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EFFECTS OF FIRE ON ENDANGERED MOUNT GRAHAM RED SQUIRRELS (*TAMIASCIURUS HUDSONICUS GRAHAMENSIS*): RESPONSES OF INDIVIDUALS WITH KNOWN FATES

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ABSTRACT—We studied demography and behavior of endangered Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) inhabiting areas within and outside low-intensity burns following the Nuttall Fire in the Pinaleno Mountains, Arizona. Body mass, proportion of individuals in reproductive condition, and distance squirrels traveled to nest did not differ between squirrels within and outside the perimeter of the fire. Within the perimeter, red squirrels had smaller home ranges and shifted territories less frequently and had shorter distances from their previously held territories than squirrels outside the perimeter. Mount Graham red squirrels evolved with patchy, low-intensity fires like those that burned in mixed-conifer forests in the Pinaleno Mountains and may be able to persist in areas affected by this level of disturbance.

RESUMEN—Estudiamos la demografía y el comportamiento de las ardillas rojas (*Tamiasciurus hudsonicus grahamensis*) amenazadas que habitan dentro y fuera de las áreas quemadas de baja intensidad que siguieron al incendio Nuttall en las montañas Pinaleno, Arizona. La masa corporal, proporción de individuos en condición reproductiva y la distancia recorrida por las ardillas al nido no difirieron entre las ardillas dentro y fuera del perímetro del incendio. Dentro del perímetro del incendio, las ardillas rojas tuvieron rangos de hogar más pequeños, se cambiaron de territorios menos frecuentemente y se desplazaron distancias más cortas desde sus territorios anteriores que las ardillas fuera del perímetro. Las ardillas rojas evolucionaron con incendios irregulares de baja intensidad como los que se presentaron en los bosques mixtos de coníferas en las montañas Pinaleno y pueden ser capaces de persistir en áreas afectadas por este nivel de perturbación.

Fire is an important driver that structures many communities in forests (Mutch, 1970; Pyne, 1982) and alters dynamics of forests, leading to adaptations in resident species to persist in these modified landscapes (Chandler et al., 1983; Pendergrass et al., 1999). Prior to European settlement, lightning-ignited fires burned over much of North America (Parsons and DeBenedetti, 1979; Chandler et al., 1983) creating floral and faunal diversity in forests (Suffling et al., 1988; McCullough et al., 1998). Beginning in the 1900s, suppression of fire has resulted in increased densities of trees, woody debris, and recruitment of non-fire-resistant species of trees (Parsons and DeBenedetti, 1979; Cole and Landres, 1996), leading to increased fuel loads, lower frequencies of fires, and a higher probability of catastrophic fire in many forests (Kauffman and Martin, 1988;

Trabaud et al., 1993; Baker, 1994; Sampson et al., 1994; Little, 1995; Keeley and Fotheringham, 2001). The importance of documenting response of forests to wild and prescribed fire is progressively more important with increased use of prescribed burns and occurrence of devastating wildfires (Weber and Taylor, 1992; Cardille et al., 2001).

Prescribed and wildfires were cited in the decline of 7% of 83 endangered species of plants and animals in the United States (Wilcove et al., 1998). Effects of fire on wildlife often have been measured in terms of overall composition of species or population-level changes, such as abundance or reproduction (Krefting and Ahlgren, 1974; Crouner and Barrett, 1979; Braithwaite, 1987; Simons, 1991; Francisco et al., 1995; Hutto, 1995; Vieira and Marinho-Filho, 1998). Information on fate of individuals rarely is

available, resulting in gaps in knowledge of mortality of individuals, shifts in behavior, or mechanisms leading to post-fire composition of populations. Documenting direct mortality and changes in demographic characteristics and movement can provide information on how to conserve or reestablish populations post-disturbance. This is particularly important for endangered or imperiled species, as each individual lost brings the population closer to extinction.

The endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) is a forest-obligate endemic to upper-elevation, spruce-fir and mixed-conifer forests of the Pinaleño Mountains, Arizona (D. E. Brown, 1984). This subspecies relies on mature forests to provide food, nests, and runways for locomotion. Forests also offer appropriate microclimate for establishing middens, which are larders for caching cones that are located centrally within space used by this territorial species (Hatt, 1929; Layne, 1954; C. C. Smith, 1968; Finley 1969). During 1575–1880, low-intensity fires burned every 6–8 years in the mixed-conifer forests of the Pinaleño Mountains (H. D. Grissino-Mayer et al., in litt.); however, suppression of fire has altered this regime and heightened the threat of catastrophic fire (United States Forest Service, in litt.). Red squirrels in this area may be able to survive wildfires similar to low-intensity fires that burned historically by escaping to nests or fleeing outside the burned area (Bendell, 1974; Koprowski et al., 2006). However, long-term success of individuals may be reduced if important foods, middens, nest sites, or structures used for escape cover are damaged by fire (Larsen et al., 1997; Koprowski et al., 2006).

In the Pinaleño Mountains, the Nuttall Fire burned 11,898 ha of mixed-conifer and spruce-fir forest during June–July 2004. In addition to wildfire, low-intensity fires were set during fire-fighting efforts. The Nuttall Fire presented a natural experiment to determine effects of fire on individuals marked prior to fire as part of a long-term study (Koprowski, 2005; Koprowski et al., 2005, 2006; Young et al., 2002). To determine how fire affected individual red squirrels within burned areas, we compared body mass and post-fire survival and reproduction within and outside the Nuttall Fire Perimeter. Body mass can be used as an index of physical condition and may affect survival (Pearson et al., 2003); reproduction and survival may decrease in fire-affected

areas due to destruction of important resources. Additionally, we looked at occupancy of middens to determine how red squirrels respond to alteration of a structure that is necessary for survival and that red squirrels show high site fidelity for (M. C. Smith, 1968; Hurly and Lourie, 1997). Destruction of middens or alteration of structure of forest around middens due to fire will likely force individuals to establish middens elsewhere. We compared use of space and nesting behavior of individuals within and outside the perimeter of the fire to determine if fire-induced alterations in habitat result in changes in movements or use of nests. Reduced food and destruction of nesting structures due to fire may result in large home ranges or increase distance squirrels travel to nest, because individuals are forced to travel further to reach these resources (J. H. Brown, 1984; Mitchell and Powell, 2004).

MATERIALS AND METHODS—We collected information on body mass, demography, use of space, and nesting behavior of Mount Graham red squirrels during May 2004–November 2005 on two study sites in the Pinaleño Mountains, Graham County, Arizona (32.6°N, 109.8°W). Both locations were sites of ongoing collection of data on ecology and biology of red squirrels (Koprowski, 2005; Koprowski et al., 2005, 2006; Young et al., 2002). The Fire Site (2,831 m elevation) was a 32.8-ha area that was exposed to low-intensity back-burns during fire-fighting efforts. About one-half of the study area was burned; 20% was lightly burned and 30% was severely burned. This site was comprised of mature-to-old-growth mixed-conifer species of trees (Froehlich and Smith, 1990; Young et al., 2002) dominated by Douglas fir (*Pseudotsuga menziesii*) with white fir (*Abies concolor*), corkbark fir (*Abies lasiocarpa* var. *arizonica*), Engelmann spruce (*Picea engelmannii*), Ponderosa pine (*Pinus ponderosa*), southwestern white pine (*Pinus strobiformis*), and quaking aspen (*Populus tremuloides*) present in smaller numbers (Froehlich and Smith, 1990). The No-fire Site (ca. 3,000 m elevation) was 72.1 ha and located 6.5 km east of the Fire Site, outside the perimeter of the fire. This site was of similar age and species composition as the Fire Site, although corkbark fir was the dominant species of tree (Leonard, 2006).

During May 2004–October 2005, we placed a Tomahawk trap (Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanuts and peanut butter at active middens and used a canvas cone to handle squirrels (Koprowski, 2002). Prior to the fire, we uniquely marked 12 adults (>200 g; 4 males, 8 females) at the Fire Site and 28 adults (15 males, 13 females) at the No-fire Site with numbered Monel ear tags and colored washers (National Band and Tag Co., Newport, Kentucky), and radiocollars (Wildlife Materials International, Inc., Carbondale, Illinois) weighing <5% of body mass (Koprowski et al., 2006). We

recorded body mass, sex, and reproductive condition of squirrels and released animals at the site of capture. Scrotal and partially scrotal males, as well as estrous, pregnant, lactating, and recently lactating females were considered reproductive. We determined proportion of animals in reproductive condition during pre-fire in spring (March–May) 2004, and post-fire in spring 2005, summer (June–August) 2004 and 2005, and autumn (September–November) 2004 and 2005.

