.17	0 – 3.37

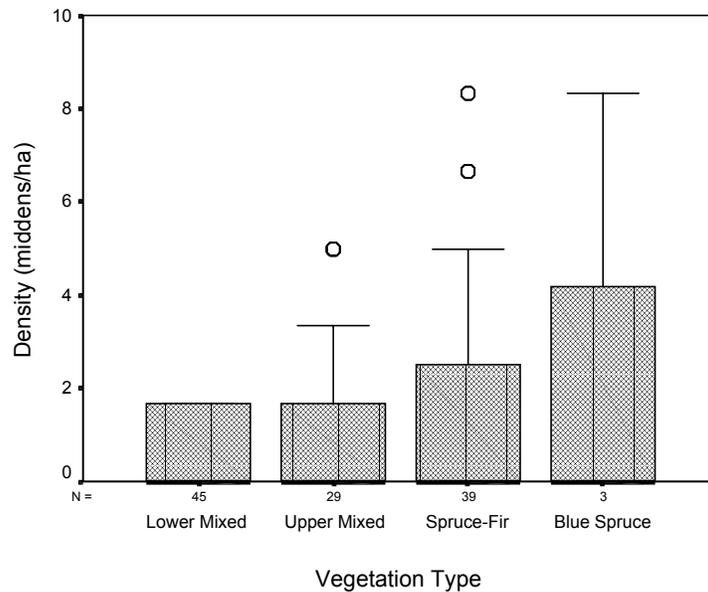


Figure 2. Density of active, primary red squirrel middens in four vegetation types on Carson National Forest in August 2003. Black bars represent medians, boxes represent quartiles, circles represent outliers. To convert from middens per ha to middens per acre, divide displayed density by 2.471.

Based on simple correlations, density of active primary middens exhibited a significant positive correlation with cover type, broad vegetation type, large subalpine fir, and all sizes of Engelmann spruce (Table 6). In contrast, density of active primary middens exhibited a significant negative correlation with white fir, Douglas fir, aspen, and small diameter downed logs (Table 6). In most cases, large numbers of small diameter (< 8 in. diameter) downed logs appeared to be the result of thinning. A multiple regression of density of active primary middens

against all independent variables was not significant ($r = 0.815$, $F = 0.903$, $P = 0.654$). In contrast, stepwise multiple regression produced six highly significant models (Tables 7 and 8). The r^2 change between each model was significant. The single best predictor of midden density was 12-16 in. DBH Engelmann Spruce (Tables 7 and 8). Additional variables that helped to improve the predictive power of the model included 20-24 in. DBH blue spruce, 12-16 in. DBH subalpine fir, 8-12 in. DBH subalpine fir, downed logs < 8 in. diameter, and > 24 in. DBH blue spruce (Table 7 and 8).

Table 6. Significant correlations between density of red squirrel middens and habitat variables.

Independent variable	r_s	P
Cover type	0.257	0.005
Vegetation type	0.204	0.028
Douglas fir		
< 4 DBH	-0.280	0.002
4-8 DBH	-0.230	0.013
8-12 DBH	-0.187	0.045
density	-0.277	0.003
White fir		
< 4 DBH	-0.335	0.000
4-8 DBH	-0.234	0.011
8-12 DBH	-0.314	0.001
density	-0.321	0.000
Subalpine fir		
12-16 DBH	0.245	0.008
Engelmann spruce		
< 4 DBH	0.316	0.001
4-8 DBH	0.288	0.002
8-12 DBH	0.286	0.002
12-16 DBH	0.341	0.000
density	0.318	0.000
Aspen		
4-8 DBH	-0.194	0.037
Downed logs		
< 8 cm diameter	-0.233	0.012

Table 7. Significant ($P < 0.001$) regression models produced through stepwise multiple regression of all independent variables against density of active, primary red squirrel middens on Carson National Forest in August 2003.

Model	r	Predictors ¹	ANOVA F
1	0.380	ES 12-16 DBH	19.279
2	0.440	ES 12-16, BS 20-24	13.575
3	0.484	ES 12-16, BS 20-24, SF 12-16	11.441
4	0.531	ES 12-16, BS 20-24, SF 12-16, SF 8-12	10.895
5	0.566	ES 12-16, BS 20-24, SF 12-16, SF 8-12, logs < 8	10.367
6	0.587	ES 12-16, BS 20-24, SF 12-16, SF 8-12, logs < 8, BS > 24	9.534

¹Letters abbreviations are Engelmann spruce (ES), blue spruce (BS), subalpine fir (SF); numbers are diameter at breast height (in) size classes.

Table 8. Coefficients for significant ($P = 0.000$) regression models produced through stepwise multiple regression of all independent variables against density of active, primary red squirrel middens on Carson National Forest in August 2003. All coefficients are significant ($P < 0.05$).

Model	Variable ¹	Coefficient	SE
1	constant	0.652	0.208
	ES 12-16	0.836	0.190
2	Constant	0.547	0.206
	ES 12-16	0.890	0.187
	BS 20-24	2.786	1.063
3	constant	0.512	0.203
	ES 12-16	0.775	0.189
	BS 20-24	2.821	1.040
	SF 12-16	0.735	0.301
4	constant	0.572	0.198
	ES 12-16	0.814	0.184
	BS 20-24	2.761	1.012
	SF 12-16	1.561	0.423
	SF 8-12	-0.511	0.189
5	constant	1.046	0.271
	ES 12-16	0.759	0.181
	BS 20-24	2.440	0.997
	SF 12-16	1.595	0.414
	SF 8-12	-0.528	0.185
	logs < 8	-0.076	0.031
6	constant	0.992	0.269
	ES 12-16	0.746	0.179
	BS 20-24	2.484	0.985
	SF 12-16	1.600	0.408
	SF 8-12	-0.519	0.182
	logs < 8	-0.071	0.030
	BS > 24	3.334	1.673

¹Variable definitions are in Table 4.

Red squirrel presence/absence.—No evidence of red squirrels was found on 36.2% of the stands sampled. Red squirrel presence varied by Forest Service GIS stand cover type. Blue spruce stands had the highest proportion of stands with red squirrels present, while Douglas fir and white fir cover types had the highest proportion of stands with red squirrels absent (Figure 3). Based on Kolmogorov-Smirnov tests, a total of seven habitat variables were significantly different in stands where red squirrels were absent as compared with stands where red squirrels were present (Table 9). These variables included number of white fir < 4 in. DBH, total number of white fir, number of Engelmann spruce 12-16 in. DBH, total number of trees, percent of white fir in stand, percent of spruce in stand, and number of downed logs < 8 in. diameter. A discriminant function analysis to model the presence or absence of red squirrels in forest stands resulted in the extraction of one canonical axis (eigenvalue= 2.679, canonical correlation = 0.853, Wilks lambda = 0.272, $df = 76$, $P = 0.039$). Variables highly correlated with red squirrel absence included < 8 in. diameter downed logs, 0 - 8 in. DBH white fir, 16-20 in. DBH Douglas fir, slope, and percent of stand white fir. In contrast, variables highly correlated with red squirrel presence included the percent of a stand composed of Engelmann spruce and the number of 12-16 in. DBH Engelmann spruce. A total of 93.1 % of the stands were correctly classified according to red squirrel presence or absence. This indicates that the model was very good at predicting the presence or absence of red squirrels based on habitat characteristics. Errors in classification were more common in stands where squirrels were not detected but were predicted to occur (9.5 %) as compared with stands where squirrels were observed but they were predicted to be absent (5.4 %). This indicates that most classification errors were probably the result of the field crews occasionally missing sign or other evidence of squirrels in some stands.

