

A Comparison of Habitat Use and Demography of Red Squirrels at the Southern Edge of Their Range

KATHERINE M. LEONARD¹ AND JOHN L. KOPROWSKI

Wildlife Conservation and Management Program, Room 325 Biological Sciences East, University of Arizona,
Tucson 85721

ABSTRACT.—Populations at the edge of their geographic range may demonstrate different population dynamics from central populations. Endangered Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*), endemic to southeastern Arizona, represent the southernmost red squirrel population and are found at lower densities than conspecifics in the center of the range. To determine if differences are due to conditions at the southern periphery of the range, we compared habitat characteristics, demography, body mass, space use and nesting behavior with another subspecies located at the southern edge of the range, the Mogollon red squirrel (*T. h. mogollonensis*). We found that mean and minimum daily temperatures were higher at Mt. Graham whereas maximum temperatures were higher in the White Mountains, male Mogollon red squirrels were heavier than male Mt. Graham red squirrels in all seasons and female Mogollon red squirrels were slightly heavier than female Mt. Graham red squirrels in spring, proportion of squirrels in reproductive condition was lower in female Mogollon red squirrels, Mogollon red squirrels had smaller home ranges, used different types of nests and traveled less distance to nest than Mt. Graham red squirrels. There were no differences in annual rainfall, seedfall, habitat characteristics or survival between mountain ranges. Localized conditions appear to account for the disparity between populations. These differences demonstrate the importance of evaluating attributes of peripheral populations for maximizing persistence and intraspecific diversity.

INTRODUCTION

The extent of a species' range is determined by many factors, both biotic and abiotic. For wide ranging species, populations at the edge of their range are frequently exposed to suboptimal and more variable conditions than populations in other parts of the range, thus local abundance is often lower at the periphery (Shelford, 1911; Kendeigh, 1974; Hengeveld *et al.*, 1979; J.H. Brown, 1984; Lawton, 1993; Safriel *et al.*, 1994; Hochberg and Ives, 1999; Gaston, 2003). Populations at the range periphery are also more likely to speciate because of increased likelihood of barriers isolating populations, and may be more prone to extinction due to this isolation and lower resource quality (Rosenzweig, 1975; Terborgh and Winter, 1980; Gaston, 2003). For these reasons, evaluating behavior of individuals in peripheral populations and available resources may help identify key resource requirements necessary for conservation prescriptions (Lesica and Allendorf, 1995; Lomolino and Channell, 1995; Fraser, 1999).

The red squirrel (*Tamiasciurus hudsonicus*) is a wide ranging species that inhabits a diverse array of environmental conditions in different parts of its range (Steele, 1998). Red squirrels are small (<300 g), diurnal tree squirrels ranging throughout northern Canada and Alaska, the northern United States and south along the Cascade, Rocky and Appalachian Mountains (Hall, 1981). This species generally inhabits conifer forests above 2,000 m elevation (D.E. Brown, 1984; Froehlich, 1990; Steele and Koprowski, 2001) and deciduous and mixed forests above 500 m in the eastern United States (Linzey and Linzey, 1971).

¹Corresponding author present address: 1010 NE 7th Place, Gainesville, Florida 32601; e-mail: kmleonard1@hotmail.com

Red squirrels are active year round and most store conifer cones when available within a central cache or midden, that is vigorously defended from conspecifics and other species (C.C. Smith, 1968; Finley, 1969; Gurnell, 1984). Middens are necessary for survival as they provide cool, moist conditions that prevent cones from drying and opening, thus furnishing a reliable food supply over winter (M.C. Smith, 1968; Hurly and Lourie, 1997). Forest structure around middens is important in creating a microclimate necessary for cone preservation in addition to providing nesting sites, cover and escape routes from predators, and access to foraging sites (Hatt, 1929; Layne, 1954; C.C. Smith, 1968; Finley, 1969). Appropriate conditions for nest and midden placement may be limited at the southern extent the red squirrel's range due to relatively high levels of solar radiation that may increase vulnerability to desiccation. Because red squirrels are dependent on appropriate midden sites for survival, this, in turn, may limit overall red squirrel numbers in a mountain range (Smith and Mannan, 1994).

The Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) exists in high elevation forests (>2000 m) of the Pinaleno Mountains of southeastern Arizona (hereafter Mt. Graham) (D.E. Brown, 1984; Hoffmeister, 1986) and represents the southernmost population of red squirrels (Steele, 1998). This population was isolated on this "mountain island" surrounded by desert and grasslands approximately 11,000 y ago at the end of the Wisconsin glaciation (Spicer, 1985). Because of geographic isolation and low population numbers (~300 individuals), the Mt. Graham red squirrel was federally listed as an endangered subspecies in 1987 (U.S. Fish and Wildlife Service, 1987).

Mt. Graham red squirrels exhibit large home ranges and use different types of nests relative to other red squirrel populations (Young *et al.*, 2002; Koprowski *et al.*, 2008; Munroe *et al.*, *in press*). The red squirrel population closest to the Mt. Graham red squirrel population is the Mogollon red squirrel (*Tamiasciurus hudsonicus mogollonensis*) (Mearns, 1907), a nonendangered subspecies found in the White Mountains of eastern Arizona, approximately 110 km from Mt. Graham. This subspecies resides in habitat that is contiguous with other forests, is slightly larger than the Mt. Graham red squirrel (Spicer, 1985) and differs in its call (Yamamoto, 1998). Both subspecies occur at or near the southern range terminus and inhabit similar forests with comparable habitat characteristics, elevations and weather conditions (Young *et al.*, 2002).

Mt. Graham red squirrels differ from red squirrels in central portions of the red squirrel range and this may be due to their location at the southern periphery of the range (Smith and Mannan, 1994). Herein we examine habitat characteristics and climatic data to determine if these southerly populations are exposed to the same environmental constraints. If both populations are exposed to similar temperatures and habitat characteristics and these factors account for demographic and behavioral disparities between Mt. Graham red squirrels and their conspecifics in the interior of the range, Mogollon red squirrels should display similar disparities. To determine if unique characteristics exhibited by Mt. Graham red squirrels may be attributed to region-wide conditions in the southwestern United States, or localized conditions specific to Mt. Graham, we compared body mass, demography, space use, nest characteristics and survival of these peripheral subspecies.