To determine if survival differed between study sites, we attempted to locate individuals visually at ≥ 1 time/month from immediately after the fire was extinguished (July 2004) through the end of the study (November 2005). Mortality was verified by using radiotelemetry to locate remains of deceased individuals. Fates of several individuals could not be verified due to failure of collar or emigration from the study site. These individuals were censored in our analyses.

We visited middens of radiocollared squirrels at the Fire Site after the fire and categorized middens as burned or unburned; burned middens had fire-scorched or charred piles of cones. Radiotelemetry and direct observation were used to determine shifts in post-fire occupancy from middens held pre-fire. If an individual was caching cones, demonstrating territorial behavior (territorial calling or chasing intruders), or was at a location other than its pre-fire midden on several visits, we considered that animal to have shifted its territory. These same criteria were used at the No-fire Site along with information from radiotelemetry plotted using ArcView (Version 3.3, Environmental Systems Research Institute, Redlands, California).

We used information on home range obtained post-fire from 8 red squirrels (1 male, 7 females) at the Fire Site and 15 red squirrels (6 males, 9 females) at the No-fire Site. Home ranges were generated for 3 periods: immediately post-fire in August–November 2004, May–July 2005, and 1-year post-fire in August–November 2005. We divided our study this way because, due to the Nuttall Fire, we could not gather radiotelemetry data at the Fire Site in summer 2004 and only have data from immediately post-fire in that year. We did not collect radiotelemetry data during winter as snow prevented regular access to the Fire Site.

We used biangulation and homing to gather radiotelemetry locations (White and Garrot, 1990). At the Fire Site, 28% of locations were gathered by biangulation and 72% were gathered by homing. At the No-fire Site, 69% of locations were gathered by biangulation and 31% were gathered by homing. Points were taken >60 min apart to ensure independence. Locations gathered with biangulation were gathered <100 m from the focal animal and with inter-bearing angles of 70 – 110° . We used the same techniques to calculate biangulation error with observers obtaining bearings on a radiocollar in a known location. We gathered locations throughout daylight hours to ensure all activity periods were represented. Most individuals were located several times per month and average number of locations/individual/day was 2 (range = 1–8). We plotted area-use curves in Ranges 6 (Anatrack Ltd., Dorset, United Kingdom) and excluded individuals whose ranges did not reach an asymptote. We used the Animal Movement Analysis extension, version 2.0 (United States Geological Survey,

Alaska Science Center, Anchorage, Alaska) in ArcView to generate 50% core areas and 95% home ranges using the fixed kernel method (Worton, 1989).

We located nocturnal nest sites by tracking individuals ≤ 2 h before sunset and followed them to the nest, observing them entering the nest whenever possible. Locations of nest trees were mapped using ArcView. We determined distance from midden to nest for individuals by direct measurement or by using the Distance and Azimuth extension (Version 1.4, Jenness Enterprises, Flagstaff, Arizona) of ArcView. We calculated distance to nest from middens pre-fire in spring and summer, immediately post-fire in summer (July–August) and autumn 2004 (September–November), and 1-year post-fire in summer (June–August) and autumn 2005 (September–November). For each individual, we used the nest closest to the midpoint of each season.

We used nonparametric Wilcoxon rank-sum tests to compare probabilities of survival, time before shifting, distance of shifts, size of home range, and distance of nest from middens of squirrels at the Fire Site and No-fire Site, as well as between squirrels with burned and unburned middens within the Fire Site. We used nonparametric sign tests to compare changes in body mass, size of home range, and distance to nest within individuals over time. We used the known-fate (White and Garrot, 1990), mark-recapture models in program MARK (White and Burnham, 1999) to calculate survival and used Akaike Information Criteria (AIC) adjusted for small samples (AICc; Anderson et al., 2000) for selection of models. Analyses were performed using JMP (SAS Institute, Inc., Cary, North Carolina) and SPSS (SPSS, Inc., Chicago, Illinois) statistical software.

