RETURN OF HISTORICAL FIRE: IMPACTS OF BURN SEVERITY AND HETEROGENEITY ON MEXICAN FOX SQUIRRELS

by

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ABSTRACT

After decades of suppression, fire is returning to forests of western United States. Understanding responses of wildlife species to fire is essential to native species conservation because contemporary fires may not have the same effects on forest structure and landscape patterns as historical fires. I used radio-telemetry to investigate effects of fire severity and heterogeneity on habitat selection of Mexican fox squirrels, *Sciurus nayaritensis chiricahuae*. Vegetation within home ranges was characterized by more open understory and larger trees than random locations. Squirrels used areas burned at low severity more than unburned areas and those burned at higher severities. Squirrels used areas of moderate burn heterogeneity more than areas of low or high heterogeneity. Return of low-severity fire can help restore habitat for Mexican fox squirrels and other native species in forests with a historical regime of low-severity fire and contribute to understanding of the role of fire in forest ecosystems.

CHAPTER 1: INTRODUCTION

In the widespread dry ponderosa pine (*Pinus ponderosa*) forests of the western United States (US), fire has been reintroduced through wildfires and prescribed burns to a landscape that historically experienced frequent, low-severity fires (Cooper, 1960; Swetnam and Baisan, 1996b). In recent decades, wildfires have burned forests at increasing frequency, severity, and extent, after nearly a century of suppression (Graham et al., 2004; Westerling et al., 2006). Climate forecasts predict conditions likely to intensify this trend (Brown et al., 2004). Prescribed burns have been used to reduce fuel loads, which may reduce size and severity of future wildfires (Brown and Smith, 2000; Finney et al., 2005; Graham et al., 2004).

To conserve forest wildlife during the reintroduction of historical fire, the effects of fire must be better understood (Driscoll et al., 2010). In addition to the direct danger imposed by fire due to extreme heat (Koprowski et al., 2006), wildlife respond to vegetation structure (DeWalt et al., 2003; North et al., 1999) and landscape pattern (Nappi and Drapeau, 2009; Vierling et al., 2008) that are modified by fire.

I examined habitat use by Mexican fox squirrels *(Sciurus nayaritensis chiricahuae)* in forests burned in the previous 15 years in the Chiricahua Mountains of southeastern Arizona as a case study to understand effects of burn severity and heterogeneity on native wildlife. I examined Mexican fox squirrel habitat use relative to vegetation structural characteristics, burn severity, and burn heterogeneity, habitat quality and feeding and nesting behavior relative to burn severity, and use of severely-burned patches relative to patch size.

CHAPTER 2: PRESENT STUDY

The methods, results, and conclusions of this study are presented in detail in the papers appended to this thesis. The following is a summary of the major conclusions in these papers.

In appendix A, I used radio-telemetry within fire-influenced forest to determine home ranges of Mexican fox squirrels and compared vegetation characteristics and burn severity within home ranges to random areas. The understory within squirrel home ranges was more open than in random locations, consistent with the structure of forests that burned at low severity historically (Brown and Smith, 2000; Cooper, 1960; Pasch and Koprowski, 2011; Swetnam and Baisan, 1996a). Trees were also larger within squirrel home ranges than at random locations. Squirrels used areas burned at low severity more than areas burned at moderate and high severities and unburned areas. Squirrels fed and nested primarily in forest burned at low-severity, but occasionally used moderately- and severely-burned areas. This chapter was written in the format for the journal *Biological Conservation*.

In appendix B, I used resource utilization functions to determine associations of use within home ranges to heterogeneity of burn severity at two spatial scales. Habitat use by Mexican fox squirrels was positively associated with moderate levels of burn heterogeneity at large scale. Heterogeneity at large scale had stronger positive association with use than heterogeneity at small scale. Squirrels used small (<0.5 ha) or narrow (<120 m) severely-burned patches, but incorporated only the edges of large patches into home ranges. This chapter was written in the format for the journal *Landscape Ecology*.

Mexican fox squirrel use of burned forests demonstrates the complexities of fire impacts on wildlife, and results contribute to an understanding of the role and impact of fire in forest ecosystems and the implications for wildlife conservation.