MATERIALS AND METHODS

STUDY SITES

From 1 May 2004 to 13 Nov. 2005 we investigated aspects of Mt. Graham red squirrel ecology at two sites at Mt. Graham, 25 km southwest of Safford, Graham County, Arizona

(32.6° N, 109.8° W). Mt. Graham 1 (approximately 3000 m elevation) was 72.1 ha and dominated by corkbark fir (*Abies lasiocarpa*) with lesser amounts of Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), Engelmann spruce (*Picea engelmannii*), Ponderosa pine (*Pinus ponderosa*), Southwestern white pine (*Pinus strobiformis*) and quaking aspen (*Populus tremuloides*) (Hutton *et al.*, 2003). Mt. Graham 2 was 32.8 ha (2831 m elevation) and located approximately 6.5 km west of Mt. Graham 1. Forest structure and composition were similar to Mt. Graham 1; however, Douglas fir was the dominant tree (Froehlich and Smith, 1990). In Jun.–Jul., 2004, the Nuttall Fire burned in forested regions of the Mt. Graham, and burned patches of Mt. Graham 2 (Koprowski *et al.*, 2006).

We studied Mogollon red squirrels at the White Mountains site (hereafter WTMN). WTMN measured 49.2 ha and is approximately 110 km north of Mt. Graham and 32 km south of Alpine, Arizona in the Blue Range Primitive Area, Apache-Sitgreaves National Forest (34.1° N, 110.0° W). At 2780 m elevation, WTMN was comprised of mature to old growth mixed conifer forest (Young *et al.*, 2002) dominated by Douglas fir with lesser amounts of white fir, corkbark fir, Engelmann spruce, blue spruce (*Picea pungens*), Ponderosa pine, Southwestern white pine and quaking aspen (Vahle, 1978). The southern portion of WTMN was affected by mid-intensity wildfire in summer 2003, however few data for this study were collected in the burned portion of this site.

STUDY SITE CHARACTERISTICS

Information on long-term daily temperature was available from weather stations at Mt. Graham 1 and approximately 2 km north of WTMN. We calculated mean, maximum and minimum daily temperatures from 1995–2005. The bulk of rainfall occurs in monsoon rains from Jun.–Sep.; we used precipitation information collected from the weather stations to determine yearly monsoonal precipitation from 1995–2005 for each mountain range.

We used seed plots with three 0.25 m² wire mesh seed traps per plot at 16 random locations at Mt. Graham 1 and 10 locations at WTMN to determine relative food availability in each mountain range from 1995 to 2004. Fallen seeds were sorted, identified to genus and counted. We included seeds of fir (*Abies* sp.), spruce (*Picea* sp.) and Douglas fir as these are known food sources of red squirrels and are easily identifiable (D.E. Brown, 1984). We pooled seeds across species and averaged number of seeds from the three traps at each plot to estimate seeds/ha.

To compare habitat characteristics between mountain ranges, we measured vegetation characteristics in 1997 along randomly placed transects at 10 locations at WTMN and 16 locations at Mt. Graham 1. From the central random point we delineated a 50 m transect in each of the four cardinal directions, marking each 10 m increment. We delineated a 50 m parallel line 5 m to the left of each of the original transects. This resulted in five 10 m × 5 m subplots in each of the four cardinal directions per random point. We counted and measured every tree ≥ 3 cm DBH and determined tree condition (live, dead) within each subplot to calculate basal area/ha, trees/ha and live trees/ha. We determined log volume/ha by measuring length and DBH at each end of every log ≥ 1 m long and ≥ 20 cm diam at one end by averaging the circumference of the two ends and using the formula for calculating volume of a cylinder. We used a spherical densiometer and the Strickler method (Strickler, 1959) to determine canopy cover at the center of each subplot.

BODY MASS AND DEMOGRAPHY

We live-trapped adult (>200 g) squirrels from Sep. 2003 to Oct. 2005 at all study sites with the exception of Mt. Graham 2, where trapping began in May 2004. We placed a Tomahawk

trap (Model 201; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanuts and peanut butter at active squirrel middens and used a canvas cone to extract and handle squirrels (Koprowski, 2002). We used numbered Monel ear tags (Model #1005-1; National Band and Tag Co., Newport, Kentucky, USA) and a colored washer (Model #1842, 3/8"; National Band and Tag Co., Newport, Kentucky, USA) to uniquely mark squirrels and recorded body mass, sex, age and reproductive condition before releasing animals at the capture site. Scrotal and partially scrotal males, as well as females in estrous, pregnant, lactating and recently lactating females were considered to be in reproductive condition. We placed radio collars (Model #SOM-2190; Wildlife Materials International, Inc., Carbondale, Illinois, USA) weighing $< 5\%$ of body mass on 46 red squirrels (27 males, 19 females) at Mt. Graham 1, 25 squirrels (11 males, 14 females) at Mt. Graham 2 and 27 squirrels (14 males, 13 females) at WTMN.

We determined body mass for spring (Mar.–May), summer (Jun.–Aug.) and fall (Sep.–Nov.) for each marked animal during 2003–2005 by including body mass collected during the capture event closest to the mid-point of each season. We also calculated proportion of animals in reproductive condition each year as the number of animals reproductive during at least one capture event.

To estimate survival, we used telemetry, nesting and trapping data to monitor the status of collared individuals over the duration of the study. Death was verified by using radiotelemetry to locate radio collars and remains of individuals. If an individual died, we calculated date of death as the mid-point between last date known alive and date the remains were discovered. Only individuals with confirmed fates were included in the analysis.

SPACE USE

Yearly home ranges were generated for 2004 and 2005. Because of the Nuttall Fire, we were unable to gather telemetry locations on red squirrels at Mt. Graham 2 in summer 2004 and only used data from the postfire period (Aug.–Nov.) during that year for all sites. We gathered telemetry data from May–Nov. 2005 at all sites.