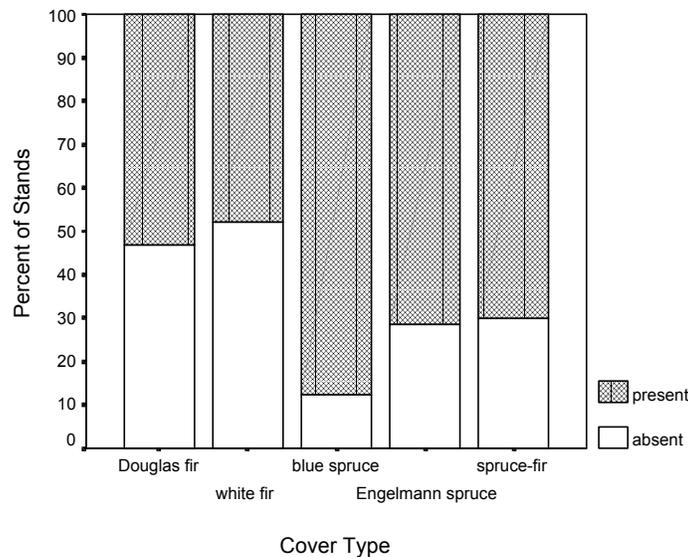


Figure 3. Percent of total stands of each cover type with red squirrels present and absent.

Table 9. Habitat variables that exhibit significant differences in stands where red squirrels were absent in comparison with stands where red squirrels were present on Carson National Forest in August 2003. Significance was determined through two-sample Kolmogorov-Smirnov tests. Densities are presented as means per acre.

	Squirrel Presence		<i>P</i>
	absent	present	
Mean density of white fir < 4 DBH	113.4	46.4	0.003
Mean density of all DBH white fir	201.0	108.2	0.036
Mean density of Engelmann spruce 12-16 DBH	15.5	41.2	0.007
Mean density of all trees	1,257.7	1,103.1	0.034
Mean percent of stand white fir	19.5	11.9	0.058
Mean percent of stand Engelmann spruce	12.7	28.2	0.022
Mean density of downed logs < 8 in diameter	386.6	231.9	0.056

Density Patterns by Cover Type

Habitat features related to red squirrel presence and abundance was investigated within each Forest Service GIS stand cover type. Sample sizes within each Forest Service GIS cover type were low. Consequently, these results should be considered preliminary. Additional study is required to establish the generality of trends reported. Table 1 presents the sample effort within each cover type by Carson National Forest district. Table 4 summarizes red squirrel densities within each Forest Service GIS cover type.

White fir.—For stands classified as white fir, midden density exhibited a significant negative correlation with < 4 in. DBH white fir ($r_s = -0.435$, $P = 0.038$) and 4-8 in. DBH aspen ($r_s = -0.473$, $P = 0.023$); there were no significant positive correlations. Stepwise multiple regression resulted in five significant predictive models for density of active middens. The single best predictor of midden density was 12-16 in. DBH aspen. Additional independent variables included in more complex models included < 4 in. DBH white fir (negative), percent forb ground cover (negative), total number of ponderosa pine (negative; Figure 4), and percent other ground cover (negative). Based on two-sample Kolmogorov-Smirnov tests no habitat variables exhibited significant differences in stands

where red squirrels were absent in comparison with stands where red squirrels were present.

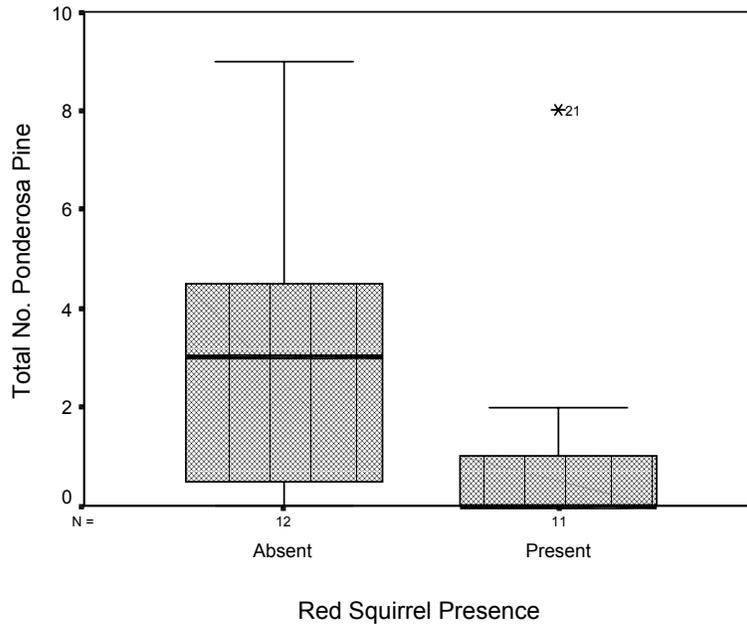


Figure 4. The total number of ponderosa pine in white fir stands where red squirrel are absent or present . Black bars represent medians, boxes represent quartiles, and the asterisk represents an extreme value. Density of ponderosa pine (per acre) of can be calculated by dividing the displayed values by 0.0194.

Douglas fir.—For stands classified as Douglas fir, midden density exhibited a significant positive correlation with > 8 in. diameter snags ($r_s = 0.366$, $P = 0.039$; Figure 5), 8-12 in. DBH aspen ($r_s = 0.376$, $P = 0.034$) and significant negative correlation with < 4 in. DBH white fir ($r_s = -0.386$, $P = 0.029$), and < 4 in. DBH aspen ($r_s = -0.356$, $P = 0.045$). Stepwise multiple regression resulted in seven significant predictive models for density of active middens. The single best predictor of midden density was 8-12 in. DBH aspen, which was a positive coefficient. Additional independent variables included in more complex models included 12-16 in. DBH aspen (negative), percent other ground cover (negative), > 8 in. DBH snags, 16-20 in. DBH Douglas fir (negative), < 4 in. DBH aspen (negative), and total number of trees. Based on two-sample Kolmogorov-Smirnov tests, the number of white fir < 4 in. DBH was the only habitat variable that exhibited a significant difference ($P = 0.016$) in stands where red squirrels were absent in comparison with stands where red squirrels were present (Figure 6).

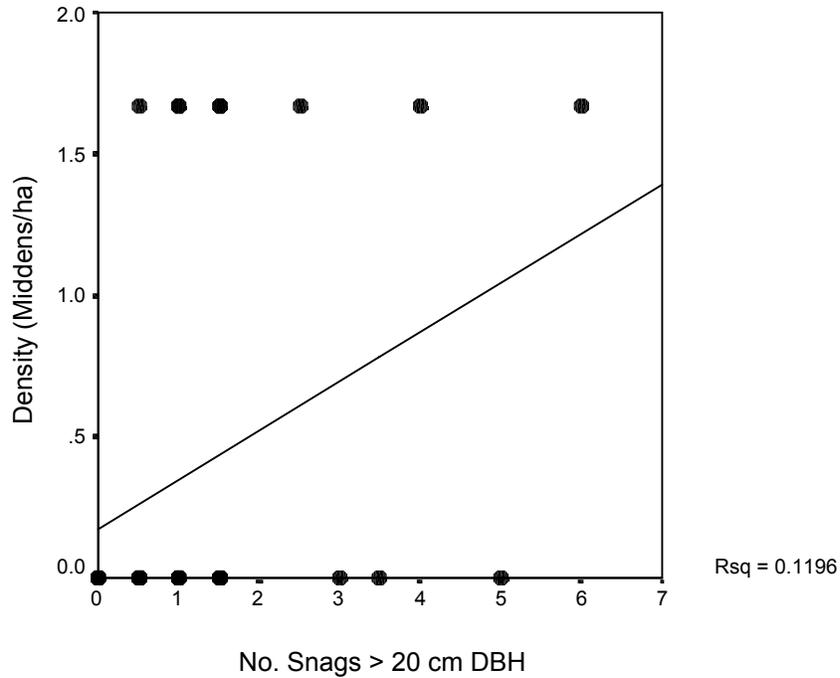


Figure 5. Linear relationship between the number of large diameter (> 8 in [= 20 cm]) snags and red squirrel midden density in stands classified as Douglas fir. To convert from middens per ha to middens per acre, divide displayed density by 2.471.