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APPENDIX A: RETURN OF HISTORICAL FIRE AS A CONSERVATION TOOL: BURN SEVERITY IMPACTS MEXICAN FOX SQUIRRELS

Abstract

After decades of suppression, fire is returning to forests of the western United States through wildfires and prescribed burns. Understanding response of wildlife species to fires is essential to conservation of native species because contemporary fires may not have the same effects as historical fires. Recent fires in the Chiricahua Mountains of southeastern Arizona provided opportunity to investigate effects of fire severity on habitat selection of a native wildlife species. We used radio-telemetry within fire-influenced forest to determine home ranges of Mexican fox squirrels, *Sciurus nayaritensis chiricahuae*, and compared vegetation and burn characteristics within home ranges to random areas available to squirrels throughout burned conifer forest. Vegetation within home ranges was characterized by lower understory density, consistent with the effects of low-severity fire, and larger trees than random locations. Squirrels positioned home ranges to include areas burned at low severity more than fire-suppressed areas and those burned at higher severities. Our results suggest that return of low-severity fire can help restore habitat for Mexican fox squirrels and other native wildlife species with similar habitat affiliations in forests with a historical regime of frequent, low-severity fire. However, areas of high-severity burn were used occasionally for feeding and nesting, suggesting these areas may provide valuable resources. Our study contributes to an understanding of the role and impact of fire in forest ecosystems and the implications for wildlife conservation as fire returns to the region.

Introduction

Fire has been suppressed in the western United States (US) since approximately 1900, altering species composition and vegetation structure in many ecosystems (Brown and Smith, 2000). In the widespread dry ponderosa pine (*Pinus ponderosa*) forests, undergrowth was historically sparse and trees were large and widely-spaced due to frequent surface fires, which killed small trees and shrubs (Brown and Smith, 2000; Cooper, 1960). A century of fire suppression has led to dense undergrowth and “dog-hair thickets” of closely-spaced stunted trees (Brown and Smith, 2000; Cooper, 1960; Covington and Moore, 1994). Many vertebrate species are sensitive to vegetation structure, specifically those properties related to vertical components and spatial distribution of vegetation (DeWalt et al., 2003; North et al., 1999; Russell et al., 2010). Long-term fire suppression and accompanying changes to forest structure are implicated in declines of >100 wildlife species in the US alone (Czech et al., 2000), such as Rocky Mountain bighorn sheep (*Ovis canadensis*, Bentz and Woodard, 1988) and red-cockaded woodpeckers (*Picoides borealis*, Wilson et al., 1995). Eastern fox squirrels (*Sciurus niger*) in the southeastern US are declining due to habitat loss of long-leaf pine (*P. palustris*) forest. Long-leaf pine forest occupies only 3% of its former range, partially due to fire-suppression that allows encroachment of hardwood forests, which are favored by eastern gray squirrels (*S. carolinensis*) and avoided by eastern fox squirrels (Conner et al., 1999).

Fire is now returning in the form of wildfires, which are more likely today to burn severely because of climate change and accumulated fuel (Cooper, 1960; Covington and Moore, 1994; Graham et al., 2004; Westerling et al., 2006), and prescribed burns, which have been used to reduce accumulated fuels (Brown and Smith, 2000; Graham et al., 2004). Severe wildfires, although expected to restore forest structure in the long term (Baker, 1994), adversely affect many native species (Wilcove et al., 1998). Not only do severe fires kill animals directly (Koprowski et al., 2006), but wildlife species are also impacted because of dramatic effects on vegetation such as widespread tree mortality and subsequent understory growth after canopy removal (Fisher and Wilkinson, 2005). For example, many forest bird species that forage in tree or shrub foliage and build nests in live trees respond negatively to severe burns (Smucker et al., 2005). In contrast, low-intensity wildfires and prescribed burns may improve conditions for wildlife species in fire-impacted forests, such as Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*, Leonard and Koprowski, 2010), Abert's squirrels (*S. aberti*, Gwinn, 2010), and Rocky Mountain bighorn sheep (Smith et al., 1999). Effects of moderate-severity fires are not well understood because moderate burn is rarely differentiated from low- or high-severity burn in studies of fire effects on wildlife species. However, effects of moderate-severity fire on some species of forest birds differed from the effects of low- and high-severity fires (Ganey et al., 1996; Kotliar et al., 2007; Smucker et al., 2005) indicating a non-linear response to fire severity.