We used biangulation and homing to identify squirrel locations (White and Garrott, 1990). The proportion of homing locations was 44% at Mt. Graham 1, 72% at Mt. Graham 2 and 94% at WTMN. Locations were taken > 60 min apart to ensure independence and we gathered locations throughout daylight hours to ensure all activity periods were represented. Locations gathered with biangulation were gathered < 100 m from the focal animal and with interbearing angles between 70 – 110° . We used the same techniques to calculate biangulation error with observers obtaining bearings on a radiocollar in a known location. At Mt. Graham 1, average bearing error ($\pm$ SE) was $5.6 \pm 4.5^\circ$, average distance error was 12 ± 6 m (Koprowski *et al.*, 2008). At Mt. Graham 2, average bearing error was $10 \pm 7^\circ$, average distance error was 60 ± 33 m. We did not calculate biangulation error at WTMN because of the low percentage of locations gathered with this technique. We plotted area-use curves in Ranges 6 (Anatrack Ltd. 2003, Dorset, U.K.) and excluded individuals whose ranges did not reach an asymptote; resulting in the inclusion of 46 animals from Mt. Graham 1 (27 males, 19 females), 22 animals (9 males, 13 females) from Mt. Graham 2 and 23 animals (11 males, 12 females) from WTMN in our home range calculations. We used the Animal Movement extension (Version 1.4, Jenness enterprises, Flagstaff, Arizona, USA) for ArcView GIS (Version 3.3, ESRI, Redlands, California, USA) to generate estimates of space use based on fixed kernel 50% cores and 95% home ranges. We used least-squares cross-validation (LSCV) to select bandwidths.

TABLE 1.—Temperature, precipitation and vegetative characteristics (mean $\pm$ sd) at weather stations and subplots at Mt. Graham and the White Mountains, Graham and Apache Counties, Arizona. Asterisk (*) indicates $P < 0.001$

Site characteristics	Mt. Graham	WTMN
	n = 320	n = 200
Mean daily temperature (1995–2005) ($^{\circ}\text{C}$) *	6.4 $\pm$ 7.1	5.6 $\pm$ 7.3
Max daily temperature (1995–2005) ($^{\circ}\text{C}$) *	13.9 $\pm$ 9.0	15.7 $\pm$ 7.7
Min daily temperature (1995–2005) ($^{\circ}\text{C}$) *	1.6 $\pm$ 6.6	−2.1 $\pm$ 7.3
Jun.–Sep. precipitation (1995–2005) (mm)	219.1 $\pm$ 113.3	276.2 $\pm$ 107.7
Trees/ha	1524.0 $\pm$ 1090.7	1143.0 $\pm$ 904.3
Live trees/ha	1280.6 $\pm$ 949.6	982.0 $\pm$ 839.3
Basal area/ha (m^2)	58.3 $\pm$ 49.1	56.5 $\pm$ 50.8
Canopy cover (%)	85.8 $\pm$ 19.1	87.5 $\pm$ 12.6
Logs/ha	255.0 $\pm$ 259.7	230.0 $\pm$ 276.2
Log volume (m^3)	347.4 $\pm$ 521.7	419.8 $\pm$ 712.0

NEST CHARACTERISTICS

To assess patterns of nest use in the two subspecies, we located nocturnal nests by tracking individuals ≤ 2 h before sunset and followed them to their nests, observing nest entrance when possible. We noted tree species and condition, type of nest (cavity, drey, log, ground) and measured diam at breast height (DBH) of cavity and drey nest trees. We determined the distance from an individual’s midden to their nest by direct measurement or by using the Distance and Azimuth extension (version 2.0) for ArcView.

For analyses, we compared characteristics of the first nest found after the start of the study for each individual; most nests were first discovered in summer, 2004. We compared nest tree features with trees sampled in 16 random plots at Mt. Graham 1 and 10 random plots at WTMN in 1997, as well as 9 random plots at Mt. Graham 2 established in 2006. Within each subplot, we noted species, condition and DBH of every tree ≥ 3 cm.

STATISTICAL ANALYSES

We used paired *t*-tests to compare temperature and rainfall between Mt. Graham 1 and WTMN. We averaged mean daily temperatures as well as maximum and minimum daily temperatures from 1995–2005. We used ANOVA and post-hoc Tukey-Kramer HSD to compare seedfall, vegetation characteristics, body mass, home range size, nest distance from middens and size of nest trees among study sites (± 1 sd). To better meet assumptions of normality, we log-transformed log volume/ha, home range and core area size, nest distance and nest tree size, but present untransformed means (± 1 sd) of values. We used chi-square tests to compare proportion of reproductively active individuals among study sites, as well as actual nest use versus expected use of tree species and live and dead trees by squirrels. We calculated number of days alive post-collaring and used Kaplan-Meier survival analysis to estimate survival (Kaplan and Meier, 1958). All analyses were performed using JMP-IN (SAS Institute Inc. 2003) and SPSS (SPSS Inc. 2005) statistical software packages.

RESULTS

STUDY SITE CHARACTERISTICS

Mean daily temperatures were $0.8 \pm 3.6^{\circ}$ higher and minimum daily temperatures were $3.7 \pm 4.3^{\circ}$ higher at Mt. Graham whereas maximum daily temperatures were $1.8 \pm 5.8^{\circ}$

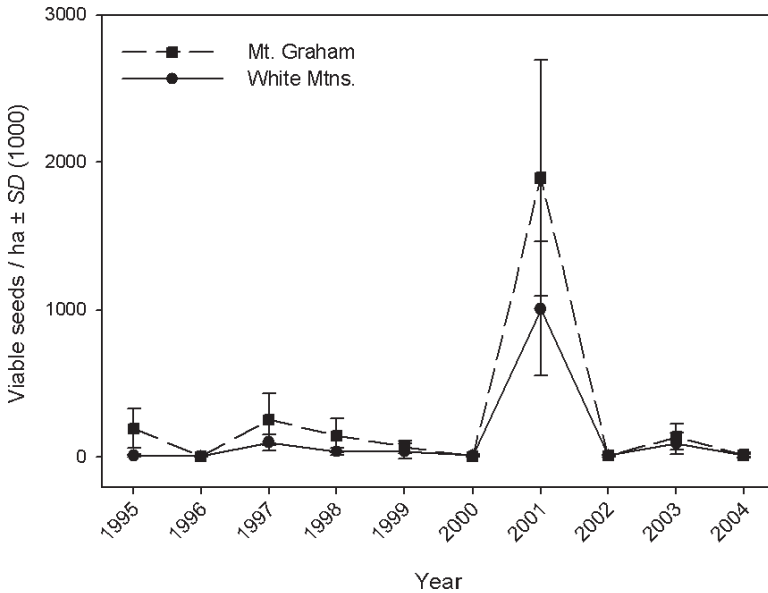


FIG. 1.—Yearly abundance (mean $\pm$ SD) of viable conifer seeds at Mt. Graham and the White Mountains, Graham and Apache Counties, Arizona, 1995–2004

higher in the White Mountains from 1995–2005 (Table 1; Mean: $t = 12.7$, $d.f. = 3527$, $P < 0.001$; Maximum: $t = -18.4$, $d.f. = 3527$, $P < 0.001$; Minimum: $t = 50.2$, $d.f. = 3527$, $P < 0.001$). Yearly monsoonal rainfall was 57.1 ± 90.8 mm higher in the White Mountains but did not differ statistically between mountain ranges ($t = -2.0$, $d.f. = 10$, $P = 0.06$).

