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## RESPONSE OF THE MOUNT GRAHAM RED SQUIRREL (*TAMIASCIURUS HUDSONICUS GRAHAMENSIS*) TO POSTFIRE CONDITIONS

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**ABSTRACT**—To assess response of Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) to postfire conditions, we monitored size of home ranges and core areas and characteristics of vegetation at middens in an area of low-intensity burn. For a larger-scale assessment, we monitored mountain-wide occupancy of middens. Although red squirrels selected unburned locations as sites for middens, mean size of home range in a lightly burned area decreased over time, suggesting high availability of resources in lightly burned areas.

**RESUMEN**—Para evaluar la respuesta de las ardillas rojas del monte Graham (*Tamiasciurus hudsonicus grahamensis*) a condiciones de post-fuego, monitoreamos el tamaño de los rangos de hogar y áreas nucleares, y las características de vegetación en basurales en un área de quema de baja intensidad. Para una evaluación a mayor escala, monitoreamos la ocupación de basurales a lo largo de la montaña. Aunque las ardillas rojas seleccionaron lugares sin quemar como sitios para basurales, el tamaño promedio del rango de hogar en un área ligeramente quemada disminuyó con el tiempo, sugiriendo alta disponibilidad de recursos en áreas ligeramente quemadas.

Disturbances span a broad range of size and frequency and contribute to structural dynamics and heterogeneity of landscapes. Short-term and long-term changes to habitat due to disturbance can influence survival and reproduction of some species (White, 1979; Sousa, 1984; Turner and Dale, 1998). Large, infrequent disturbances, such as vast wildfires, are important ecologically due to considerable scale and duration of impact. Severe fires can alter structure of forests dramatically (Jones et al., 2001) and, therefore, affect fauna (Fisher and Wilkinson, 2005). However, large wildfires often burn with varying intensities and create a mosaic of conditions in forests (Turner and Dale, 1998).

Suppression of fires over the past century in the southwestern United States has altered fire regimes and structure of forests drastically by allowing accumulation of fuel (Swetnam et al., 2001). Forests that once experienced frequent, low-intensity, stand-maintenance fires are now susceptible to high-intensity, stand-replacing fires (Sousa, 1984). The response of small mammals to wildfire is variable over successional stages. During the initiation stage, 0–10 years post-disturbance, abundance of small mammals usually increases with age of stand, in accordance with species-specific habitat associations (Lee, 2002; Fisher and Wilkinson, 2005).

Tree squirrels depend on mature trees for food, nests,

and cover (Gurnell, 1987; Steele and Koprowski, 2001); therefore, squirrels flee wildfires and can suffer negative short-term effects of fire due to reduced food and nesting resources in burned areas (Koprowski et al., 2006). Red squirrels (*Tamiasciurus hudsonicus*) occur in the southwestern United States where vast wildfires have occurred (Grissino-Mayer et al., 1994; Koprowski et al., 2006) and, therefore, provide an appropriate model to examine questions of habitat selection following wildfire. In the western part of their range, individuals defend a territory centered on a conspicuous cache of cones, or midden (Gurnell, 1987), formed by concentrated feeding (Finley, 1969). Locations of middens are associated with characteristics of vegetation in forests, such as density of stand, sometimes represented as basal area and canopy cover (Finley, 1969; Vahle and Patton, 1983). Large, primary middens are used continually and might be indicative of quality habitat. Consequently, abandoned, small, or temporary middens might indicate less-optimal or marginal habitat (Gurnell, 1987).

The Mount Graham red squirrel (*T. h. grahamensis*) is a subspecies isolated in high-elevation, spruce-fir (*Picea-Abies*) and mixed-conifer forests of the Pinaleño Mountains in southeastern Arizona and was listed as endangered in 1987 (Hoffmeister, 1986; United States Fish and Wildlife Service, 1993). Factors contributing to endan-

gered status include possible competition with introduced Abert's squirrels (*Sciurus aberti*), isolated location, and reduced availability of habitat due to disturbances such as infestation by insects, logging, construction, and fire (Koprowski et al., 2005). The population is at the southern terminus of the geographic range of the species, where climate is hotter and drier than at higher latitudes (Hoffmeister, 1986; Smith and Mannan, 1994). Hence, the Pinaleno Mountains might be more prone to wildfires than other portions of the range. Monitoring the response of Mount Graham red squirrels to postfire conditions during the initiation stage of post-disturbance succession could provide beneficial information for management of forests, which is particularly important for peripheral and endangered species.

In 1993, 3,769 ha of potential habitat for red squirrels existed on Mount Graham. Potential habitat was identified by a pattern-recognition model based on presence of middens or evidence of red squirrels in mixed-conifer and spruce-fir forests. Largely due to the Clark Peak fire in 1996, habitat of red squirrels decreased 3.2% during 1993–1997. Damage by insects was the primary cause of loss of habitat during 1997–2003 (Hatten, 2009). In 2004, the Nuttall Complex fire burned 11,898 ha in the Pinaleno Mountains, reaching into both types of forests used by squirrels. Remaining habitat is sparse as a result of these and other natural and anthropogenic disturbances (Koprowski et al., 2006; Hatten, 2009).