The history of suppression and recent reintroduction of fire brings a unique management and conservation challenge as the response of wildlife species is considered in addition to wildfire risk (Tiedemann and Klemmedson, 2000; Wilcove et al., 1998). Understanding effects of fire on wildlife species is of utmost importance in informing decisions to return fire to the landscape because of the widespread reintroductions of fire that are necessary and the potential impacts to wildlife species (Allen et al., 2002; Horton and Mannan, 1988; Hutto et al., 2008; Russell et al., 2010).

We examined use by Mexican fox squirrels *(Sciurus nayaritensis chiricahuae)* in forest burned in the previous 15 years in southeastern Arizona as a case study to understand effects of burn severity on native wildlife species. Mexican fox squirrels living in areas of small prescribed burns have smaller home ranges, indicative of higher quality habitat, than squirrels in fire-suppressed areas (Pasch and Koprowski, 2011), which suggests that low-severity fire may be beneficial to squirrels. Because much of the southwestern US historically sustained frequent, low-severity fire (Swetnam and Baisan, 1996a), we predicted that Mexican fox squirrels would select structural characteristics associated with low-severity fire and would position home ranges to include forest burned at low severity more than other burn severity categories, including unburned, fire-suppressed areas. Because tree squirrels require mature trees for food and shelter (Gurnell, 1987; Steele and Koprowski, 2001), and few large trees survive severe fires (Smucker et al., 2005; Turner et al., 2003), we predicted Mexican fox squirrels would not use severely burned forest.

Methods

Study System

The Mexican fox squirrel *(Sciurus nayaritensis)* is a large tree squirrel (~700 g) found throughout the Sierra Madre Occidental of Mexico, northward into the US only in the Chiricahua Mountains (Best, 1995). This northernmost population is a unique subspecies *(S. n. chiricahuae)* known as the Chiricahua fox squirrel (Best, 1995), and is classified as a sensitive species by the United States Forest Service (USFS, USDA Forest Service, 2000). The Mexican fox squirrel is the only arboreal squirrel species in the Chiricahuas (Cahalane, 1939), and the population has been isolated in the mountain range since the "sky island" landscape, characterized by insular forest at high elevations separated from other mountains by arid lowlands (Gehlbach, 1993), formed in northwestern Mexico and southwestern US at least 7000 years ago (Van Devender and Spaulding, 1979). The endemic subspecies appears well adapted to the forest characteristics associated with the natural fire regime and able to serve as a model for other native wildlife species that respond to similar vegetation characteristics. Tree squirrels require mature trees for food and shelter and serve as reliable indicators of forest condition (Gurnell, 1987; Steele and Koprowski, 2001). Mexican fox squirrels use all forested vegetation types in the Chiricahuas, but are most often associated with riparian and conifer forests (Cahalane, 1939).

The Chiricahua Mountains of southeastern Arizona encompass 37 000 ha and range from 1500 m to 2795 m in elevation. Historically, forests in the Chiricahua Mountains sustained frequent, low-severity fire (Swetnam and Baisan, 1996a). After nearly 100 years of fire suppression, fires have recently heavily impacted the range (Coronado National Forest Supervisors Office, 2006), primarily in conifer forests (ponderosa pine and mixed conifer forests, Douglas-fir, *Pseudotsuga menziesii*, with white fir, *Abies concolor*, and Engelman spruce, *Picea engelmannii*). Forests unburned for nearly a century were rare historically (Swetnam and Baisan, 1996a); unburned areas are herein labeled as “fire-suppressed”.