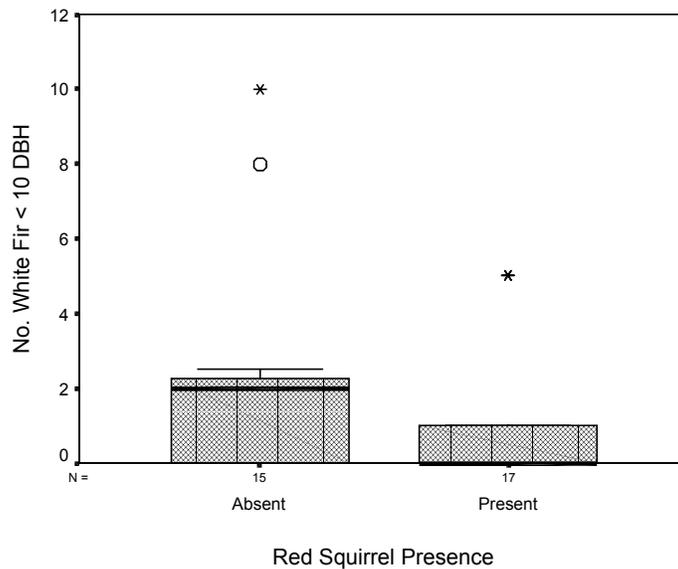


Figure 6. Number of < 4 in (= 10 cm) DBH white fir present in Douglas fir stands where red squirrels were absent and present. Black bars represent medians, boxes represent quartiles, circles represent outliers, and asterisks represent extreme values. Density of white fir (per acre) of can be calculated by dividing the displayed values by 0.0194.

Blue spruce.—For stands classified as blue spruce, the only significant correlation with madden density was with 4-8 in. DBH (=10-20 cm DBH) blue spruce ($r_s = -0.589$, $P = 0.016$), which was negative. A stepwise multiple regression was not possible due to sample size limitations. Based on two-sample Kolmogorov-Smirnov tests, two habitat variables exhibited significant differences in stands where red squirrels were absent in comparison with stands where red squirrels were present, including number of small (4-8 in. DBH) blue spruce and the total number of blue spruce (Figures 7 and 8).

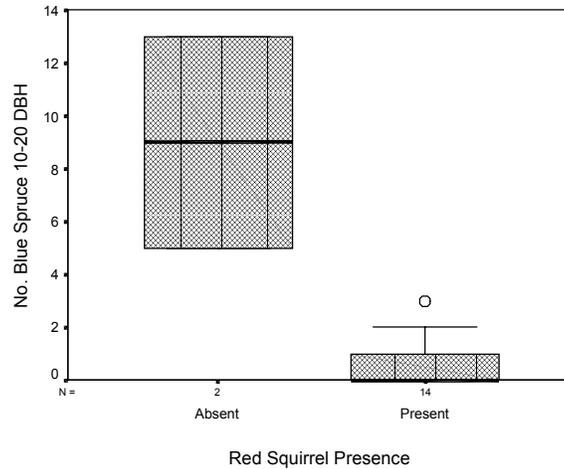


Figure 7. Number of small diameter (4-8 in DBH [=10 – 20 cm DBH]) blue spruce in blue spruce stands where red squirrels are absent and present. Black bars represent medians, boxes represent quartiles, and the circle represents an outlier. Density of blue spruce (per acre) of can be calculated by dividing the displayed values by 0.0194.

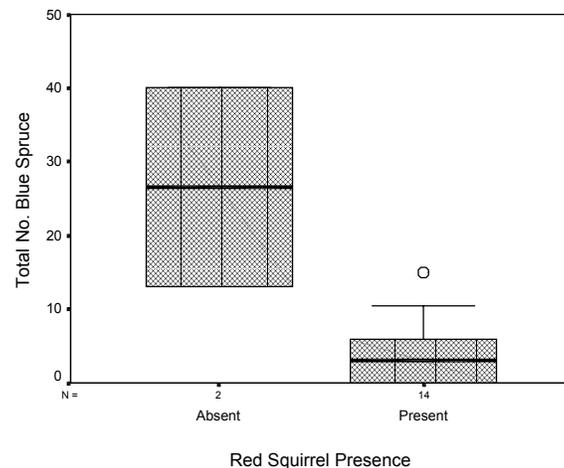


Figure 8. The total number of blue spruce in blue spruce stands where red squirrels are absent and present. Black bars represent medians, boxes represent quartiles, and the circle represents an outliers. Density of blue spruce (per acre) of can be calculated by dividing the displayed values by 0.0194.

Engelmann spruce.—For stands classified as Engelmann spruce, midden density exhibited a significant positive correlation with percent grass ground cover ($r_s = 0.760$, $P = 0.002$) and a significant negative correlation with elevation ($r_s = -0.568$, $P = 0.034$; Figure 9). Stepwise multiple regression resulted in nine significant predictive models for density of active middens. The single best predictor of midden density was percent grass ground cover. This result should be evaluated with extreme caution because it suggests habitat characteristics that conflict with known habitat requirements for this species (i.e., dense canopy cover with little ground cover). Future studies should be designed to specifically address this relationship. Additional independent variables included in more complex models included 20-24 in. DBH white fir (negative), 4-8 in. DBH subalpine fir, 4-8 in. DBH white fir, percent other ground cover, 8-12 in. DBH subalpine fir, total number of Engelmann spruce (negative), < 4 in. DBH aspen (negative), and percent litter ground cover. Based on two-sample Kolmogorov-Smirnov tests two habitat variables exhibited significant differences in stands where red squirrels were absent in comparison with stands where red squirrels were present, including percent litter ground cover ($P = 0.080$; Figure 10) and number of Engelmann spruce 16-20 in. DBH ($P = 0.080$; Figure 11).

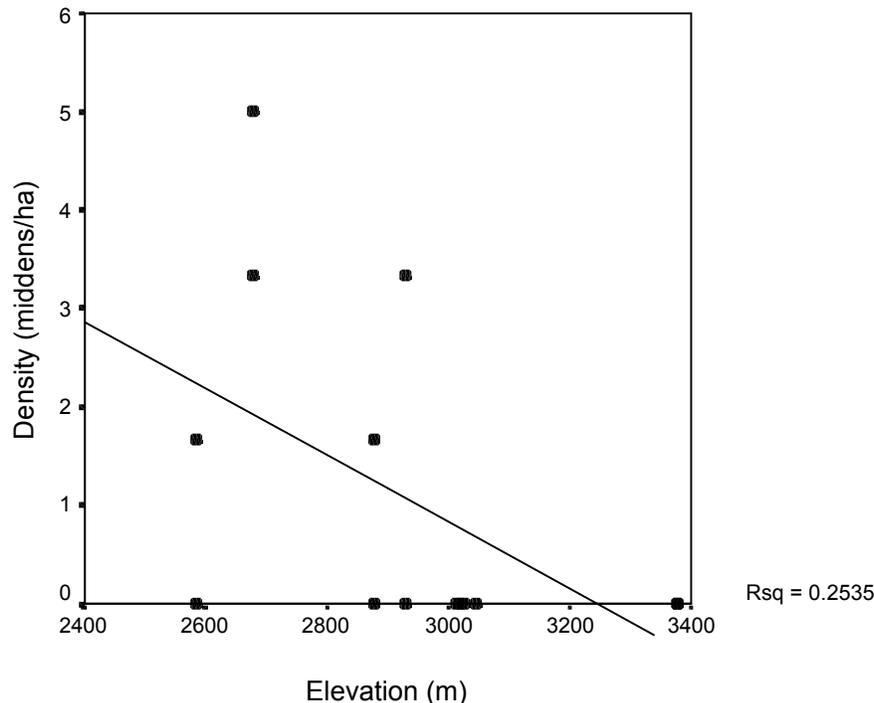


Figure 9. Linear relationship between elevation and red squirrel midden density in Engelmann spruce stands on Carson National Forest in August 2003. To convert from middens per ha to middens per acre, divide displayed density by 2.471. Elevation can be converted to feet by multiplying meters by 3.28.