With a rate of loss of 35% over 14 days, direct mortality of Mount Graham red squirrels due to the Nuttall Complex fire exceeds many annual rates of loss in populations and, thus, seems relatively high. However, most red squirrels survived (Koprowski et al., 2006). Insight into response of this critically endangered subspecies to postfire conditions during the initiation stage of succession will allow managers to make more informed decisions concerning management of forests. In addition, methods of research and management might be applicable to other peripheral or endangered small mammals (Rushton et al., 2006; Koprowski et al., 2008). Our objectives were to assess use of space, characteristics of habitats associated with middens, and continued occupancy of middens of Mount Graham red squirrels in areas burned by the Nuttall Complex fire.

**MATERIALS AND METHODS**—We studied Mount Graham red squirrels during June 2006–October 2007 within the perimeter of the Nuttall Complex fire (11,898 ha) in the Pinaleno Mountains, 25 km SW Safford, Graham County, Arizona (32.6°N, 109.8°W). The population we studied spanned two vegetational zones: spruce-fir and mixed-conifer forests. Spruce-fir forests were at higher elevations (>3,000 m) and were dominated by Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*). Mixed-conifer forests were at lower elevations with corkbark fir, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), southwestern white pine (*P. strobiformis*), white fir (*Abies*

*concolor*), and quaking aspen (*Populus tremuloides*) as dominant species as described by Froehlich and Smith (1990) and Leonard and Koprowski (2009).

In 2005, Arizona Game and Fish Department conducted a complete census of all known middens and used United States Forest Service Burned Area Emergency Response indicators to assess middens for severity of burn (no burn, light, moderate, severe). We used a random-stratified subset of middens of various severities of burn to conduct surveys of occupancy throughout the perimeter of the burn. We monitored individual squirrels and assessed characteristics of vegetation associated with middens at Merrill Peak, an area of 32.8 ha at 2,831 m elevation, which experienced a heterogeneous burn during the Nuttall Complex fire. We used a slightly modified set of indicators to assess severity of burns at middens and surrounding vegetation (Table 1). Ground fire and damage to crown were assessed easily by these methods; however, whether damage to crown was due to heat from ground fires or from canopy fire is more difficult to assess but not of concern as both are consequences of wildfire.

In censusing surveys and analyses of vegetation, we determined occupancy of middens according to presence of evidence of red squirrels, including fresh diggings, cachings, cones recently stripped of scales, sightings, and resident behaviors, which are territorial vocalizations, chasing of other squirrels, or caching cones (Gurnell, 1987; Mattson and Reinhart, 1997). We trapped and monitored squirrels at Merrill Peak. We used live traps (Model 202, 48.3 by 15.2 by 15.2 cm, Tomahawk Live Trap, Tomahawk, Wisconsin) to capture squirrels at middens, transferred individuals to a handling bag, and assessed mass, sex, age, and reproductive status. We fitted adults (>200 g) with radiocollars (Model SOM 2190, Wildlife Materials International Inc., Carbondale, Illinois) and marked all squirrels for long-term identification with uniquely numbered metal ear tags (Model 1005-1, National Band and Tag Co., Newport, Kentucky) and color-coded plastic washers (Model 1841 3/8-inch, National Band and Tag Co., Newport, Kentucky).

To investigate home range and use of space, we used a receiver and Yagi antenna (models TRX-2000S and F164-165-

TABLE 1—Indicators used to determine severity of burns on surrounding vegetation and at middens of Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*).

| Severity of burn | Indicators   |
|------------------|--|
| Unburned         | No indication of burn.   |
| Light            | Trees are alive, with green needles. Lower branches may be scorched. Individual trees may be burned. Height of scorch <1 m.  |
| Moderate         | Trees were killed, with red needles. Needles on portions of trees may be consumed by fire. Needles on individual trees and on small pockets of trees may be completely consumed by fire. Height of scorch 1–2.3 m. |
| Severe           | Trees were killed. Needles and small branches were consumed entirely by fire. Only the boles may be left on some trees. Leaves, fine branches, and coarse branches were consumed by fire. Height of scorch >2.3 m. |

3FB, respectively, Wildlife Materials International Inc., Carbondale, Illinois) to locate radiocollared red squirrels ( $n = 25$ ; 9 males, 16 females) in daylight hours (0600–1800 h). Consecutive locations for each individual within the same day were separated by a minimum of 1 h to reduce autocorrelation as suggested by Leonard and Koprowski (2009).

We calculated seasonal (summer and autumn) home ranges for individuals ( $n = 10$ : six males, four females) with  $\geq 25$  locations/season in 2007. Summer was defined as June–July, when feeding at dispersed locations predominated. Autumn was August–October, when clipping and caching of cones occurred. We used ArcView GIS 3.3 (Environmental Systems Research Institute, Redlands, California) and used the Animal Movements Analysis extension (Hooge and Eichenlaub, 2000), with smoothing parameters calculated by least-squares-cross-validation to determine 95% size of home range using the fixed-kernel method and 50% size of home range (core area) using the fixed-kernel method (Millspaugh and Marzluff, 2001). To assess if severity of burn affects size of home range or core area, we noted severity of burn of each midden ( $n = 10$ ; seven with no burn, three with light burn).

We used SPSS statistical software to conduct statistical analyses (SPSS 17; SPSS, Inc., Somers, New York). We used the logarithm transformation on size of home range and core area to meet assumptions of normality and homogeneity of variance. We report means as untransformed values for both size of home ranges and core areas by season and severity of burns. Sex does not affect size of home range in red squirrels (Koprowski et al., 2008); therefore, we combined sexes (six males, four females) to increase size of sample in categories of severity of burns.