Seedfall was not different between mountain ranges (Fig. 1, ANOVA, $F_{1,178} = 0.65$, $P = 0.421$) but differed by year ($F_{9,178} = 22.9$, $P < 0.0001$) with an interactive effect of year and mountain range ($F_{9,178} = 4.5$, $P < 0.0001$).

Trees/ha (Table 1; $t = 1.00$, $d.f. = 518$, $P = 0.317$), live trees/ha ($t = 1.31$, $d.f. = 518$, $P = 0.190$), basal area/ha ($t = 1.29$, $d.f. = 518$, $P = 0.199$), logs/ha ($t = 0.96$, $d.f. = 518$, $P = 0.339$), log volume ($t = 0.54$, $d.f. = 518$, $P = 0.59$) and canopy cover ($t = -1.08$, $d.f. = 518$, $P = 0.282$) did not differ between mountain ranges.

BODY MASS AND DEMOGRAPHY

Males at WTMN were more than 10 g heavier than males at Mt. Graham in all seasons with males in both mountain ranges heaviest in spring (Fig. 2, ANOVA, Site: $F_{2,208} = 41.17$, $P < 0.001$; Season: $F_{2,208} = 7.52$, $P < 0.001$; Site $\times$ Season: $F_{4,208} = 2.28$, $P = 0.062$) (Tukey-Kramer, all $P < 0.001$).

Female mass differed by season among the three study sites with a marginal interaction between study site and season (Fig. 2, ANOVA, Site: $F_{2,271} = 9.15$, $P < 0.001$; Season: $F_{2,271} = 4.17$, $P = 0.016$; Site $\times$ Season: $F_{4,271} = 2.27$, $P = 0.062$). Mass was not different between study sites at Mt. Graham (Tukey-Kramer, $P = 0.599$). Females at WTMN were heavier than squirrels at Mt. Graham 1 in spring (Tukey-Kramer, $P < 0.001$), but did not differ from squirrels at Mt. Graham 2 (Tukey-Kramer, $P = 0.139$). Females were slightly heavier in summer than fall (Tukey-Kramer, $P = 0.067$) but did not differ among other seasons (Tukey-Kramer, all $P > 0.05$).

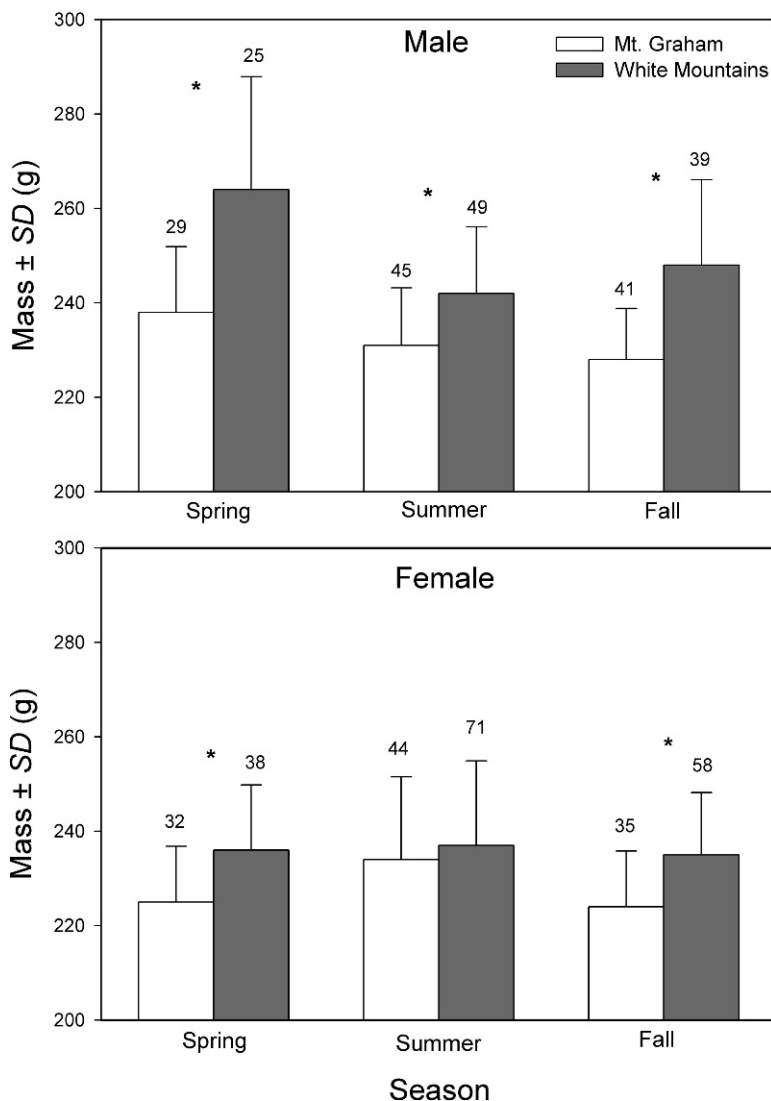


FIG. 2.—Seasonal body mass (mean $\pm$ SD) of male and female Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) and Mogollon red squirrels (*T. h. mogollonensis*) at Mt. Graham and the White Mountains, Graham and Apache Counties

The frequency of males in reproductive condition did not differ by year ($\chi^2 = 0.19$, *d.f.* = 1, $P = 0.662$) or study site ($\chi^2 = 5.26$, *d.f.* = 2, $P = 0.072$) (Proportion in reproductive condition (%) 2004: Mt. Graham = 93%, *n* = 29; WTMN = 85%, *n* = 33; 2005: Mt. Graham = 93%, *n* = 27; WTMN = 94%, *n* = 32).