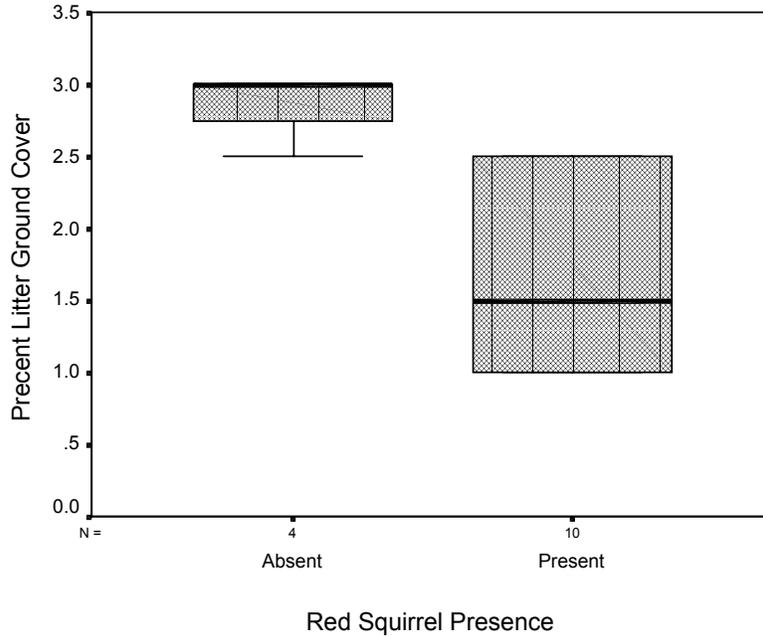


Figure 10. Litter ground cover in Engelmann spruce stands where red squirrels are absent and present. Black bars represent medians and boxes represent quartiles. Ground cover classes have the following percentage equivalents: 1 = 0 - 5%, 2 = 5 - 25%, 3 = 25 - 50 %, 4 = 50 - 75%, 5 = 75 - 95%, and 6 = 95 - 100% grass cover.

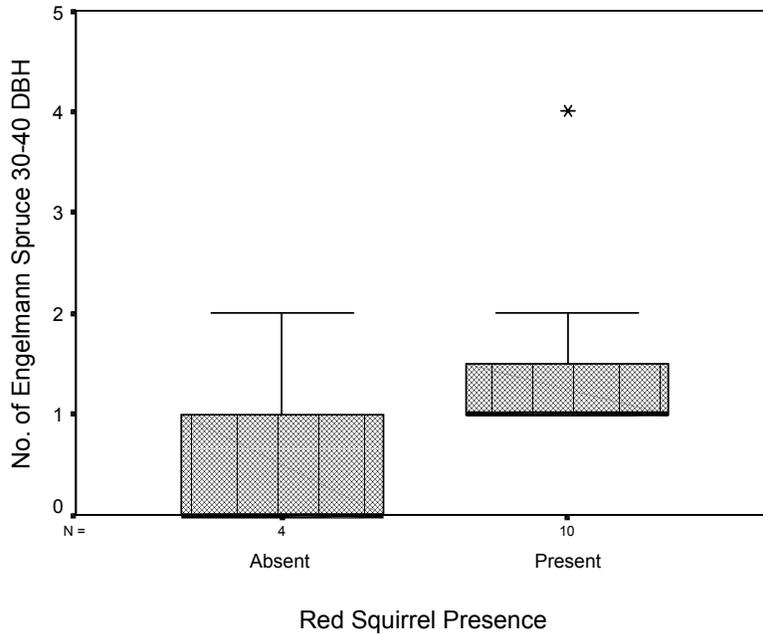


Figure 11. The number of large diameter (12-16 in DBH [= 30-40 cm DBH]) Engelmann spruce in Engelmann spruce stands where red squirrels are absent and present. Black bars represent medians, boxes represent quartiles, and the asterisk represents an extreme value. Density of Engelmann spruce (per acre) of can be calculated by dividing the displayed values by 0.0194.

Engelmann spruce-Subalpine fir.—For stands classified as spruce-fir, midden density exhibited a significant positive correlation with 12-16 in. DBH subalpine fir ($r_s = 0.458$, $P = 0.011$), 16-20 in. DBH subalpine fir ($r_s = 0.373$, $P = 0.042$), 12-16 in. DBH Engelmann spruce ($r_s = 0.428$, $P = 0.018$), and percent Engelmann spruce in stand ($r_s = 0.441$, $P = 0.015$). There was a significant negative correlation with percent grass ground cover ($r_s = -0.477$, $P = 0.008$), percent aspen in stand ($r_s = -0.365$, $P = 0.047$), and < 8 in. diameter downed logs ($r_s = -0.403$, $P = 0.027$). Stepwise multiple regression resulted in two significant models. The simplest model only included 12-16 in. DBH Engelmann spruce as a predictor of midden density ($r = 0.459$, $P = 0.011$, MD = $0.384 + 1.590[12-16 \text{ DBH ES}]$). Within these stands, the majority (79.9%) of spruce were less than 12 in. DBH; only 7.9 % of spruce trees were larger than 16 in. DBH. The second model included the addition of slope to the model ($r = 0.575$, $P = 0.004$, MD = $-1.047 + 1.597 [12-16 \text{ in. DBH ES}] + 0.118[\text{slope}]$). Based on two-sample Kolmogorov-Smirnov tests only the total number of trees exhibited a significant difference ($P = 0.051$) in stands where red squirrels were absent in comparison with stands where red squirrels were present (Figure 12).

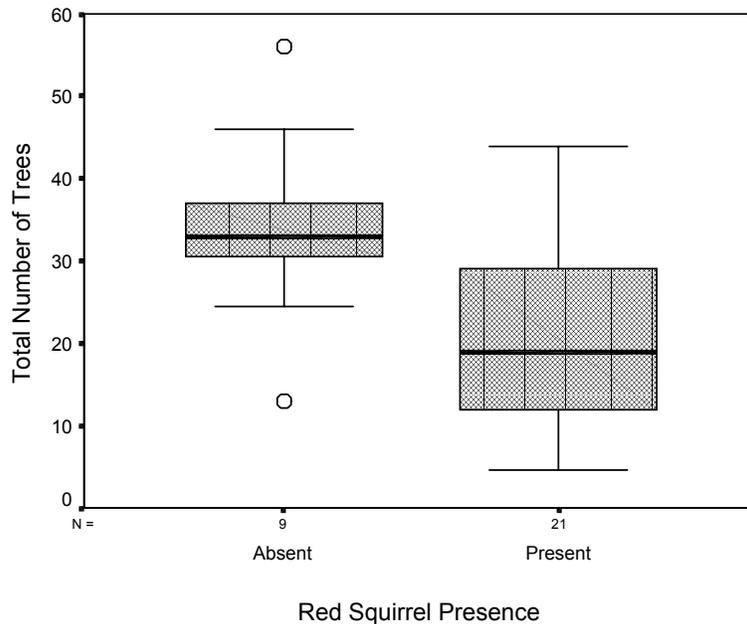


Figure 12. The total number of trees in spruce-fir stands where red squirrels are absent and present. Black bars represent medians, boxes represent quartiles, and the circles represent outliers. Density of trees (per acre) of can be calculated by dividing the displayed values by 0.0194.