We conducted surveys of feeding sign throughout burned forested areas of the Chiricahuas and conducted radio-telemetry in two study areas. We located one study area (2600 m elevation) at the perimeter of a large (>10 000 ha) wildfire that burned in 1994, in an area with fire- suppressed forest and variable-sized patches of forest burned severely, moderately, and at low severity nearby. We located a second study area at the perimeter of a prescribed burn (>2800 ha) from 2005-06, which burned at low severity. The perimeter was selected so that both fire-suppressed forest and forest burned at low severity were available for use by squirrels. Because we were interested in long-term effects of fire regardless of ignition source, we considered all fires that occurred ≤15 years ago to be equivalent. Vegetation was comprised primarily of ponderosa pine forest with smaller components of Madrean oak-pine (Chihuahuan and Apache pines, *Pinus leiophylla* var. *chihuahuana* and *P. engelmannii*, with evergreen oaks, *Quercus emoryi*, *Q. arizonica*, and *Q. hypoleucoides*), mixed conifer, and riparian forest (deciduous woodland associated with drainages, Gehlbach, 1993; Sawyer and Kinraide, 1980). Our study was conducted in 2007 through 2009.

Determination of home ranges

To describe squirrel habitat use, we employed radio-telemetry to determine home ranges of squirrels in 2 study areas burned with varying severities near the perimeters of recent fires (≤15 years, Coronado National Forest Supervisors Office, 2006). We selected trapping areas in conifer forest (ponderosa pine and mixed conifer) because these areas were both used by squirrels and recently burned. We evaluated 10 potential live-trapping areas for squirrel activity indicated by feeding sign and live-trapped in 5 areas. We were able to calculate home ranges for squirrels in 2 study areas.

We distributed Tomahawk live traps baited with peanuts and peanut butter throughout trapping areas at the base of large trees and at water sources. We transferred captures to a handling cone (Koprowski, 2002) and fitted adults (>550 g) with a radio-collar (Model SOM 2380, Wildlife Materials, Inc., Carbondale, IL). We used a Yagi antenna and receiver (Models F164-165-3FB and TRX-2000S, Wildlife Materials, Inc., Carbondale, IL) to locate individuals during daylight hours by homing (White and Garrott, 1990) and recorded locations with a Global Positioning System (GPS) unit (eTrex Legend Cx, Garmin International, Inc., Olathe, Kansas). We located individuals at ≥120-min. intervals to minimize autocorrelation (White and Garrott, 1990) and obtained locations evenly throughout periods of squirrel activity (Koprowski and Corse, 2005) during all seasons from May 2007 through November 2008. We applied fixed-kernel methods with least squares cross-validation to set the smoothing parameter (Gitzen and Millspaugh, 2003; Seaman and Powell, 1996), and used the Animal Movement Analysis extension of ArcView (Hooge and Eichenlaub, 2001) to calculate 95% home ranges for squirrels with 29 or more telemetry locations, a point at which accumulation curves generally asymptote (Ranges 6 software, Kenward et al., 2003). We performed a 2-factor ANOVA to evaluate effects of sex and study area on home range size (95% kernel). Parameter estimates are shown ± half-width 95% confidence interval unless otherwise noted. Trapping and handling were approved by The University of

Arizona Institutional Animal Care and Use Committee (protocols 01-056 and 07-077) with permits from Arizona Game and Fish Department and United States Forest Service (USFS).

Map of burn severity

We used a supervised classification of the differenced Normalized Burn Ratio (dNBR, Key and Benson, 2005) to construct a map of fire severity from pre- and post-fire Landsat Thematic Mapper images. We categorized burn severity into 3 classes (low, moderate, severe) based on dNBR values, and classified areas outside USFS burn perimeters (Coronado National Forest Supervisors Office, 2006) as fire-suppressed. We used ground assessments at 344 points generated for vegetation measurements (described below) to supervise the classification process. Fifteen years is not sufficient time for large trees to regrow; therefore, severity classifications should be stable for >15 years post-fire. We used ERDAS Imagine (ERDAS, 2008) for image processing, ESRI ArcMap (ESRI, 2008) for GIS processing, and obtained Landsat TM images from Arizona Regional Image Archive (ARIA support team, 2008).