Because we monitored the same individuals across both seasons, we used a repeated-measures ANOVA to examine effect of season, severity of burn, and interaction of season and severity of burn on size of home ranges and core areas. We conducted a power analysis to determine size of samples needed in our evaluation of size of home range. We compared mean size of home ranges and core areas of red squirrels over all of North America, the White Mountains in Arizona, unburned forest on Mount Graham, insect-damaged forest on Mount Graham, prefire at Merrill Peak, 1-year postfire, and 3 years postfire.

We collected data for vegetation in plots at 13 occupied middens, 17 unoccupied middens, and 15 random locations generated in ArcView 3.3 to assess characteristics of vegetation important for selection of habitat in a burned area. To investigate whether characteristics of vegetation differed at distances from midden, plots were designed with a circular plot (radius = 10 m, area = 0.03 ha) centered on the midden or random location from the focal tree as described by Smith and Mannan (1994) and 10-m by 5-m subplots extending in 40-m transects in each cardinal direction from the circular plot (Fig. 1).

We measured physical and vegetational characteristics at each location. We recorded species, diameter at breast height (DBH), and if a snag was dead or alive for all trees  $> 3$  cm DBH. We assessed severity of burn and measured percentage of slope and aspect of slope from the center of circular and subplots on transects. Aspect of slope was recorded as N ( $315^\circ < \text{aspect} \leq 45^\circ$ ), E ( $45^\circ < \text{aspect} \leq 135^\circ$ ), S ( $135^\circ < \text{aspect} \leq 225^\circ$ ), and W ( $225^\circ < \text{aspect} \leq 315^\circ$ ). We used a spherical densiometer as described by Strickler (1959) to determine canopy cover at 0, 5,

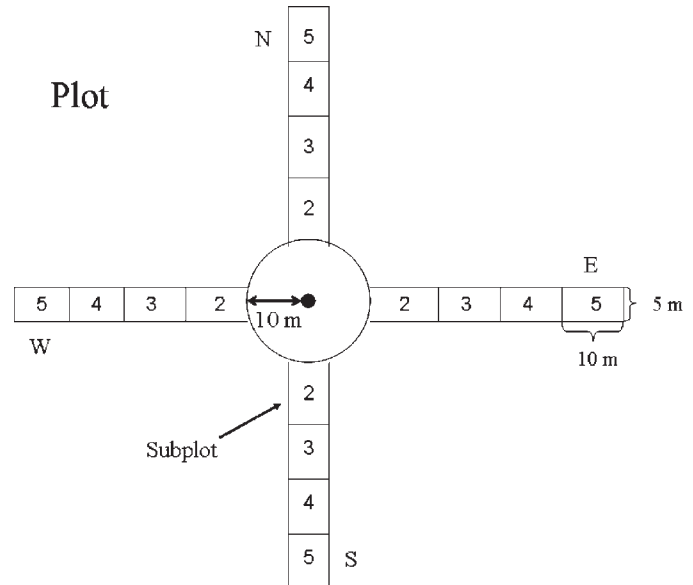


FIG. 1—Configuration of plot and subplots used to characterize physical attributes of habitat occupied by Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) at Merrill Peak, Pinaleno Mountains, Graham County, Arizona.

and 10 m from the center in circular plots and at the center of each subplot on transects.

We examined physical and vegetational characteristics of all three types of sites (occupied midden, unoccupied midden, and random location). We categorized middens as occupied if we saw evidence of occupancy at any time during our study. When assessing differences in structure of vegetation, we included all physical characteristics and distance from center of plot as covariates. We performed analyses on whole plots, then subplots grouped by distance from center of plots, to investigate characteristics of habitat at various spatial scales.

We used MINITAB 13 (MINITAB, Inc., State College, Pennsylvania) for analyses and, to reduce impacts of multicollinearity, excluded variables that had high correlation (correlation  $> 0.75$ ). In our analysis to determine variables most important in distinguishing middens and random locations, and in our analysis of occupied and unoccupied middens, total basal area per ha and basal area of live trees per ha were highly correlated; we used total basal area per ha. In our analysis of middens and random locations, number of dead trees and basal area of dead trees also were correlated highly; we used number of dead trees.

We performed logistic regression on data from whole plots, combining all data from subplots, to determine variables that were most important in predicting whether a site was an occupied or unoccupied midden, and a midden or random location. Because we had no a priori models to explain differences between middens and random locations, we used stepwise selection ( $P < 0.15$  for entry,  $P > 0.15$  for removal) of variables to include in a logistic-regression model.

We used two-tailed  $t$ -tests to test for differences in physical and vegetational characteristics for subplots grouped by distance from center of each plot for middens versus random locations and occupied versus unoccupied middens. We used data from 15 middens that were selected randomly from all occupied and

unoccupied middens for comparison of locations of middens and random locations.