The frequency of females in reproductive condition did not differ between study sites at Mt. Graham ($\chi^2 = 0.52$, *d.f.* = 1, $P = 0.47$). The proportion of females in reproductive condition was higher at Mt. Graham in 2004 ($\chi^2 = 29.3$, *d.f.* = 1, $P < 0.001$) and in 2005 (χ^2

= 8.8, *d.f.* = 1, *P* = 0.003). (Proportion in reproductive condition (%) 2004: Mt. Graham = 79%, *n* = 33; WTMN = 19%, *n* = 52; 2005: Mt. Graham = 51%, *n* = 70; WTMN = 29%, *n* = 112).

Survival did not differ between Mt. Graham 1 and Mt. Graham 2 (Kaplan-Meier $\chi^2 = 0.595$, *d.f.* = 1, *P* = 0.441). At the end of the study, 71% of collared squirrels with known fates (16 out of 24 males, 18 out of 24 females) were alive at Mt. Graham and 88% (8 out of 8 males, 7 out of 9 females) were alive at WTMN. The fates of 9 females and 14 males at Mt. Graham and 2 females and 5 males at the White Mountains were unknown and these animals were excluded from the analysis. The average number of days alive was 360 ± 27 at Mt. Graham (*n* = 48), and 365 ± 34 d at WTMN (*n* = 17). Number of days alive post-collaring did not differ between mountain ranges (Kaplan-Meier $\chi^2 = 0.136$, *d.f.* = 1, *P* = 0.713).

SPACE USE

Home ranges and core areas were larger across sexes for squirrels at Mt. Graham compared to those at WTMN (Fig. 3). Home ranges differed by study site, sex and year with an interactive effect between year and study site (ANOVA, 95% Home range: Sex $F_{1,158} = 7.42$, *P* = 0.007; Year $F_{1,158} = 8.16$, *P* = 0.005; Site $F_{2,158} = 48.18$, *P* < 0.0001; Year x Site $F_{2,158} = 11.41$, *P* < 0.0001; 50% Core area: Sex $F_{1,158} = 6.54$, *P* = 0.012; Year $F_{1,158} = 3.61$, *P* = 0.059; Site $F_{2,158} = 39.00$, *P* < 0.0001; Year x Site $F_{2,158} = 9.77$, *P* < 0.0001).

NEST CHARACTERISTICS

Nest distance from middens did not differ between Mt. Graham 1 and Mt. Graham 2 (*t* = -0.96, *d.f.* = 56, *P* = 0.340). Mt. Graham red squirrels traveled further from their middens to nest than Mogollon red squirrels (*t* = 2.91, *d.f.* = 82, *P* = 0.005) (Mt. Graham: Mean = 31.0 ± 46.4 m, range = 0–272 m, *n* = 58; WTMN: Mean = 9.0 ± 7.1 m, range = 0–27 m, *n* = 26).

Size of nest trees did not differ between Mt. Graham 1 and Mt. Graham 2 (*t* = -0.35, *d.f.* = 28, *P* = 0.728) or between mountain ranges (*t* = -0.25, *d.f.* = 53, *P* = 0.803). Squirrels used trees that were on average larger than those measured in the random sample (Table 2; Mt. Graham: *t* = -10.02, *d.f.* = 511, *P* < 0.0001; WTMN: *t* = -6.32, *d.f.* = 239, *P* < 0.0001).

Squirrels nested in dead trees more frequently than live trees at Mt. Graham 1 whereas squirrels at Mt. Graham 2 and WTMN nested in live trees more frequently (Table 2). Squirrels at Mt. Graham 2 and WTMN nested in live and dead trees in proportion to their abundance on the landscape (Mt. Graham 2: $\chi^2 = 0.064$, *d.f.* = 1, *P* = 0.800; WTMN: $\chi^2 = 0.637$, *d.f.* = 1, *P* = 0.420), whereas squirrels at Mt. Graham 1 used a higher proportion of dead trees than that present in the random sample ($\chi^2 = 99.3$, *d.f.* = 1, *P* < 0.0001).

Squirrels at Mt. Graham 1 nested in aspens more frequently than other tree species, whereas squirrels at Mt. Graham 2 nested in aspens and Douglas firs most frequently and squirrels at WTMN nested in Douglas firs most frequently (Table 2). Squirrels in both mountain ranges used aspens and squirrels at WTMN used Douglas fir more frequently than expected based on abundance on the landscape (Mt. Graham 1: $\chi^2 = 25.79$, *d.f.* = 1, *P* = 0.002; Mt. Graham 2: $\chi^2 = 17.30$, *d.f.* = 1, *P* = 0.016; WTMN: $\chi^2 = 26.58$, *d.f.* = 1, *P* < 0.001).

Squirrels in both mountain ranges nested in cavities and dreys most frequently, however the proportion of nest type used differed between subspecies ($\chi^2 = 29.18$, *d.f.* = 4, *P* < 0.001). Several individuals at Mt. Graham used ground and log nests, whereas use of these nests was not observed at WTMN. Red squirrels at Mt. Graham used cavities most frequently, whereas squirrels at WTMN used more dreys (Proportion of nest type used (%) (Cavity,