Habitat use relative to vegetation characteristics

We examined associations of use by Mexican fox squirrels at forest-wide scale relative to vegetation characteristics in burned forest and related key characteristics to burn severity. We compared vegetation within home ranges to random areas potentially available to squirrels throughout burned forest in the Chiricahua Mountains. Forest was potentially available if it was within 500 m of locations used by squirrels (indicated by telemetry locations, dreys, sightings, tracks in snow, or feeding sign) because this distance would be easily traveled by squirrels that routinely travel >1 km in a single day (Koprowski and Corse, 2005). Available forested areas were sampled at thirty 8-ha (mean home range size for first year of study) circular random sites. Random sites were placed in burned forest or within 200 m of burn perimeters, which was the distance radio-collared squirrels penetrated fire-suppressed areas.

We placed twelve 10 m x 4 m plots randomly within each home range and random site. We recorded information on vegetation characteristics within each randomly-oriented plot. We recorded number of logs >2 m long and >20 cm in diameter partially or completely within the plot, number of shrubs (any woody plant including small trees with stem <10 cm in diameter at breast height, DBH), percent understory density ≤2 m high (in increments of 5%), number of trees ≥10 cm DBH, tree density (m^2/ha, measured with variable plot method accounting for slope), and percent canopy cover measured with spherical densitometer at plot center. We also recorded subjective burn severity (fire-suppressed = 0, low severity = 1, moderate severity = 2, and severe burn = 3) and burn scar height on live tree closest to plot center. Our burn classification was similar to Jennes et al. (2004), but incorporated canopy continuity, an important habitat component for tree squirrels (Pasch and Koprowski, 2011; Steele and Koprowski, 2001). Low-severity burns were evidenced by burn scars on tree trunks but intact canopy, moderate burns, by tree mortality and interrupted canopy, and severe burns, by complete or nearly complete tree mortality such that remaining live trees were isolated from each other so that branches did not overlap. Fire-suppressed areas were those outside the fire perimeter as defined by the USFS.

We employed stepwise logistic regression to select important vegetation characteristics to differentiate home ranges from random sites. To make the home range or random site the sampling unit, we used the mean of each vegetation characteristic for 12 plots within a home range or random site as explanatory variables and used the median for ordinal burn severity. Variables were log transformed as necessary to meet assumptions of normality and one variable of each pair of highly correlated variables ($r \geq 0.75$) was omitted. We calculated mean tree size for the home range or random site from mean tree count and mean tree density.

To relate important vegetation characteristics to burn severity, we regressed mean vegetation measurement for home ranges and random sites as a function of median burn severity for that home range or random site. In addition to a linear fit, we evaluated a 2nd order polynomial fit to discern whether characteristics varied across burn severity in non-linear fashion. We also evaluated potential interaction of burn severity and home range/random site indicator variable to determine whether use of forest characteristics differed by burn severity. We selected models based on whole-model *p*-values.

Habitat use relative to burn severity

To examine associations of use by Mexican fox squirrels at home-range scale relative to burn severity, we compared burn severities within home ranges to burn severities of surrounding areas available to squirrels in our study. We overlaid home ranges onto our map of burn severity, determined composition of home ranges relative to burn severity, and used compositional analysis (Aebischer et al., 1993; Smith, 2005) to determine if squirrels select or avoid burn severities in the placement of home ranges (second-order selection, Johnson, 1980). To define areas available to squirrels in our study, we used a 784-m buffer (the greatest distance an animal was known to travel during the study from its capture point) around locations of traps that captured a squirrel for which we calculated a home range. Home ranges of Mexican fox squirrels can be 50 ha in size with considerable interspecific overlap (Pasch and Koprowski, 2006), and squirrels can regularly move ≥1 km daily (Koprowski and Corse, 2005; Pasch and Koprowski, 2006). We delineated available areas for each study area separately, and compared each home range to the available area for the study area in which it was located.

Habitat quality relative to burn severity

To assess habitat quality relative to burn severity, we used home-range size as an indicator of habitat quality, such that a smaller home range suggests higher quality habitat (Ford, 1983). To assess how low-severity fire affects home-range size relative to long-term fire suppression, we regressed home-range size against the ratio of the proportion of each squirrel's home range that was burned at low severity relative to the proportion that was fire-suppressed. Home-range sizes and ratios were log-transformed to meet assumptions of normality. Log-ratio transformations of proportional compositions are linearly independent (Aitchison, 1986).