Inactive Middens

Density of inactive primary middens varied from 0 - 0.146 per acre (= 0 - 3.33 per hectare) with a mean of 0.07 per acre (= 0.17 per ha; Table 10). Density of inactive primary middens did not vary significantly by Forest Service GIS stand cover type (Kruskal-Wallis nonparametric test $P = 0.865$, $df = 5$, $\chi^2 = 1.884$) or general vegetation type (Kruskal-Wallis nonparametric test $P = 0.671$, $df = 5$, $\chi^2 = 1.551$). There was no significant correlation between the percentage of each cover type sampled and the density of inactive middens ($r_s = 0.638$, $P = 0.173$). However, there was a highly significant correlation between the percentage of each cover type sampled and the percentage of inactive middens ($r_s = 0.986$, $P = 0.000$).

Table 10. Occurrence of inactive primary middens in different cover types on Carson National Forest in August 2003.

Forest Service cover type	Cover type		Inactive middens		
	No. stands	Percent surveyed	Density middens/ha	SE	Percent of middens
Douglas fir	32	27.6	0.126 (=0.312/ha)	0.047	30.0
White fir	23	19.8	0.146 (=0.362)	0.059	25.0
Blue spruce	16	13.8	0.126 (=0.312/ha)	0.092	15.0
Engelmann spruce	14	12.1	0.048 (=0.119/ha)	0.048	5.0
Spruce-fir	30	25.9	0.112 (=0.278/ha)	0.057	25.0
Aspen	1	0.9	0	0	0.0

Discussion

Forest-wide Patterns

Based on midden counts, red squirrel densities on Carson National Forest in August 2003 were within the range of variation found in other studies. Table 11 presents a summary of red squirrel densities found during other selected studies in other habitats and geographic regions. Most previous studies have reported relatively low red squirrel densities (e.g., < 1.0 per hectare; = < 0.4 per acre). These compare with the relatively low densities of red squirrels found in white fir and Douglas fir stands on Carson National Forest during this study. However, the mean density of red squirrels in the more favored spruce-fir and blue spruce stands on Carson National Forest were as high, or higher, than the maximum density reported in most previous studies. When the range of variation in density is considered, the density found in some spruce-fir and blue spruce stands on Carson National Forest (i.e., 8.33/ha; = 3.37/acre; see Table 4) greatly exceeded the maximum density reported in Table 11 (i.e., 6.8/ha in Alberta spruce).

This study was somewhat unique in the geographic coverage and habitat variation included. Most previous studies were conducted in single habitat types. Consequently, this study provides unique and important data on the relationship between different habitat types and red squirrel densities. Anecdotal and empirical evidence has suggested that red squirrel densities are highest in habitats dominated by spruce (*Picea* spp.). The reason for this is thought to be because spruce trees generally produce large numbers of highly nutritious cones that can be stored efficiently. Several results of this study confirm those previous observations. First, mean midden density was highest in the three cover types where spruce was dominant (blue spruce, Engelmann spruce, spruce-fir; Table 4) and lowest in cover types where spruce was absent or a minor component (Douglas fir, white fir; Table 4). Similarly, across all transects, red squirrel midden density increased with increasing numbers of Engelmann spruce, but decreased with increasing numbers of Douglas fir and white fir (Table 6). Finally, the single best predictor of red squirrel midden density was large diameter (12-16 in. DBH [= 30-40 cm]) Engelmann spruce, even though trees of this large size were relatively uncommon.

Within the cover types dominated by spruce, red squirrel midden densities were higher in blue spruce and spruce-fir cover types as compared to Engelmann spruce (Table 4). This may be a function of higher moisture availability, which promotes cone and fungi production as well as cone storage. Engelmann spruce is a dominant component of most subalpine forest habitat series (Dick-Peddie 1993). The Engelmann spruce-subalpine fir forests series is typical of mid-elevations in the subalpine zone (Dick-Peddie 1993). Relative to both higher and lower subalpine forests that have Engelmann spruce as a dominant tree, spruce-fir forests generally have higher mean annual precipitation and snow blown from higher elevations often accumulates in these regions (Dick-

Peddie 1993). Although blue spruce may occur in a variety of situations in the upper montane coniferous forest zone, this tree typically grows in riparian situations at mid elevations where soils are well watered throughout the year (Dick-Peddie 1993).

Table 11. Comparison of red squirrel densities reported in previous studies with those observed on Carson National Forest in August 2003. To convert values to density per acre, divide value by 2.471.

Location	Habitat	Density (per ha)	Reference
Western North America			
Alberta	aspen	0.05 - 0.1	Kemp and Keith 1970
Alberta	spruce	1.6 - 6.8	Rusch and Reeder 1978
	jack pine	0.9 - 2.6	
	aspen	0 - 1.0	
Alaska	white/black spruce	1.2 - 1.6	Wolff and Zasada 1975
	shelterwood	0.5	
	clearcut	0	
Alaska	white spruce after 2 cone failure	0.6 - 0.8 0.2	Smith 1968
Arizona, Mt. Graham	spruce-fir	0.05 - 1.0	Young et al. 1999
	mixed	0.1 - 1.4	
Arizona, Mt. Graham	spruce-fir	0.31	Spicer et al. 1985
	mixed	0.02	
Arizona, west-central	mixed	1.0 - 2.5	Vahle and Patton 1983
British Columbia		1.1 - 2.0	Smith 1965
Colorado	lodgepole pine	0.1	Gurnell 1984
Montana	mixed conifers	0.8 - 2.0	Halvorson 1965
New Mexico	Douglas fir	0.4	current study
	white fir	0.4	
	blue spruce	2.4	
	Engelmann spruce	1.1	
	spruce-fir	2.0	
Eastern North America			
New Brunswick	spruce	2.5	Klugh 1927
New York	spruce	1.1	Fitzwater 1941
multiple studies	various	0.1 - 2.5	cited in Rusch and Reeder 1978

Stands where squirrels were absent had significantly higher numbers of sapling white fir (< 4 in. DBH [= 10 cm]), total numbers of white fir, percent of white fir in stand, total number of trees of all species, and numbers of small diameter downed logs (< 8 in. diameter [= < 20 cm]; Table 9). This indicates that white fir stands are particularly poor habitat for red squirrels. Further, this evidence suggests that forests with high tree density, such as those dominated by dense stands of small diameter trees, are avoided. One management technique for these forests is to thin small diameter trees. However, stands where thinning has occurred (as evidenced by a high density of small diameter downed logs) were also avoided. In contrast, stands with higher numbers of large diameter (12-16 in. DBH [=30-40 cm]) Engelmann spruce and with a higher percentage of spruce in the stand were more likely to have squirrels present (Table 9). These univariate results were reflected in the discriminant function model. Habitat variables highly associated with an absence of red squirrels included the numbers of small diameter white fir, the percent stand composition of white fir, and the number of large diameter Douglas fir. In contrast, variables highly associated with the presence of red squirrels included the relative proportion of Engelmann spruce in a stand as well as more specifically the numbers of large diameter (12-16 in. DBH [= 30-40 cm]) Engelmann spruce.