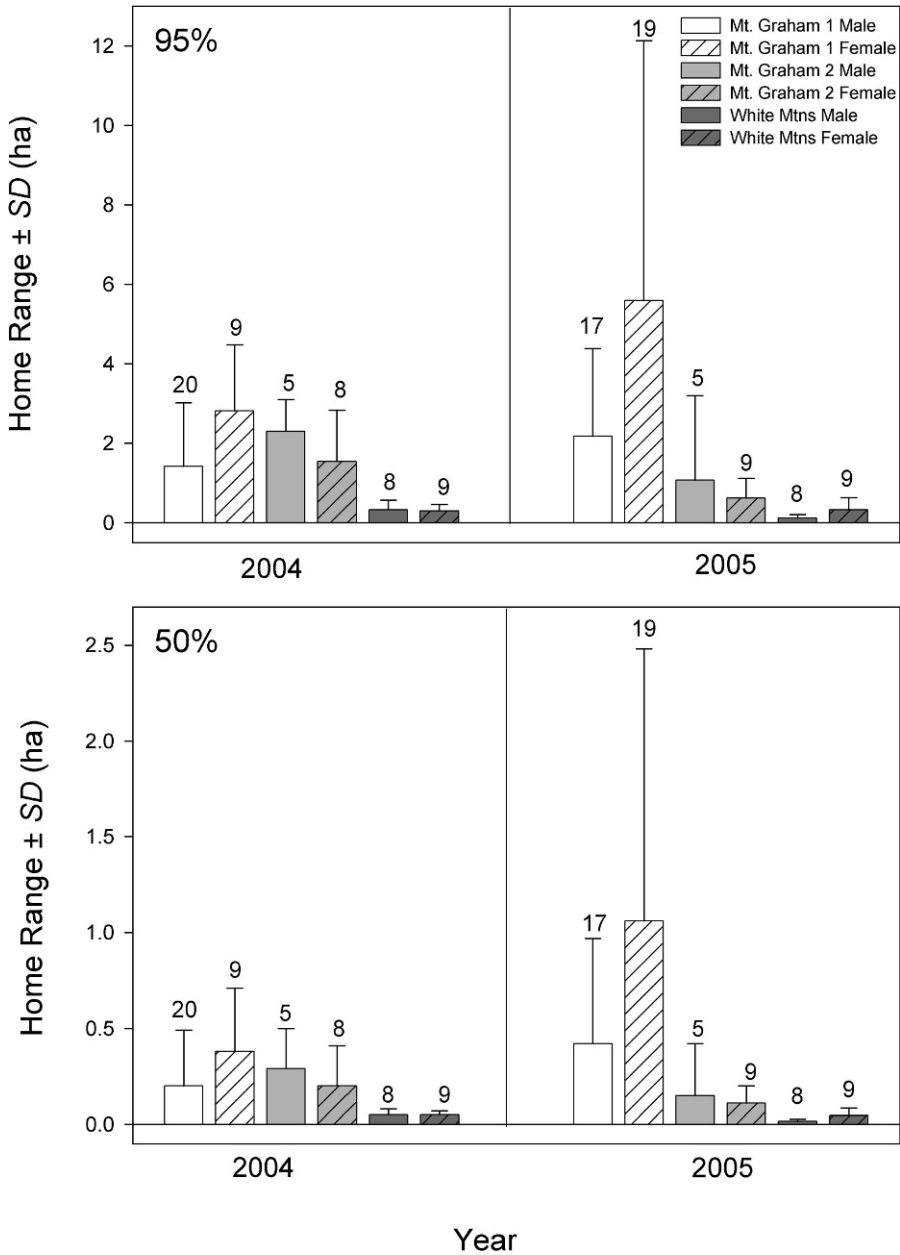


FIG. 3.—Size of fixed kernel 95% home ranges and 50% core areas (mean $\pm$ sd) of male and female Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) and Mogollon red squirrels (*T. h. mogollonensis*) at Mt. Graham and the White Mountains, Graham and Apache Counties, Arizona, 2004–2005, all seasons combined. Sample sizes indicated above bars

TABLE 2.—Characteristics and proportion of occurrence of Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) and Mogollon red squirrel (*T. h. mogollonensis*) nests and random trees at Mt. graham and the White Mountains, Graham and Apache Counties, Arizona

	Mt. Graham		WTMN	
	Nest	Random	Nest	Random
N	56	3746	26	1143
DBH ± SD (cm)	49.0 ± 17.8	17.2 ± 14.5	51.4 ± 21.5	18.2 ± 17.2
Proportion of live trees (%)	56	76	81	86
Proportion of tree species (%)				
Aspen	56	10	19	6
Douglas Fir	17	12	42	18
Fir sp	13	52	19	40
Pine sp	8	7	8	5
Spruce sp	6	17	12	29
Other/unknown	0	2	0	2

drey, ground, log: Mt. Graham: n = 60; 70.0%, 15.0%, 13.3%, 1.7%; WTMN: n = 26; 30.8%, 69.3%, 0%, 0%).

DISCUSSION

Mt. Graham red squirrels and Mogollon red squirrels are closely related, are in close proximity, occur at similar elevations and in similar forest types and persist at the southern end of the species' range (D.E. Brown, 1984; Young *et al.*, 2002). Despite these similarities, these populations differ in some aspects of their ecology, with Mogollon red squirrels demonstrating more similar densities, space use and nesting behavior with conspecifics in central portions of their distribution (Young *et al.*, 2002; Munroe *et al.*, *in press*).

Daily mean and minimum temperatures were higher at Mt. Graham; it is unknown if this slight difference influences desiccation of stored cones, but if so, this could explain differences in midden site availability and, therefore, amount of squirrels each mountain range can support. Mt. Graham and the White Mountains had similar seedfall, vegetation structure and forest composition, therefore, differences in habitat characteristics are not likely the reason for observed divergence between populations.

BODY MASS AND DEMOGRAPHY

Adult survival was similar between mountain ranges and reproductive potential was higher at Mt. Graham, contrary to expectations based upon the low density and endangered status of Mt. Graham red squirrels. However, juvenile survival was not assessed. Red squirrels have a high (>60%) mortality rate in their first year of life (Halvorson and Engeman, 1982; Stuart-Smith, 1993; Haughland and Larsen, 2004), because unfamiliarity with their surroundings while searching for a territory increases their vulnerability to predation (Larsen and Boutin, 1994; Stuart-Smith and Boutin, 1995; Kreighbaum and Van Pelt, 1996; Bertreux and Boutin, 2000), this threat may be higher at Mt. Graham if suitable midden sites are limited as juveniles would be forced to search more widely for midden sites. Furthermore, despite prevalence of squirrels in reproductive condition, the number of young added to the population may be low, as Mt. Graham red squirrels appear to have smaller litters than red squirrels in the center of the range (Munroe *et al.*, *in press*).