Plots were selected randomly and data for whole plots, therefore, were independent. However, data from grouped 10-m subplots were not completely independent due to proximity of subplots per transect. The probability of committing one or more type I errors per family of tests (i.e., per characteristic of vegetation) was 0.33. We used a Bonferroni correction, restricting  $\alpha = 0.01$  (Abdi, 2007), to correspond with a traditional uncorrected  $\alpha = 0.05$ . However, because of the danger of committing type II errors and suggesting that a potentially important event such as fire has no impact when it might for this critically endangered species, we consider tests with  $P < 0.05$  as significant to indicate potential biological impacts of what may be marginal statistical significance.

From 1,293 previously known middens (Rushton et al., 2006), we surveyed a random sample ( $n = 223$ ) of middens stratified by severity of burn ( $n = 56$  no burn,  $n = 56$  light burn,  $n = 47$  moderate burn,  $n = 64$  severe burn) during 14 October–4 November 2006 and 13–28 October 2007 within the perimeter of the Nuttall Complex fire that occurred in 2004. During each census, observers categorized middens as occupied or unoccupied.

We calculated a percentage of occupied middens within each category of burn for both years and performed a Pearson's  $\chi^2$  analysis on a number of occupied middens between years. We performed a  $\chi^2$  goodness-of-fit analysis on a number of occupied middens between each category of burn. To assess continued occupancy of middens, we performed a Pearson's  $\chi^2$  analysis on frequency of occupied middens across categories of burns by middens that were occupied for only 1 year and those occupied both years. We assigned scores of occupancy to middens according to number of years occupied postfire (0 years = never occupied, 1 year = occupied 1 year, 2 years = occupied 2 years). We performed a  $t$ -test on mean scores of occupancy of burned and unburned middens to determine if percentage of continually occupied middens was different between burned and unburned categories.

**RESULTS**—Mean size of core areas in summer was  $0.059 \pm 0.017$  ha for red squirrels using unburned middens ( $n = 7$ ) and  $0.039 \pm 0.034$  ha for red squirrels using lightly burned middens ( $n = 3$ ). Mean size of core areas in autumn was  $0.064 \pm 0.024$  ha for reds squirrels using unburned middens ( $n = 7$ ) and  $0.145 \pm 0.070$  ha for red squirrels using lightly burned middens ( $n = 3$ ). Mean size of home range in summer was  $0.317 \pm 0.119$  ha for red squirrels using unburned middens ( $n = 7$ ) and  $0.178 \pm 0.140$  ha for red squirrels using lightly burned middens ( $n = 3$ ). Mean size of home range in autumn was  $0.285 \pm 0.089$  ha for red squirrels using unburned middens ( $n = 7$ ) and  $0.609 \pm 0.296$  ha for red squirrels using lightly burned middens ( $n = 3$ ).

A main effect of season on both size of home ranges and core areas was apparent (repeated-measures ANOVA: size of home range,  $F_{1,8} = 15.37$ ,  $P = 0.004$ ; size of core area,  $F_{1,8} = 14.02$ ,  $P = 0.006$ ). No main effect of severity of burn on size of home range or size of core area was detected (repeated-measures ANOVA: size of home

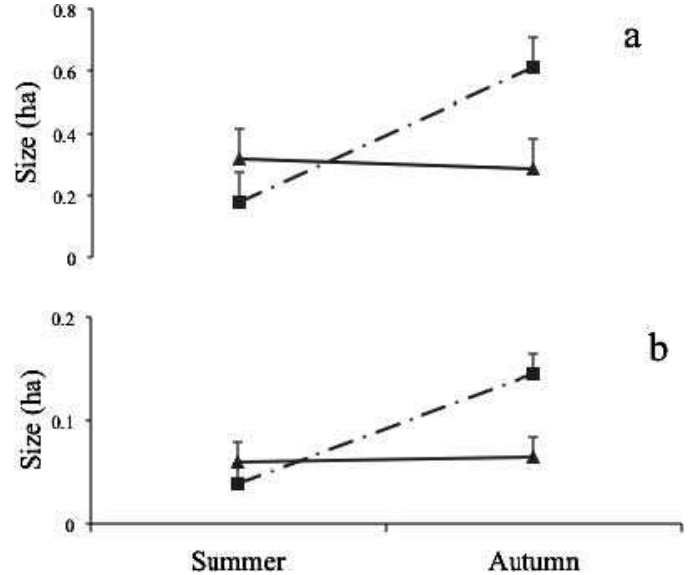


FIG. 2—Mean sizes of a) home ranges and b) core areas of Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) by severity of burn (▲ = no burn, ■ = light burn) and season, Merrill Peak, Pinaleno Mountains, Graham County, Arizona, 2007.

range,  $F_{1,8} = 0.232$ ,  $P = 0.643$ ; size of core area,  $F_{1,8} = 0.196$ ,  $P = 0.670$ ). However, an interaction existed between season and severity of burn for both size of home ranges and core areas (repeated-measures ANOVA: size of home range,  $F_{1,8} = 10.30$ ,  $P = 0.012$ ; size of core area,  $F_{1,8} = 14.18$ ,  $P = 0.006$ ; Fig. 2), thereby complicating interpretation. Given the small sample, our power was reduced such that a sample of 30 animals was required to obtain a power of  $1 - \beta = 0.8$  on size of home range.

Of the 10 variables used to characterize habitat of middens, four were selected via stepwise logistic regression. Slope, canopy cover, severity of burn, and aspect were important variables for distinguishing middens from random locations. Three variables were selected in distinguishing locations of occupied from unoccupied middens; dead trees, aspect, and total number of trees (Table 2).