Patterns within Specific Cover Types

White fir.—Factors influencing the density of red squirrels differed in various stand cover types. White fir stands had the lowest density of red squirrel middens and highest proportion of stands without red squirrel (Figure 1 and 3). Within these stands red squirrels were more likely to occur in stands where ponderosa pine did not occur (Figure 4). Ponderosa pines require relatively warm temperatures. Thus, this suggests that red squirrel preferentially occupy higher elevations and colder sites in white fir cover types. Second, within stands classified as white fir, there was a negative relationship between midden density and the number of sapling (< 4 in. DBH [= 10 cm]) white fir and aspen. Both of these factors suggest an early successional stage forest. Aspen is an important seral tree in most Southwestern mixed conifer and boreal forest (Dick-Peddie 1993). Forests dominated by deciduous trees, including aspen, are poor red squirrel habitat. Resident squirrels in quality conifer forest habitats are highly territorial and do not allow young squirrels to establish home ranges within their defended territory. Thus, when young red squirrel leave the maternal territory, they are often forced to live in suboptimal habitats. Rusch and Reeder (1978) concluded that deciduous forests were primarily occupied by young animals and that survival rates were relatively low.

Douglas fir.—A similar pattern was observed in stands classified as Douglas fir cover type. In this cover type, midden density decreased with increasing numbers of sapling white fir and aspen. As in the white fir cover type, the abundance of these small diameter trees suggests an early serial stage. In

contrast, an increasing number of large snags (> 8 in. DBH [= 20 cm]) was associated with higher midden density. When available, red squirrels will use hollow snags for nest sites. The best predictor of midden density was the number of moderate sized (8-12 in. DBH [= 20-30 cm]) aspen in a stand. The reason for this pattern is not clear and may be a spurious result. The spurious nature of this result is supported by the fact that the large number of both smaller (< 4 in. DBH) and larger (12-16 in. DBH) aspen was associated with stands where red squirrels were absent.

Blue spruce.—In stands classified as blue spruce, midden density and presence of squirrels was negatively related to the number of blue spruce trees. Stands with large numbers of spruce, especially small diameter (8-12 in. DBH [= 10-20 cm]) blue spruce, had fewer squirrels. Again, this suggests that even in a preferred habitat type such as blue spruce, stands with dense small diameter trees are unfavorable. A major reason for this likely is due to limited cone production in young trees.

Engelmann spruce.—In stands classified as Engelmann spruce, midden density increased with increasing percent grass ground cover. At greater than 50 % grass cover, midden density was typically greater than 1.2 per acre (= 3 per hectare), a high density in comparison with other habitats (Table 11). Based on the relatively high r^2 value, this was one of the strongest relationships observed in this study. This result contradicts other studies that have suggested that red squirrels prefer conifer forests with little herbaceous ground cover. The rationale for this conclusion is that red squirrels require cool, moist places for cone storage. Thus, it has been suggested that factors that open the canopy cover to allow solar radiation to penetrate to the forest floor would result in warming and drying that would decrease cone storage and possibly fungus production. It is likely that such openings would also promote grass growth. Canopy cover was not a significant predictor of red squirrel midden density in any analysis. The reason for the pattern observed in this study cannot be determined with available data. It should also be noted that there was a relatively small sample of Engelmann spruce stands. Additional studies will be required to fully understand this pattern.

In the Engelmann spruce cover type, red squirrels tended to be absent from stands that had a high percent of litter ground cover. The relationship with litter ground cover is likely related to the opposite relation between grass cover and midden density. However, this pattern does support the idea that ground cover conditions reflect suitability of these stands for red squirrel. Finally, red squirrel tended to be absent from stands that had few or no large diameter (12-16 in. DBH [= 30-40 cm]) Engelmann spruce.

Engelmann spruce-subalpine fir.—In spruce-fir stands, red squirrel midden densities were highest in stands with large numbers of large diameter Engelmann spruce (12-16 in. DBH [= 30-40 cm]) and subalpine fir (12-20 in. DBH [= 30-50 cm]) and a high percent of Engelmann spruce in the stand.

However, as observed in other cover types, red squirrel tended to be absent in stands with large numbers of trees. Both these observations indicate the importance of mature forest for maintaining high red squirrel densities. In contrast with the Engelmann spruce cover type, the density of red squirrel middens decreased with increasing grass cover. This result is more consistent with observations of other studies that indicate a dark forest with little ground cover is favored by this squirrel. The percent aspen in the stand and numbers of downed small diameter logs were also associated with lower densities of red squirrel middens. Aspen is a seral species and their presence indicates openings in the forest canopy. On most study areas, a large number of small diameter downed logs usually appeared to have resulted from relatively recent forest thinning (e.g., based on the presence of stumps and cut ends of logs).

Conclusions

Red squirrel midden densities observed on Carson National Forest in August 2003 were within the range of variation reported in other locations and habitats. Red squirrel densities in some blue spruce and spruce-fir stands were among some of the highest reported in this species. Although extrinsic factors such as climate and logging are known to effect red squirrel populations, evidence suggests that red squirrel populations may be more stable than other species such as Abert's squirrel. This is due to the extreme territorialism of the species. Each squirrel maintains and guards a territory that generally can provide enough stored food resource in the midden to last through a food production shortage. This behavior regulates both home range size and densities such that smaller home ranges and higher densities occur in locations with higher food resource.

Results indicated a habitat preference for stands dominated by spruce (i.e., blue spruce, Engelmann spruce, spruce-fir). Lower elevation mixed conifer stands (i.e., dominated by Douglas fir or white fir) were relatively unfavorable and had substantially lower red squirrel densities. The habitat preference is because spruce cones provide a highly nutritious and accessible food source that can be stored. In addition to the preference for stands dominated by spruce, results indicate that red squirrels favored stands with larger (e.g., > 12 in. DBH) trees, even though these were uncommon in most stands. Red squirrels generally avoided stands that contained large numbers of small diameter (e.g., < 8 in. DBH [= 20 cm]) trees, even in favored habitat types such as blue spruce (e.g., Fig. 8). The reason for this is likely because larger trees are at a maturity with maximal cone production. Specific habitat parameters often were found to be related to red squirrel density or occurrence in the various cover types. While these patterns may be indicative of general factors that influence red squirrel occurrence, it should be recognized that sample sizes were typically small or modest. Additional studies can help refine habitat relationship patterns in order to better direct forest management in ways that will benefit this species.

Recommendations

- 1) Annual midden density monitoring of red squirrel should continue long-term.
- 2) Annual midden density monitoring of red squirrels should include all or a consistent subset of the stands monitored in 2003. This will provide a control for inter-stand variation.
- 3) In order to preserve the comparability of year-to-year samples, subsequent monitoring methodology should conform to that used in 2003.
- 4) Additional studies should be implemented to better address habitat relations of red squirrels in specific stand cover types.
- 5) Additional studies should be implemented that address the impacts of specific forest management strategies.
- 6) Long-term data on conifer cone/seed and fungal production should be conducted in conjunction with red squirrel monitoring.

Acknowledgments

Thanks to Deanna Williams and Chirre Keckler for facilitating this project and to Jeffery Muehleck for GIS support. Stace Walker provided information on the Jicarilla District. Tim Snow provided information on Mount Graham red squirrel monitoring protocols and Bob Vahle provided important advice about sampling red squirrels. I am especially grateful for the hard work of the primary field crewmembers, Andrew Hope and Jason Malaney. The efficiency and quality of the field data collection was largely due to their efforts.