SPACE USE

Large home ranges may reflect a scarcity of available resources or may be a result of relaxation of territorial behavior due to low population densities (J. H. Brown, 1984; Mitchell and Powell, 2004); Mt. Graham red squirrels have much larger home ranges than their nearest neighbors in the White Mountains and red squirrels in other parts of their range (Froehlich, 1990; Koprowski *et al.*, 2008). Range-wide, the average red squirrel home range is 0.53 ha (Munroe *et al.*, *in press*). In comparison, 67% of animals at Mt. Graham had home ranges > 1 ha in at least one year, and the largest individual home range was 26.9 ha. In contrast, the largest home range at WTMN was 0.82 ha and no squirrels at WTMN had a home range > 1 ha. Abundance of spruce, fir and Douglas fir seeds, the primary red squirrel food sources, was similar between mountain ranges so it is unlikely Mt. Graham red squirrels moved further to obtain scarce food supplies.

NEST CHARACTERISTICS

Mt. Graham red squirrels appear to prefer cavities over dreys (Young *et al.*, 2002), whereas Mogollon red squirrels used predominantly dreys. Mt. Graham red squirrels traveled over 3 times farther to nest than Mogollon red squirrels, therefore, this preference may be evidenced by Mt. Graham red squirrels traveling further distances from middens to nest in cavities. Alternatively, in the White Mountains, high midden density and territorial neighbors may constrain movement and limit access to nesting sites, or cavities may be limited in the White Mountains, forcing animals to build dreys. Animals nesting in dreys may be disadvantaged if cavities afford more protection from predators and weather (Hatt, 1929; Hamilton, 1939; Hatt, 1943; Layne, 1954; Fancy, 1980); however, dreys also may reduce the need to travel long distances to nest as dreys can be constructed in trees large enough to support a nest and provide adequate protection in the form of canopy cover (Fitzwater and Frank, 1944).

CONCLUSION

Evaluating the status and reasons for decline in endangered species such as the Mt. Graham red squirrel is necessary to preserve the important genetic, behavioral and morphological diversity declining species or populations may contribute (Lesica and Allendorf, 1995; Fraser, 1999). Understanding these causes may be even more important in peripheral populations because of the potential for peripheral habitat to serve as refugia in declining species (Lomolino and Channell, 1995).

Despite similar food resources and habitat characteristics, Mt. Graham red squirrels exhibit important differences from neighboring red squirrel populations, indicating that localized processes such as slightly elevated temperatures and isolation may be responsible for the disparity. Because of isolation, there are no opportunities for increasing available habitat or gene flow, making this subspecies more susceptible to extinction if disturbance further reduces habitat. The disparities between Mt. Graham red squirrels and their nearby conspecifics demonstrate the importance of evaluating local conditions and population dynamics before initiating conservation efforts. Conservation strategies that use general data gathered in the center of the geographic range may fail to address the reasons for population decline at the edge, where conditions and limiting factors often are different (Ruggiero *et al.*, 1994; Haight, 1995; Brown *et al.*, 1996; Kloor, 1999; Gaston, 2003).

Acknowledgments.—We thank S. R. Bertelsen, S. Blount, A. Casey, A. J. Edelman, V. L. Greer, N. Hallmark, S. R. B. King, R. W. Mannan, M. Merrick, K. E. Munroe, B. S. Pasch, K. Pokorny, N. Ramos-Lara, M. Rheude, T. Snow, R. J. Steidl, B. Weise, D. J. Wood, M. Yurenka, C. A. Zugmeyer and University

of Arizona Red Squirrel Monitoring Program employees and volunteers. We also thank Carl Edminster, Randall Smith, Lawrence Jones and Thomas Skinner.

LITERATURE CITED

- BERTREAUX, D. AND S. BOUTIN. 2000. Breeding dispersal in female North American red squirrels. *Ecology*, **81**:1311–1326.
- BROWN, D. E. 1984. Arizona's tree squirrels. Arizona Game and Fish Department, Phoenix.
- BROWN, J. H. 1984. On the relationship between abundance and distribution of species. *The Amer. Nat.*, **124**:255–279.
- , G. C. STEVENS AND D. M. KAUFMAN. 1996. The geographic range: size, shape, boundaries and internal structure. *Ann. Rev. Ecol. System.*, **27**:597–623.
- FANCY, S. G. 1980. Nest-tree selection by red squirrels in a boreal forest. *Can. Field-Nat.*, **94**:198.
- FINLEY, R. B. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. *Univ. Kansas Mus. Misc. Pub.*, **51**:233–273.
- FITZWATER, JR., W. D. AND W. J. FRANK. 1944. Leaf nests of gray squirrel in Connecticut. *J. Mammal.*, **25**:160–170.
- FRASER, D. F. 1999. Species at the edge: the case for listing of “Peripheral” species. Proc. Biology and Management of Species and Habitats at Risk, Kamloops, British Columbia.
- FROELICH, G. F. 1990. Habitat use and life history of the Mt. Graham red squirrel. Masters thesis, University of Arizona. 61 p.
- AND N. S. SMITH. 1990. Habitat use by the Mt. Graham red squirrel. Phoenix. p. 118–125.
- GASTON, K. J. 2003. The Structure and dynamics of geographic ranges. Oxford University Press, New York, New York, USA.
- GURNELL, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. *Anim. Behav.*, **32**:1119–1131.
- HAIGHT, R. G. 1995. Comparing extinction risk and economic cost in wildlife conservation planning. *Ecological Applications*, **5**:767–775.
- HALL, E. R. 1981. The mammals of North America. 2nd ed. John Wiley and Sons, New York. 600 p.
- HALVORSON, C. AND R. M. ENGEMAN. 1982. Survival analysis for a red squirrel population. *J. Mammal.*, **64**:332–336.
- HAMILTON, W. J. 1939. Observation on the life history of the red squirrel in New York. *Amer. Midl. Nat.*, **22**:732–745.
- HATT, R. T. 1929. The red squirrel: Its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. *Roosevelt Wild Life Ann.*, **2**:1–146.
- . 1943. The pine squirrel in Colorado. *J. Mammal.*, **24**:311–345.
- HAUGHLAND, D. L. AND K. W. LARSEN. 2004. Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. *J. Mammal.*, **85**:225–236.
- HENGVELD, R., S. A. L. M. KOIJMAN AND C. TAILLIE. 1979. A spatial model explaining species-abundance curves, p. 333–347. In: J. K. Ord, G. P. Patil and C. Taillie (eds.). Statistical distributions in ecological work. International Co-operative Publishing House, Fairland, Maryland, USA.
- HOCHBERG, M. E. AND A. R. IVES. 1999. Can natural enemies enforce geographical range limits? *Ecography*, **22**:268–276.
- HOFFMEISTER, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson. 602 p.
- HURLY, T. A. AND S. A. LOURIE. 1997. Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. *J. Mammal.*, **78**:529–537.
- HUTTON, K. A., J. L. KOPROWSKI, V. L. GREER, M. I. ALANEN, C. A. SCHAUFFERT AND P. J. YOUNG. 2003. Use of mixed conifer and spruce-fir forests by an introduced population of Abert's squirrels (*Sciurus aberti*). *Southwest. Nat.*, **48**:257–260.
- KAPLAN, E. L. AND P. MEIER. 1958. Nonparametric estimation from incomplete observations. *Amer. Stat. Assoc. J.*, **53**:457–481.
- KENDEIGH, S. C. 1974. Ecology with special reference to animals and man. Prentice Hall, Englewood Cliffs, New Jersey, USA.