At locations of middens compared to random sites in the 10-m circular plots, severity of burn tended to be greater ( $t_{28} = 2.05$ ,  $P = 0.049$ ). In addition, DBH of individual trees were 3–258 cm and basal area was larger ( $t_{28} = -2.65$ ,  $P = 0.013$ ). There were more dead trees ( $t_{28} = 2.25$ ,  $P = 0.033$ ). Locations of middens also tended to have more canopy cover than random sites at 30–40 m ( $t_{22} = 2.48$ ,  $P = 0.020$ ) and 40–50 m ( $t_{19} = 2.17$ ,  $P = 0.040$ ) from centers of plots.

Areas with occupied middens had more canopy cover than those with unoccupied middens at 10–20 m ( $t_{27} = 2.69$ ,  $P = 0.012$ ) and 20–30 m ( $t_{27} = 2.55$ ,  $P = 0.017$ ) from centers of plots. Areas with occupied middens had more live trees than those with unoccupied middens at 10–20 m ( $t_{27} = 3.26$ ,  $P = 0.003$ ). At 20–30 m, occupied middens

TABLE 2—Stepwise logistic-regression model to assess odds of a site being a midden of a Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*;  $n = 15$ ) versus a random location ( $n = 15$ ) or a midden being occupied ( $n = 13$ ) versus unoccupied ( $n = 17$ ) after a low-intensity, patchy burn at Merrill Peak, Pinaleño Mountains, Graham County, Arizona, autumn 2007.

| Source                            | Estimate | SE    | P      | Odds ratio |
|-----------------------------------|----------|-------|--------|------------|
| Midden versus random location     |          |       |        |            |
| Slope                             | -0.055   | 0.030 | 0.068  | 0.947      |
| Canopy cover                      | -0.039   | 0.015 | 0.009  | 0.962      |
| Severity of burn                  | -0.790   | 0.341 | 0.021  | 0.454      |
| Aspect                            | -0.229   | 0.072 | 0.001  | 0.795      |
| Midden occupied versus unoccupied |          |       |        |            |
| Total number of trees             | 0.113    | 0.029 | <0.001 | 1.120      |
| Number of dead trees              | -0.120   | 0.025 | <0.001 | 0.890      |
| Aspect                            | -0.146   | 0.086 | 0.092  | 0.860      |

had slightly more live trees than unoccupied middens ( $t_{26} = 2.17$ ,  $P = 0.039$ ).

Occupancy did not differ between years in our stratified-random sample of 223 middens. In the no-burn category, 20 (35.7%) middens, 13 (23.2%) in light burn, 1 (2.1%) in moderate burn, and 0 (0%) in severe burn were occupied in 2006. In 2007, 25 (44.6%) middens in the no-burn category, 16 (28.6%) in light burn, 0 in moderate burn, and 1 (1.6%) in severe burn ( $\chi^2_3 = 2.05$ ,  $P = 0.563$ ) were occupied. We combined data from both years and determined that occupancy of middens was influenced by severity of burn ( $G_{adj} = 208.43$ ,  $P < 0.001$ ).

In the no-burn category, 17 (54.8%) middens were occupied for only 1 year and 14 (45.2%) for both years. In the light-burn category, 7 (38.9%) were occupied for 1 year and 11 (61.1%) for both years. For both the moderate-burn and severe-burn categories, only one midden was occupied for 1 year and none was occupied for both years ( $\chi^2_3 = 3.16$ ,  $P = 0.367$ ). Unburned middens were occupied more continually after wildfire than burned middens (Fig. 3;  $t_{221} = 6.49$ ,  $P < 0.001$ ; mean occupancy score was 0.62 years lower for burned than unburned middens, 95% CI from 0.43 to 0.81).

**DISCUSSION**—Large home ranges might indicate a scarcity of available resources (Mitchell and Powell, 2004), as size of territory of red squirrels is regulated by food (C. C. Smith, 1968). Mean size of home range of red squirrels in North America is <0.6 ha (Munroe et al., 2009). The Mogollon red squirrel (*Tamiasciurus hudsonicus mogollensis*), studied in Apache-Sitgreaves National Forest ca. 110 km N Mount Graham, also had a small home range of ca. 0.40 ha (Leonard and Koprowski, 2009). Mean size of home ranges for Mount Graham red squirrels exceed 3.0 ha in unburned forest, surpassing the largest home ranges reported for North American red squirrels (Froehlich and Smith, 1990; Kreighbaum and Van Pelt, 1996; Koprowski et al., 2008; Zugmeyer and Koprowski, 2009). This suggests that Mount Graham red squirrels must range widely due to

limited availability of resources. Following low-intensity, heterogeneous fire, size of home ranges decreased to range-wide levels and remained so for  $\geq 3$  years (Fig. 4; Leonard and Koprowski, 2009; this study). The fact that size of home ranges after the fire was similar to those of populations of red squirrels in healthy forests suggests that initial quality of habitat increased following the Nuttall Complex fire in the lightly burned forests where we examined home ranges.