RESULTS—Body mass of animals at the Fire and No-fire sites did not differ over time ($\chi^2 = 0.257$, $df = 1$, $P = 0.308$). All males with data available pre-fire and 1-year post-fire were in reproductive condition in both time periods at both sites (No-fire $n = 9$; Fire $n = 1$). Two females at the No-fire Site were not in reproductive condition when captured pre-fire, but were reproductive 1-year later. All other females at both study sites were in reproductive condition during both pre-fire and post-fire periods (No-fire $n = 9$; Fire $n = 4$).

Four of 9 red squirrels at the Fire Site and 10 of 24 at the No-fire Site were alive 16 months post-fire. Monthly survival did not differ between study sites (Fig. 1; $\chi^2 = 0.776$, $P = 0.38$). The most-parsimonious model included an interactive effect between time and site. Fates of three individuals at the Fire Site and five at the No-fire Site were unknown and, therefore, censored in the analysis.

Of the nine red squirrels alive post-fire at the Fire Site, middens of five of them (one male, four females) were burned. Four of these

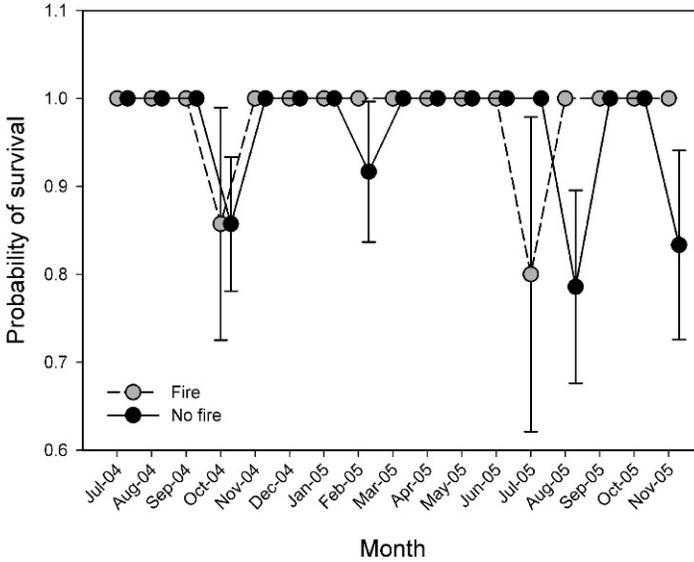


FIG. 1.—Mean monthly probability of survival ($\pm SE$) of Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) within and outside the Nuttall Fire Perimeter, Pinaleno Mountains, Graham County, Arizona, 2004–2005.

animals established middens elsewhere post-fire. Only one with a burned midden, a female, shifted middens more than once; we discovered her remains 20 m from her burned cone scale pile ca. 3 months post-fire. No animals with unburned middens at the Fire Site shifted territories during the study. Three of the four animals that shifted did so immediately after their middens burned, whereas one established a new midden ca. 1 month post-fire. One male with a burned midden moved his nest 9 m away and established a new midden beneath his nest during winter. One female shifted middens twice post-fire, once to her last-known pre-fire nest, where she cached cones in autumn and once in early December, where she established a cone-scale pile at the base of a large tree. Excluding this female, no squirrels with burned middens shifted more than once. On average, red squirrels that shifted middens moved <50 m from their pre-fire middens ($n = 4$, mean = 42.4 ± 20.0 m, range = 9.0–99.5 m).

At the No-fire Site, 10 (six males, four females) of the 28 animals that were alive during pre-fire shifted territories. The first shift occurred several days after the fire was extinguished at the Fire Site ($n = 10$, mean = 136.2 ± 48 days, range = 3–353 days) and four animals shifted more than once (median = 1 shift, range = 1–5 shifts).

Squirrels at the No-fire Site shifted later ($Z = -2.13$, $df = 12$, $P = 0.033$) and further ($n = 10$, mean = 157.9 ± 50.8 m, range = 34.0–519.9 m; $Z = -1.91$, $df = 12$, $P = 0.056$) than squirrels at the Fire Site.