- KLOOR, K. 1999. Lynx and biologists try to recover after disastrous start. *Science*, **285**:320–321.
- KOPROWSKI, J. L. 2002. Handling tree squirrels with a safe and efficient restraint. *Wildl. Soc. Bull.*, **30**:101–103.
- , K. M. LEONARD, C. A. ZUGMEYER AND J. L. JOLLEY. 2006. Direct effects of fire on endangered Mt. Graham red squirrels. *Southwest. Nat.*, **51**:59–63.
- , S. R. B. KING AND M. MERRICK. 2008. Home ranges are expanded in a peripheral population: space use of endangered Mt. Graham red squirrels. *Endang. Spec. Res.*, **4**:227–232.
- KREIGHBAUM, M. E. AND W. E. VAN PELT. 1996. Mount Graham red squirrel juvenile dispersal telemetry study. Phoenix: Arizona Game and Fish Department, Nongame and Endangered Wildlife Program. Report no. 489.
- LARSEN, K. W. AND S. BOUTIN. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology*, **75**:214–223.
- LAWTON, J. H. 1993. Range, population abundance and conservation: trends in ecology and evolution. **8**:409–413.
- LAYNE, J. N. 1954. The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. *Biol. Monog.*, **24**:227–266.
- LESICA, P. AND F. W. ALLENDORF. 1995. When are peripheral populations valuable for conservation? *Conser. Biol.*, **9**:753–760.
- LINZEY, A. V. AND D. W. LINZEY. 1971. Mammals of Great Smoky Mountains National Park. The University of Tennessee Press, Knoxville. 114 p.
- LOMOLINO, M. V. AND R. CHANNELL. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. *J. Mammal.*, **76**:335–347.
- MEARNS, E. A. 1907. Mammals of the Mexican boundary of the United States. Species accounts of Arizona grey squirrel and red squirrel. *Smithson. Inst. Bull.*, **56**, 530 p.
- MITCHELL, M. S. AND R. A. POWELL. 2004. A mechanistic home range model for optimal use of spatially distributed resources. *Ecol. Model.*, **177**:209–232.
- MUNROE, K. E., J. L. KOPROWSKI AND V. L. GREER. The mating and social systems in red squirrels: do Mt. Graham red squirrels fit the pattern? *In*: The last refuge of the Mt. Graham red squirrels: Ecology of endangerment. *In Press*.
- ROSENZWEIG, M. L. 1975. On continental steady states of species diversity, p. 124–140. *In*: M. L. Cody and J. M. Diamond (eds.). *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- RUGGIERO, L. F., G. D. HAYWARD AND J. R. SQUIRES. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. *Conser. Biol.*, **8**:364–372.
- SAFRIEL, U. N., S. VOLIS AND S. KARK. 1994. Core and peripheral populations and global climate change. *Israel J. Plant Sci.*, **42**:331–345.
- SHELFORD, V. E. 1911. Physiological animal geography. *J. Morph.*, **22**:551–618.
- SMITH, A. A. AND R. W. MANNAN. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. *J. Wildl. Manag.*, **58**:437–445.
- SMITH, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. *Ecol. Monog.*, **38**:31–63.
- SMITH, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. *J. Wildl. Manag.*, **32**:305–317.
- SPICER, R. B. 1985. Status of the Mount Graham red squirrel, *Tamiasciurus hudsonicus grahamensis*, of southeastern Arizona. Arizona Game and Fish Department, 47 p.
- STEELE, M. A. 1998. *Tamiasciurus hudsonicus*. *Mammal. Spec.*, **586**:1–9.
- AND J. L. KOPROWSKI. 2001. North American tree squirrels. Smithsonian Institution, Washington D.C., USA.
- STRICKLER, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. USDS Forest Service General Technical Report. RM-217.
- STUART-SMITH, A. K. 1993. The effect of predation and availability of food on survival rates. M.S. Thesis, University of Alberta, Edmonton.

- AND S. BOUTIN. 1995. Behavioural differences between surviving and depredated juvenile red squirrels. *Ecoscience*, **2**:35–40.
- TERBORGH, J. AND B. WINTER. 1980. Some causes of extinction, p. 119–133. *In*: M. E. Soulé and B. A. Wilcox (eds.). *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts, USA.
- U.S. FISH AND WILDLIFE SERVICE. 1987. Endangered and threatened wildlife and plants; determination of endangered status for the Mount Graham red squirrel. *Federal Register*, **52**:20994–20999.
- VAHLE, J. R. 1978. Red squirrel use of Southwestern mixed coniferous habitat. M.S. Thesis, Arizona State University., 100 p.
- WHITE, G. C. AND R. A. GARROTT. 1990. Analysis of Wildlife radiotracking data. Academic Press. p. 145–205.
- YAMAMOTO, O. S. 1998. Variation in the bark call of the red squirrel (*Tamiasciurus hudsonicus*). *West. Nor. Amer. Nat.*, **61**:395–402.
- YOUNG, P. J., V. L. GREER AND S. K. SIX. 2002. Characteristics of bolus nests of red squirrels in the Pinaleno and White Mountains of Arizona. *Southwest. Nat.*, **47**:267–275.

SUBMITTED 20 DECEMBER 2007

ACCEPTED 11 SEPTEMBER 2008