To assess how inclusion of severely-burned patches affected habitat quality, we compared sizes of home ranges with patches of severe burn to sizes of home ranges without patches of severe burn.

Feeding and nesting behavior relative to burn severity

We assessed squirrel use of areas burned recently by surveying transects ($n = 48$) of 500 m length for signs of squirrels feeding. We located transects randomly relative to vegetation type and burn severity within perimeters of recent (≤15 y) wildfires and prescribed burns. We documented feeding sign (scales or cores of conifer cones), which indicated presence of *S. n. chiricahuae* in exclusion of other seed predators in the Chiricahua Mountains (Cahalane, 1939; Elbroch, 2003), within 2 m of start point and at each 25-m increment along a transect. We also assessed burn severity subjectively at each survey point.

We used a GPS to record the location of any leaf or cavity nest of squirrels found while conducting telemetry within study areas. Burn severity at each nest or cavity was determined from a burn severity map and compared with chi-square goodness-of-fit tests to burn severities within available study areas (Marcum and Loftsgaarden, 1980) defined by 784-m buffer around trap locations. We applied Yates correction for small expected values.

Results

Determination of home ranges

We radio-collared 19 adult squirrels (11 females; 8 males) and located squirrels 575 times ($\bar{x}$ = 30.3 ± 8.2 locations per individual). We calculated home ranges for 14 squirrels (9 female, 5 male) with ≥29 telemetry locations ($\bar{x}$ = 39.8 ± 3.0). Home-range sizes did not differ between males and females ($F_{1,11}$ = 2.45, p = 0.15), or between study areas ($F_{1,11}$ = 0.39, p = 0.55).

Habitat use relative to vegetation characteristics

Home ranges had more open understory (effect likelihood ratio test, χ^2= 3.76, *d.f.* = 1, p = 0.053) and larger trees (χ^2= 4.54, *d.f.* = 1, p = 0.033) than random sites (logistic regression, whole model χ^2= 10.87, *d.f.* = 2, p = 0.004, Figure 1). The most open understory was found in areas burned at low severity, with minimum understory density at median burn severity = 1.17 (SE 0.59 to 2.21) where 1 = low-severity burn and 2 = moderate-severity burn (multiple regression, 2nd-order polynomial, R^2 = 0.34, $F_{3,40}$ = 6.72, p = 0.0009, Figure 2). Not only was average understory density lower in home ranges than at random sites, but squirrels used open understory throughout their home ranges. Only one home range had one plot with understory density ≥65%, whereas over half (60%) of all random sites had ≥1 plots with understory density ≥65%. For mean tree size, the best-fit model included an interaction of burn severity and use, so that tree size was larger in home ranges than random sites in fire-suppressed areas but larger in random sites than home ranges in severely burned areas (multiple regression, R^2 = 0.28,

$F_{3,40}$ = 5.31, p = 0.004, Figure 3). When each burn severity category was analyzed separately, tree size did not differ between home ranges and random sites at low-severity burn (t_{21} = 1.13, p = 0.3) or high-severity burn (t_1 = 0.24, p = 0.9), but tree size was larger in home ranges than random sites in fire-suppressed areas (t_{11} = 3.59, p = 0.004, Figure 3).

Habitat use relative to burn severity

Squirrels used low-severity burns more than other categories of burn severity (Figure 4), and moderate burn was used less than low-severity burn and fire-suppressed forest (Λ = 0.0729, -N ln Λ = 36.67, *d.f.* = 3, $p < 0.0001$, n = 14, Table 1).

Habitat quality relative to burn severity

Home-range size showed a slight negative relationship to the ratio of forest burned at low severity relative to fire-suppressed forest within squirrel home ranges (linear regression, R^2= 0.13, $F_{1,12}$ = 1.79, p = 0.21, Figure 5). Size did not differ for home ranges with patches of severe burn compared to home ranges without patches of severe burn (t_{12} = 0.66, p = 0.52, home ranges with severe burn were 4.43 ha ± 14.73 larger than home ranges without severe burn).