Size of home ranges and core areas did not differ between Fire and No-fire sites immediately post-fire (Table 1). Most home ranges at the Fire Site decreased in size over time, whereas size of home ranges at the No-fire Site tended to increase. When comparing sizes of home ranges and core areas immediately post-fire and 1-year later, use of space did not change at the No-fire Site (Sign test, $n = 12$, $df = 11$, $P = 0.388$), whereas all home ranges at the Fire Site decreased in size ($n = 4$, $df = 3$, $P = 0.124$).

At the Fire Site, average bearing error was 10° ($\pm 7^\circ$ SD) and average distance error was 60 m (± 33 m SD). At the No-fire Site, average bearing error was 5.6° ($\pm 4.5^\circ$ SD) and average distance error was 12 m (± 6 m SD; Koprowski et al., 2008).

Red squirrels traveled greater distances from midden to nest at the No-fire Site than at the Fire Site during summer and autumn 2004 (Fig. 2; pre-fire, $Z = -1.732$, $df = 34$, $P = 0.083$; summer 2004, $Z = -2.497$, $df = 32$, $P = 0.013$; autumn 2004, $Z = -2.282$, $df = 28$, $P = 0.023$), but did not differ from animals at the No-fire Site in

TABLE 1—Mean size of home range ($\pm SE$) and results of comparisons between Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) within and outside the Nuttall Fire Perimeter, Pinaleno Mountains, Graham County, Arizona, 2004–2005; * $P < 0.05$.

Parameter	Fire site	No-fire site	Statistics
Size of home range (ha), August–November 2004	1.48 \pm 0.32 ($n = 8$)	2.01 \pm 0.39 ($n = 22$)	$Z = -0.352$, $df = 28$, $P = 0.725$
Size of home range (ha), May–July 2005	0.62 \pm 0.25 ($n = 5$)	3.21 \pm 0.55 ($n = 15$)	$Z = -2.880$, $df = 18$, $P < 0.01^*$
Size of home range (ha), August–November 2005	0.36 \pm 0.09 ($n = 4$)	2.88 \pm 0.81 ($n = 13$)	$Z = -2.887$, $df = 15$, $P < 0.01^*$
Size of core area (ha), August–November 2004	0.19 \pm 0.07 ($n = 8$)	0.27 \pm 0.07 ($n = 22$)	$Z = -0.399$, $df = 28$, $P = 0.673$
Size of core area (ha), May–July 2005	0.14 \pm 0.05 ($n = 5$)	0.47 \pm 0.10 ($n = 15$)	$Z = -2.270$, $df = 18$, $P = 0.023^*$
Size of core area (ha), August–November 2005	0.07 \pm 0.02 ($n = 4$)	0.51 \pm 0.19 ($n = 13$)	$Z = -2.548$, $df = 15$, $P = 0.011^*$

summer or autumn 2005 (summer 2005, $Z = -0.349$, $df = 18$, $P = 0.727$; autumn 2005, $Z = -1.327$, $df = 16$, $P = 0.184$). Post-fire spring is excluded from these analyses as data for nests were only available for one individual at the Fire Site. Many individuals at both sites used the same nest in different seasons, although only one individual at the Fire Site used the same nest for the entire study. Most pre-fire nests were located in summer 2004. When comparing this period to post-fire distance to nest 1-year later, distance did not change at the Fire Site (Fig. 2; Sign test, $n = 4$, $df = 3$, $P = 0.624$) but tended to decrease at the No-fire Site ($n = 13$, $df = 12$, $P = 0.092$).

DISCUSSION—Number of shifts of middens, size of home range, and distance traveled to nest differed between the Fire and No-fire sites. However, the Nuttall Fire did not appear to affect reproductive condition, body mass, or survival of red squirrels in areas with low severity of fire. This suggests promise for persistence of Mount Graham red squirrels affected by fire; however, small samples may reduce our ability to detect fire-induced responses of individuals.

Mount Graham red squirrels evolved with regular low-intensity, summer fires similar to the Nuttall Fire (H. D. Grissino-Mayer et al., in litt.). We saw that this timing allowed individuals with burned middens sufficient time before winter to establish new middens and food caches adequate for survival over winter.