Trends were similar in size of core areas and home ranges in regard to interaction of season and severity of burn. Seasonality affects size of home ranges of Mount Graham red squirrels; core areas and home ranges are larger in summer than in autumn (Koprowski et al., 2008). The interaction between seasonality and severity of burn in influencing size of core areas and home ranges appeared to be due to size of territory of unburned

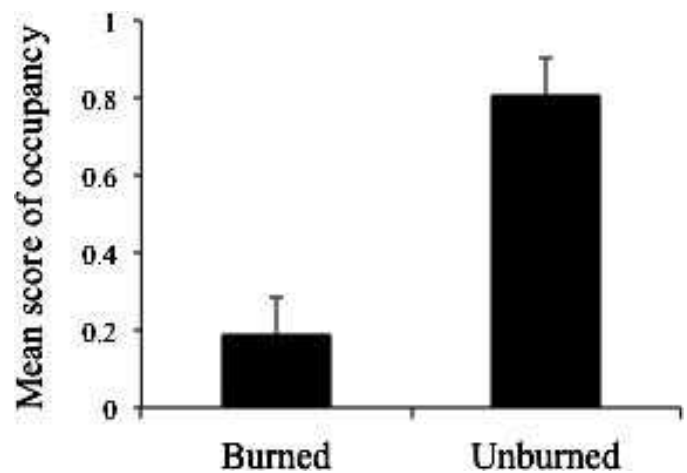


FIG. 3—Number of years (mean  $\pm$  SE) of occupancy for burned and unburned middens by Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) within the perimeter of the Nuttall Complex fire, Pinaleño Mountains, Graham County, Arizona, 2006 and 2007. Scores for occupancy of middens were assigned as 0 = never occupied, 1 = occupied 1 year, 2 = occupied 2 years.

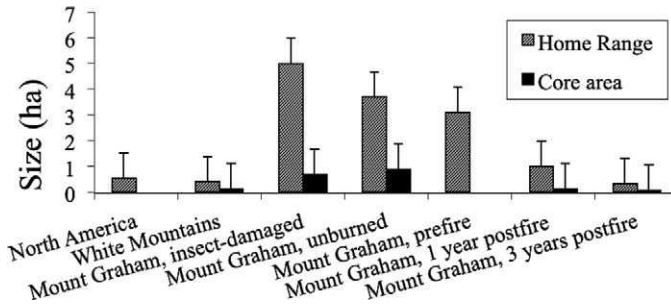


FIG. 4—Mean sizes of home ranges and core areas between red squirrels across North America, Mogollon red squirrels (*Tamiasciurus hudsonicus mogollonensis*) in the White Mountains, Apache County, Arizona, and Mount Graham red squirrels (*T. h. grahamensis*) in the Pinaleno Mountains, Graham County, Arizona, in unburned, insect-damaged, prefire, and postfire forests. Data for size of core area across North America and for prefire on Mount Graham were not available.

middens changing little among seasons, whereas territories with lightly burned middens were larger in autumn than in summer. During autumn, red squirrels need to invest energy in defending larderhoards at middens (Gurnell, 1984). Resources in burned areas could be scarcer during autumn or loss of part of the midden might reduce stores from the previous year that usually would augment the crop of cones in the current year (M. C. Smith, 1968). The effect of severity of burn alone may be difficult to determine because all burned middens that remained in use were only lightly burned and, therefore, might not have been much different than unburned middens. However, red squirrels chose lightly burned areas for middens more often than moderately or severely burned areas. This suggests that red squirrels are sensitive to burns and avoid heavily burned areas but can still persist in lightly burned areas. One explanation might be that red squirrels evolved with frequent ground fires (Kiltie, 1989) and can escape into the canopy (Kirkpatrick and Mosby, 1981) in the event of a low-intensity fire. In contrast, crown-fires were not common historically in the southwestern United States (Brown and Smith, 2000); thus, red squirrels might not have evolved effective ways of surviving severe burns (Koprowski et al., 2006).

Characteristics of vegetation such as basal area and canopy cover are important in areas used by red squirrels (Finley, 1969; Vahle and Patton, 1983). In undamaged, mixed-conifer forests on Mount Graham, greater total basal area, more dead trees, and more canopy cover were important attributes of locations of middens compared to random sites (Smith and Mannan, 1994). Merrill Peak experienced relatively low-intensity burns compared to other areas covered by the Nuttall Complex fire. Severity of burn was slightly greater at middens within the 10-m-circular plots; however, the mean was within the low-burn category. DBH of dead trees was greater at middens prior to (Froehlich and Smith, 1990) and following fire. At the 10-m scale, characteristics of middens seem less different

from random locations on Merrill Peak compared to other transition-zone forests on Mount Graham (Smith and Mannan, 1994). Mixed-conifer forests can have many combinations of densities, sizes, and compositions of trees (Vahle and Patton, 1983), and forests on Merrill Peak might be more homogenous than other transition-zone areas of Mount Graham.

Smith and Mannan (1994) reported that red squirrels appeared to choose areas with a more closed canopy farther from middens in addition to close to middens. Our analysis revealed that occupied middens tended to have higher canopy cover at 10–30 m from centers of plots than unoccupied middens. In addition, when we compared middens to random sites, middens had higher canopy cover at 30–50 m from centers of plots. Canopy cover can provide access routes and protection from predators (Hughes and Ward, 1993) and also increase crown area for production of seeds (Smith and Mannan, 1994).