References

- Arbogast, B. S., R. A. Browne, and P. D. Weigl. 2001. Evolutionary genetics and Pleistocene biogeography of North American tree squirrels (*Tamiasciurus*). *Journal of Mammalogy*, 82:302-319.
- Armstrong, D. M. 1972. Distribution of mammals in Colorado. Monograph of the Museum of Natural History, University of Kansas, 3:1-415.
- Bailey, V. 1931 (=1932). Mammals of New Mexico. *N. Am. Fauna*, 53:1-412.
- Brown, D.E. 1984. Arizona's tree squirrels. Arizona Game and Fish Department, Phoenix, 114 pp.
- Brown, D.E. 1994. Biotic Communities: southwestern United States and northwestern Mexico. Univ. Utah Press, Salt Lake City, 342 pp.
- Dick-Peddie, W.A. 1993. New Mexico vegetation past present and future. University of New Mexico Press, Albuquerque, 244 pp.
- Ferner, J.W. 1974. Habitat relationships of *Tamiasciurus hudsonicus* and *Sciurus aberti* in the Rocky Mountains. *The Southwestern Naturalist*, 18:470-473.
- Findley, J.S. 1961. Geographic variation in New Mexican chickarees. *Journal of Mammalogy*, 42:313-322.
- Findley, J. S., A. H. Harris, D. E. Wilson, and C. Jones. 1975. Mammals of New Mexico. Univ. New Mexico Press, Albuquerque, 360 pp.
- Finley, R.B. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. University of Kansas, Museum of Natural History, Miscellaneous Publications, 51:233-273.
- Fitzgerald, J.P., C.A. Meaney, and D.M. Armstrong. 1994. Mammals of Colorado. University Press of Colorado, Niwot, CO. 467 pp.
- Flyger, V. and J. E. Gates. 1982. Pine squirrels *Tamiasciurus hudsonicus* and *T. douglasii*. Pages 230-238 in (J.A. Chapman and G. A. Feldhamer, editors) *Wild mammals of North America: biology, management, and economics*. The Johns Hopkins University Press, Baltimore.
- Fredrick, T., R. Sanderson, M. McCluhan, M. Pruss and T. Snow. 2003. Mount Graham red squirrel survey manual. Nongame and Endangered Wildlife Program, Arizona Game and Fish Department, 12 pp.
- Gurnell, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in subalpine lodgepole pine forest. *Animal Behaviour*, 32:1119-1131.
- Hall, E.R. 1981. *The mammals of North America*. Second Edition. Reprinted in 2001 by Blackburn Press, Caldwell, New Jersey.
- Hatt, R.T. 1943. The pine squirrel of Colorado. *Journal of Mammalogy*, 24:311-345.
- Kemp, G.A., and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. *Ecology*, 51:763-779.
- Kilham, L. 1954. Territorial behaviour of red squirrel. *Journal of Mammalogy*, 35:252-253.

- Koford, R.R. 1992. Does supplemental feeding of red squirrels change population density, movements, of both? *Journal of Mammalogy*, 73:930-932.
- Linday, S.L. 1987. Geographic size and non-size variation in rocky Mountain *Tamiasciurus hudsonicus*: significance in relation to Allen's rule and vicariant biogeography. *Journal of Mammalogy*, 68:39-48
- Rusch, D.A. and W.G. Reeder. 1978. Population ecology of Alberta red squirrels. *Ecology*, 59:400-420.
- Shaw, W.T. 1936. Moisture and its relation to the cone-storing habit of the western pine squirrel. *Journal of Mammalogy*, 17:337-349.
- Smith, A.A., and R.W. Mannan. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. *Journal of Wildlife Management*, 58:437-445.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. *Ecological Monographs*, 38:31-63.
- Smith, C.C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs*, 40:349-371.
- Smith, C. C. and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, 15:329-351.
- Smith, M.C. 1968. Red squirrel responses to spruce cone failure. *The Journal of Wildlife Management*, 32:305-316.
- Spicer, R. B., J. C. deVos, R. L. Glinski. 1985. Status of the Mount Graham red squirrel *Tamiasciurus hudsonicus grahamensis* (Allen), of southeastern Arizona. Final Report for the Office of Endangered Species, US Fish and Wildlife Service, 48 pp.
- Steele, M.A. 1998. *Tamiasciurus hudsonicus*. *Mammalian Species*, 586:1-9.
- Sun, Chin. 1997. Dispersal of young red squirrels (*Tamiasciurus hudsonicus*). *The American Midland Naturalist*, 138:252-259.
- Vahle, J.R., and D.R. Patton. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. *Journal of Forestry*, 81:14-15.
- Wilson, D.E., and F.R. Cole. 2000. Common names of mammals of the world. Smithsonian Institution Press, Washington, DC.
- Wolff, J. O. and J. C. Zasada. 1975. Red squirrel response to clearcut and shelterwood systems in interior Alaska. Pacific Northwest Forest and Range Experience Station, USDA Forest Service Research Note PNW-255:1-7.
- Yeager, L.E. 1937. Cone piling by the Michigan red squirrel. *Journal of Mammalogy*, 18:191-194.
- Young, P.J., V.L. Greer, J.E. Lowry, E. Bibles, N. Ferguson, and E. Point. 1999. The Mount Graham red squirrel monitoring program: 1989-1998. unpublished report, University of Arizona, 148 pp.

Appendix 1

Monitoring Effort and Logistics

Two field crewmembers were able to complete 58 monitoring sites (= 116 transects) in 13 days, not including travel to and from Carson National Forest. This included part of a training period, which involved a total of three field crewmembers during the first two days of fieldwork. Additional training was conducted prior to the initiation of fieldwork. The number of transects completed per day ranged from 1 to 16 with an average of 8.9 transects completed per day. This should be considered a highly efficient rate. The field crewmembers in this study had extensive prior field experience in rugged, forested terrain and were comfortable working alone. Consequently, a major reason for the fast completion rate was because most transects were sampled by a single field crewmember. In future monitoring, safety and other considerations may necessitate that field crewmembers work in teams. This would significantly reduce the rate at which monitoring transects could be sampled. Other major reasons for the study efficiency was because field crewmembers camped near monitoring areas, worked long hours (typically at least 10 –12 hours per day) and in very inclement weather, and were physically fit and able to negotiate rugged terrain at high elevations. Several factors limited the speed by which sampling could be conducted. Fewer transects could be completed on days with longer drive times among sites or on days that required breaking camp and traveling to new monitoring areas. Another major factor that impeded work was inclement weather. The timing of the monitoring coincided with the onset of the monsoon season, which resulted in rain showers virtually every afternoon. Extreme weather conditions (especially due to lightening) resulted in delays. Relative to Abert's squirrel monitoring, red squirrel monitoring is extremely demanding on the field crew. Terrain was generally very rugged, elevation was high, and weather was often bad.

Appendix II. Transect locations, cover types, and density of active, primary middens sampled on Carson National Forest in August 2003. Latitude and longitude are in decimals of the degree (i.e., site 1a is N 36° 40.445', W 106° 8.689').

site No.	NF District	site No.	Start Latitude	Start Longitude	bearing	Cover type	Midden Density
1a	Tres Piedras	1a	36.40.445	106.08.689	226	DF	0
1b	Tres Piedras	1b	36.39.976	106.09.145	32	DF	0
2a	Tres Piedras	2a	36.62.319	106.11.881	90	DF	1.67
2b	Tres Piedras	2b	36.42.319	106.11.881	270	DF	0
3a	Tres Piedras	3a	36.38.435	106.08.428	270	DF	1.67
3b	Tres Piedras	3b	36.38.435	106.08.428	180	DF	0
4a	Tres Piedras	4a	36.40.958	106.12.872	108	ES	0
4b	Tres Piedras	4b	36.40.892	106.12.501	310	ES	0
5a	Tres Piedras	5a	36.39.591	106.09.508	270	S/F	0
5b	Tres Piedras	5b	36.39.656	106.09.459	270	S/F	0
6a	Tres Piedras	6a	36.39.568	106.12.429	270	BS	3.33
6b	Tres Piedras	6b	36.39.568	106.12.429	240	BS	0
7a	Tres Piedras	7a	36.39.872	106.09.397	30	WF	0
7b	Tres Piedras	7b	36.39.822	106.09.397	180	WF	0
8a	Canjilon	8a	36.36.327	106.22.664	110	WF	0
8b	Canjilon	8b	36.36.327	106.22.664	132	WF	1.67
9a	Canjilon	9a	36.36.145	106.23.574	110	WF	0
9b	Canjilon	9b	36.36.060	106.23.620	110	AA	0
10a	Canjilon	10a	36.33.675	106.23.404	0	DF	0
10b	Canjilon	10b	36.33.675	106.23.404	45	DF	0
11a	Canjilon	11a	36.33.395	106.23.726	270	DF	0
11b	Canjilon	11b	36.33.395	106.23.726	315	DF	0
12a	Canjilon	12a	36.34.005	106.20.180	350	SF	1.67
12b	Canjilon	12b	36.33.985	106.20.122	350	SF	8.33
13a	Canjilon	13a	36.34.368	106.20.176	90	SF	6.67
13b	Canjilon	13b	36.34.307	106.20.122	30	SF	5
14a	El Rito	14a	36.28.366	106.17.047	310	WF	1.67
14b	El Rito	14b	36.28.366	106.17.047	0	WF	0
15A	El Rito	15A	36.28.239	106.17.023	270	ES	5
15b	El Rito	15b	36.28.239	106.17.023	90	ES	3.33
16a	El Rito	16a	36.31.854	106.13.991	0	DF	1.67
16b	El Rito	16b	36.31.854	106.13.991	40	DF	1.67
17a	El Rito	17a	36.32.218	106.14.044	270	S/F	0
17b	El Rito	17b	36.32.161	106.14.063	270	S/F	1.67
18a	El Rito	18a	36.30.366	106.14.914	0	DF	0