Scorched substrate, increased edge, and reduced canopy cover may limit potential sites for middens by destroying forest characteristics

necessary for preservation of cones (Hatt, 1929; Layne, 1954; C. C. Smith, 1968; Finley, 1969). At the Fire Site, no squirrel with unburned middens moved territories; individuals that shifted likely did so because of fire, establishing middens in nearby, unburned habitat that was likely within their pre-fire home ranges. Individuals may reduce exploratory forays to find available sites for middens within the perimeter of the fire because lower canopy cover and increased edge make squirrels more vulnerable to predation (Rusch and Reeder, 1978; Kaufman et al., 1983).

Large home ranges may reflect a scarcity of resources (J. H. Brown, 1984; Mitchell and Powell, 2004). If fire reduced availability of resources within the perimeter of the fire, we might expect individuals to use larger areas to obtain resources that were available pre-fire; we did not see this pattern as all home ranges decreased in size at the Fire Site. Avoidance of predators may explain small home ranges if squirrels reduced overall movement to avoid this threat (Lagos et al., 1995; Sullivan et al., 1996; Anderson and Boutin, 2002).

Animals in the burned area that survived fire likely did so by taking refuge in nests (Koprowski et al., 2006), and several squirrels with burned middens used nests to cache cones, demonstrating the importance of these structures. If fire destroyed potential nesting sites, we may expect animals to move further post-fire to find nests. At the Fire Site, distance to nests during post-fire was not different from pre-fire and was shorter or the same as at the No-fire Site. Nest trees of Mount Graham red squirrels that survived the

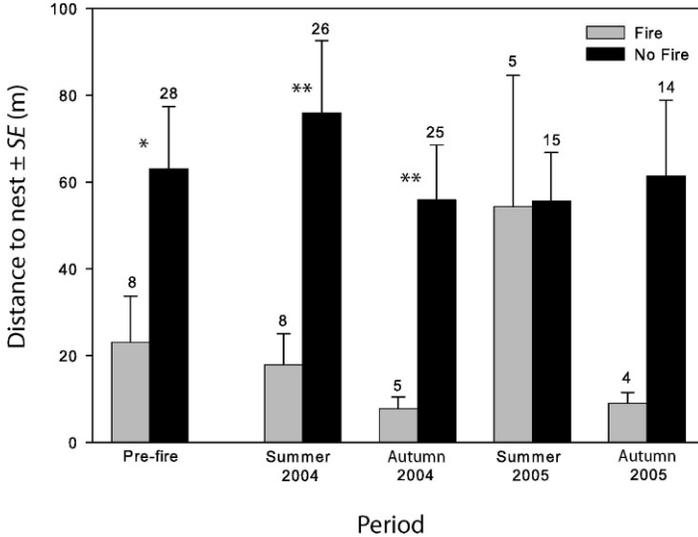


FIG. 2—Distance (mean \pm SE) from middens to nocturnal nests of Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) within and outside the Nuttall Fire Perimeter, Pinaleno Mountains, Graham County, Arizona, 2004–2005. Size of samples are indicated above bars: * $P < 0.1$, ** $P < 0.05$.

fire were unburned or scorched only at the base; thus, leaving areas of lightly burned forest or unburned-relict forest should allow sufficient access to these important structures.

Red squirrels are believed to evacuate burned areas, using them opportunistically to forage post-fire, but mostly avoiding fire-damaged forests during initial succession (Fisher and Wilkinson, 2005). This occurred in spruce-fir forests in the Pinaleno Mountains where the Nuttall Fire burned more intensely and uniformly (Koprowski et al., 2006, C. A. Zugmeyer, pers. comm.); however, squirrels remained in areas of low-intensity burns in mixed-conifer forests due to high site-fidelity and access to unburned habitat. This supports the recommendation of Fisher and Wilkinson (2005) to leave residual, unburned patches when using prescribed fire. As we saw with Mount Graham red squirrels, monitoring fates of individuals affected by fire may allow determination of specific tolerances and implementation of appropriate fire-management practices that permit persistence of resident animals.

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