We elucidated similar distinguishing characteristics in our increased plots on 40-m transects in each cardinal direction, as researchers who used 10-m-circular plots, for middens when compared to random sites and occupied compared to unoccupied middens. Our results also suggest that characteristics such as high basal area and canopy cover are important for persistence of Mount Graham red squirrels as reported previously (Finley, 1969; Vahle and Patton, 1983). Therefore, a range of scales of assessment may be important in detecting characteristics of habitat associated with middens of red squirrels in various areas of Mount Graham.

Responses by populations of small mammals to fire are related to uniformity and intensity of fire; availability of food and cover are important influences (Krefting, 1974; Smith et al., 2000). In the short term, patches of lightly burned vegetation can provide refugia for small mammals, whereas severe burns can kill most of the trees, thereby limiting cover and resources (Smith et al., 2000). Red squirrels form middens beneath preferred feeding sites (Finley, 1969; Hurly and Lourie, 1997) and generally avoid recent stand-replacing fires (Smith et al., 2000). We determined that severity of burn influenced occupancy of middens in our analyses. On a mountain-wide scale with a mosaic burn in mixed-conifer and spruce-fir forests, occupancy of middens by Mount Graham red squirrels tended to be higher at unburned sites and low in moderately and severely burned sites. Red squirrels prefer undisturbed sites for middens (Vahle and Patton, 1983) and middens that are continually used might indicate quality of habitat, whereas abandoned or temporary middens might indicate less-preferred or poor-quality habitat (Finley, 1969; Gurnell, 1987).

Wildfires, due to their unprecedented scale and intensity (Parsons and DeBenedetti, 1979; Allen, 1994), may present detrimental consequences for this critically endangered subspecies. At a local scale, burned areas

have some negative impacts on Mount Graham red squirrels; animals tend not to occupy burned middens or select burned areas as sites for middens. However, an overall decrease in mean size of home range in a lightly burned area during 3 years following wildfire indicates the possibility that availability of resources might have increased. Over time, a mixture of few large burns with many small burns and variation within the burned areas perpetuates the mosaic nature of landscapes (Smith et al., 2000). Therefore, by providing resources and sites for middens, an area with unburned and lightly burned patches might be advantageous to Mount Graham red squirrels during the initiation stage of post-disturbance succession. Populations that survive the initial detrimental impacts of fire might have several years of enhanced resources, during which conservation efforts can focus on promoting long-term persistence.

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#### LITERATURE CITED

- ABDI, H. 2007. The Bonferroni and Šidák corrections for multiple comparisons. Pages 103–107 in *Encyclopedia of measurement and statistics* (N. J. Salkind, editor). Sage Publications, Thousand Oaks, California.
- ALLEN, L. S. 1994. Fire management in the sky islands. Pages 386–388 in *Biodiversity and management of the Madrean Archipelago: the sky islands of the southwestern United States and northwestern New Mexico* (L. F. DeBano, G. J. Gottfried, R. H. Hamre, C. B. Edminster, P. F. Ffolliott, and A. Ortega-Rubio, technical coordinators). United States Department of Agriculture Forest Service, General Technical Report RM-GTR-264:1–669.
- BROWN, J. K., AND J. K. SMITH. 2000. Wildland fire in ecosystems: effects of fire on flora. United States Department of Agriculture Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-42-2:1–257.
- FINLEY, R. B. J. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Pages 233–273 in *Contributions in mammalogy* (J. K. Jones, Jr., editor). Miscellaneous Publications, Museum of Natural History, University of Kansas 51:1–428.
- FISHER, J. T., AND L. WILKINSON. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35:51–81.
- FROELICH, G. F., AND N. S. SMITH. 1990. Habitat use by the Mt. Graham red squirrel. Pages 118–125 in *Managing wildlife in the Southwest symposium* (P. R. Krausman and N. S. Smith, editors). Arizona Chapter of the Wildlife Society, Phoenix.
- GRUSSINO-MAYER, H. D., C. H. BAISAN, AND T. W. SWETNAM. 1994. Fire history in the Pinaleño Mountains of southeastern Arizona: effects of human-related disturbances. Pages 399–407 in *Biodiversity and management of the Madrean Archipelago: the sky islands of the southwestern United States and northwestern New Mexico* (L. F. DeBano, G. J. Gottfried, R. H. Hamre, C. B. Edminster, P. F. Ffolliott, and A. Ortega-Rubio, technical coordinators). United States Department of Agriculture Forest Service, General Technical Report RM-GTR-264:1–669.
- GURNELL, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. *Animal Behaviour* 32:1119–1131.
- GURNELL, J. 1987. The natural history of squirrels. Facts on File, Inc., New York.
- HATTEN, J. R. 2009. Mapping and monitoring Mt. Graham red squirrel habitat with GIS and thematic mapper imagery. Pages 170–184 in *The last refuge of the Mt. Graham red squirrel: ecology of endangerment* (H. R. Sanderson and J. L. Koprowski, editors). University of Arizona Press, Tucson.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. University of Arizona Press, Tucson.
- HOOGE, P. N., AND B. EICHENLAUB. 2000. Animal movement extension to Arcview, version 2.0. Alaska Science Center-Biological Science Office, United States Geological Survey, Anchorage.
- HUGHES, J. J., AND D. WARD. 1993. Predation risk and distance to cover affect foraging behavior in Namib Desert gerbils. *Animal Behaviour* 46:1243–1245.
- HURLY, T. A., AND S. A. LOURIE. 1997. Scatterhoarding and larderhoarding by red squirrels: size dispersion, and allocation of hoards. *Journal of Mammalogy* 78:529–537.
- JONES, J., R. D. DEBRUYN, J. J. BARG, AND R. J. ROBERTSON. 2001. Assessing the effects of natural disturbance on a Neotropical migrant songbird. *Ecology* 82:2628–2635.
- KILTE, R. A. 1989. Wildfire and the evolution of dorsal melanism in fox squirrels, *Sciurus niger*. *Journal of Mammalogy* 70:726–739.
- KIRKPATRICK, R. L., AND H. S. MOSBY. 1981. Effect of prescribed burning on tree squirrels. Pages 99–101 in *Prescribed fire and wildlife in southern forests* (G. W. Wood, editor). Belle Baruch Forest Science Institute, Clemson, South Carolina.
- KOPROWSKI, J. L., M. I. ALANEN, AND A. M. LYNCH. 2005. Nowhere to run and nowhere to hide: response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biological Conservation* 126:491–498.
- KOPROWSKI, J. L., S. R. B. KING, AND M. MERRICK. 2008. Expanded home ranges in a peripheral population: space use by endangered Mt. Graham red squirrels. *Endangered Species Research* 4:227–232.
- KOPROWSKI, J. L., K. M. LEONARD, C. A. ZUGMEYER, AND J. L. JOLLEY. 2006. Direct effects of fire on endangered Mt. Graham red squirrels. *Southwestern Naturalist* 51:59–63.
- KREFTING, L. W. 1974. Small mammals and vegetation changes after fire in a mixed-conifer hardwood forest. *Ecology* 55:1391–1398.
- KREIGHBAUM, M. E., AND W. E. VAN PELT. 1996. Mount Graham red squirrel juvenile dispersal telemetry study. *Arizona Game and*