site No.	NF District	site No.	Start Latitude	Start Longitude	bearing	Cover type	Midden Density
18b	El Rito	18b	36.30.366	106.14.914	310	DF	0
19a	El Rito	19a	36.28.590	106.13.865	50	WF	0
19b	El Rito	19b	36.28.579	106.13.865	90	WF	0
20a	El Rito	20a	36.28.459	106.13.824	90	WF	1.67
20b	El Rito	20b	36.28.459	106.13.626	140	WF	0
21a	El Rito	21a	36.32.545	106.14.369	290	BS	0
21b	El Rito	21b	36.32.545	106.14.369	310	BS	0
22a	El Rito	22a	36.30.212	106.12.952	60	DF	1.67
22b	El Rito	22b	36.30.285	106.12.929	60	DF	1.67
23a	El Rito	23a	36.30.704	106.12.677	290	S/F	1.67
23b	El Rito	23b	36.30.704	106.12.677	80	S/F	0
24a	Camino Real	24a	36.03.181	105.28.776	70	S/F	1.67
24b	Camino Real	24b	36.03.154	105.28.657	100	S/F	0
25a	Camino Real	25a	36.03.320	105.29.938	0	S/F	0
25b	Camino Real	25b	36.03.320	105.29.938	180	S/F	0
26a	Camino Real	26a	36.08.875	105.32.546	190	WF	0
26b	Camino Real	26b	36.08.875	105.32.546	240	WF	0
27a	Camino Real	27a	36.07.885	105.32.309	80	DF	0
27b	Camino Real	27b	36.07.916	105.32.281	80	DF	1.67
28a	Camino Real	28a	36.17.535	105.22.596	280	ES	0
28b	Camino Real	28b	36.17.535	103.22.596	120	ES	1.67
29a	Camino Real	29a	36.18.598	105.19.126	120	ES	0
29b	Camino Real	29b	36.18.552	105.19.094	120	ES	0
30a	Camino Real	30a	36.08.002	105.31.553	170	ES	0
30b	Camino Real	30b	36.08.002	105.31.553	140	ES	1.67
31a	Camino Real	31a	36.17.104	105.19.490	0	S/F	0
31b	Camino Real	31b	36.17.061	105.19.422	0	S/F	0
32a	Camino Real	32a	36.18.979	105.19.099	320	DF	0
32b	Camino Real	32b	36.18.979	105.19.099	340	DF	0
33a	Camino Real	33a	36.18.756	105.25.666	250	BS	1.67
33b	Camino Real	33b	36.18.756	105.25.66	90	BS	5
34a	Camino Real	34a	36.18.838	105.27.490	250	BS	0
34b	Camino Real	34b	36.18.838	105.27.490	100	BS	0
35A	Camino Real	35a	36.21.928	105.23.626	30	BS	5
35b	Camino Real	35b	36.22.043	105.23.142	320	BS	1.67
36a	Camino Real	36a	36.21.850	105.24.594	40	DF	0
36b	Camino Real	36b	36.21.850	105.24.594	70	DF	0
37a	Camino Real	37a	36.19.886	105.24.576	20	DF	0
37b	Camino Real	37b	36.19.886	105.24.576	40	DF	0
38a	Camino Real	38a	36.25.493	105.20.432	350	BS	5
38b	Camino Real	38b	36.25.492	105.20.432	190	BS	8.33

site No.	NF District	site No.	Start Latitude	Start Longitude	bearing	Cover type	Midden Density
39a	Camino Real	39a	36.18.769	105.25.666	330	WF	0
39b	Camino Real	39b	36.18.769	105.25.666	280	WF	0
40a	Camino Real	40a	36.16.338	105.19.298	120	S/F	0
40b	Camino Real	40b	36.16.289	105.19.308	120	S/F	0
41a	Camino Real	41a	36.13.141	105.29.665	270	WF	0
41b	Camino Real	41b	36.13.141	105.29.665	230	WF	0
42a	Camino Real	42a	36.14.015	105.28.764	20	ES	3.33
42b	Camino Real	42b	36.14.015	105.28.764	190	ES	0
43a	Camino Real	43a	36.12.885	105.31.642	340	WF	1.67
43b	Camino Real	43b	36.12.885	105.31.642	80	WF	0
44a	Questa	44a	36.47.015	105.10.902	14	WF	0
44b	Questa	44b	36.47.050	105.10.922	14	WF	0
45a	Questa	45a	36.45.765	105.12.027	270	DF	0
45b	Questa	45b	36.45.721	105.12.023	270	DF	0
46a	Questa	46a	36.44.940	105.20.550	220	S/F	3.33
46b	Questa	46b	36.44.940	105.20.550	90	S/F	1.67
47a	Questa	47a	36.47.549	105.15.567	250	BS	1.67
47b	Questa	47b	36.47.579	105.15.567	90	BS	3.33
48a	Questa	48a	36.47.421	105.11.571	340	S/F	0
48b	Questa	48b	36.47.418	105.11.495	340	S/F	0
49a	Questa	49a	36.45.857	105.22.832	205	ES	0
49b	Questa	49b	36.45.857	105.22.832	156	ES	0
50a	Questa	50a	36.43.995	105.29.739	180	DF	0
50b	Questa	50b	36.43.995	105.29.739	90	DF	0
51a	Questa	51a	36.45.251	105.26.151	60	S/F	3.33
51b	Questa	51b	36.45.239	105.26.070	60	S/F	6.67
52a	Questa	52a	36.44.440	105.25.373	30	S/F	0
52b	Questa	52b	36.44.447	105.25.240	30	S/F	0
53a	Questa	53a	36.44.029	105.24.939	0	DF	0
53b	Questa	53b	36.43.966	105.24.853	0	DF	1.67
54a	Questa	54a	36.45.672	105.22.313	130	S/F	1.67
54b	Questa	54b	36.45.672	105.22.313	270	S/F	1.67
55a	Questa	55a	36.46.808	105.21.181	246	S/F	8.33
55b	Questa	55b	36.46.808	105.21.181	120	S/F	6.67
56a	Questa	56a	36.43.244	105.24.518	280	WF	1.67
56b	Questa	56b	36.43.185	105.24.511	290	WF	0
57a	Questa	57a	36.44.182	105.26.774	250	BS	3.33
57b	Questa	57b	36.44.182	105.26.774	80	BS	0
58a	Questa	58a	36.43.510	105.23.729	210	DF	0
58b	Questa	58b	36.43.548	105.23.745	210	DF	0