- Fish Department, Nongame and Endangered Wildlife Program Technical Report 89:1–25.
- LEE, P. 2002. Stages of forest succession. Pages 3.1–3.3 in *The ecological basis for stand management in Alberta* (S. Song, editor). Alberta Research Council, Vegreville, Alberta, Canada.
- LEONARD, K. M., AND J. L. KOPROWSKI. 2009. A comparison of habitat use and demography of red squirrels at the southern edge of their range. *American Midland Naturalist* 162:125–138.
- MATTSON, D. J., AND D. P. REINHART. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology* 34:926–940.
- MILLSPAUGH, J. J., AND J. M. MARZLUFF. 2001. *Radio tracking and animal populations*. Academic Press, San Diego, California.
- MITCHELL, M. S., AND R. A. POWELL. 2004. A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modeling* 177:209–232.
- MUNROE, K. E., J. L. KOPROWSKI, AND V. L. GREER. 2009. Reproductive ecology and home range size of red squirrels: do Mt. Graham red squirrels fit the pattern? Pages 287–298 in *The last refuge of the Mt. Graham red squirrel: ecology of endangerment* (H. R. Sanderson and J. L. Koprowski, editors). University of Arizona Press, Tucson.
- PARSONS, D. J., AND S. H. DEBENEDETTI. 1979. Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management* 2:21–33.
- RUSHTON, S. P., D. J. A. WOOD, P. W. W. LURZ, AND J. L. KOPROWSKI. 2006. Modeling the population dynamics of the Mt. Graham red squirrel: can we predict its future in a changing environment with multiple threats? *Biological Conservation* 131:121–131.
- 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 three squirrels *Tamiasciurus*. *Ecological Monographs* 38:31–63.
- SMITH, J. K., L. J. LYON, M. H. HUFF, R. G. HOOPER, E. S. TELFER, AND D. S. SCHREINER. 2000. Wildland fire in ecosystems: effects of fire on fauna. United States Department of Agriculture Forest Service, General Technical Report RMRS-GTR-42-1:1–84.
- SMITH, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. *Journal of Wildlife Management* 32:305–317.
- SOUSA, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353–391.
- STEELE, M. A., AND J. L. KOPROWSKI. 2001. *North American tree squirrels*. Smithsonian Institution Press, Washington, D.C.
- STRICKLER, G. S. 1959. Use of the spherical densiometer to estimate density of forest canopy on permanent sample plots. United States Department of Agriculture Forest Service, General Technical Report RM-217:1–5.
- SWETNAM, T. W., C. H. BAISAN, AND J. M. KAIB. 2001. Forest fire histories of the Sky Islands of La Frontera. Pages 95–119 in *Changing plant life of La Frontera* (G. L. Webster and C. J. Bahre, editors). University of New Mexico Press, Albuquerque.
- TURNER, M. G., AND V. H. DALE. 1998. Comparing large, infrequent disturbances: what have we learned? *Ecosystems* 1:493–496.
- UNITED STATES FISH AND WILDLIFE SERVICE. 1993. *Mount Graham red squirrel recovery plan*. United States Fish and Wildlife Service, Phoenix, Arizona.
- VAHLE, J. R., AND D. R. PATTON. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. *Journal of Forestry* 81:14–15.
- WHITE, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229–299.
- ZUGMEYER, C. A., AND J. L. KOPROWSKI. 2009. Severely insect-damaged forest: a temporary trap for red squirrels? *Forest Ecology and Management* 257:464–470.

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