Feeding and nesting behavior relative to burn severity

Feeding sign was detected at 71 (7.1%) of 1007 survey points on 48 transects. Of 71 survey points with feeding sign, 7 (9.9%) were in areas burned severely. Squirrels fed in severely-burned areas less than available (whole model χ^2 = 8.49, *d.f.* = 3, p = 0.037, Bonferroni z-tests, $p < 0.05$, $Z_{0.00625} = -2.50$).

Fifty-four leaf nests and 7 cavity nests were located within our study areas during telemetry activities. Of all nests found (leaf and cavity), most were located in areas burned at low severity (72.1%). However, 3 of 54 leaf nests (5.6%) were found in moderately burned areas. Leaf nests were located at points burned at low severity more than available and in severely-burned areas less than available (whole model χ^2 = 17.06, *d.f.* = 3, p = 0.0007, Bonferroni z-tests, $p < 0.05$, $Z_{0.00625} = -2.50$). Two of 7 cavity nests found (28.6%) were located in moderately-burned areas, and 2 (28.6%) were located in severely burned areas. Burn severity at cavities did not differ from random (χ^2 = 2.59, *d.f.* = 3, p = 0.46).

Discussion

Home ranges of Mexican fox squirrel had more open understory than random sites, especially in areas recently burned at low severity, consistent with the evolutionary history of the species in forests that historically burned frequently at low severity (Brown and Smith, 2000; Cooper, 1960; Pasch and Koprowski, 2011; Swetnam and Baisan, 1996a). Many wildlife species respond to forest structural components that are modified by fire (DeWalt et al., 2003; North et al., 1999). Species with similar vegetation requirements and preferences are likely to respond similarly to fire (Driscoll et al., 2010). Other species that prefer open understory in addition to Mexican fox squirrels, such as Steller's jay (*Cyancitta stellarri*), respond positively to low-severity fire (Kotliar et al., 2007), whereas species that prefer dense understories or thick leaf litter, such as spotted towhee (*Pipilo maculates*) or northern flying squirrels (*Glaucomys sabrinus*), respond negatively to low-severity fire (Kirkpatrick et al., 2006; Meyer et al., 2007). Squirrels also used areas with larger trees than random sites. Repeated frequent, low-severity fire increases average tree size relative to fire-suppressed areas by killing the smallest trees (Cooper, 1960; Regelbrugge and Conard, 1993; Saab et al., 2006; Schmidt et al., 2006). Moderate fires leave only the largest trees alive and even severe fires may spare some large trees (Schmidt et al., 2006; Smucker et al., 2005).

As predicted, Mexican fox squirrels used areas burned at low severity more than fire-suppressed areas and areas burned at moderate and high severities. Mexican fox squirrels have smaller core areas in fire-prescribed forest than in fire-suppressed forest (Pasch and Koprowski, 2011), suggesting forest burned at low severity is of higher quality (Ford, 1983) than fire-suppressed forest. Other species adapted to vegetation types that historically experienced frequent, low-severity fires may also benefit from reintroduction of low-severity fire, including Mount Graham red squirrels (Leonard and Koprowski, 2010), Abert's squirrels (Gwinn, 2010), Florida panthers (*Puma concolor coryi*, Dees et al., 2001), Rocky Mountain bighorn sheep (Smith et al., 1999), white-tailed deer (*Odocoileus virgineanus*, Ivey and Causey, 1984), several songbird species and deer mice (*Peromyscus maniculatus*, Bock and Bock, 1983). Although longer periods and repeated fires will probably be required to fully restore forest to historical conditions (Baker, 1994), squirrels responded positively to single episodes of low-severity fire, suggesting a fire-based restoration process may improve habitat.

Squirrels did not avoid severely burned forest as we had predicted; severely-burned forest was included within home ranges approximately in proportion to availability. Home range size, an indicator of habitat quality (Ford, 1983), did not differ for squirrels that included severe burn in their ranges, which suggests that severely burned patches are not of substantially lower quality or may provide an important resource. Possible explanations for use of severely burned areas by squirrels include feeding, cavity nesting for females raising young, or edge attraction. Squirrels infrequently used severely burned areas for both feeding and nesting, diminishing the possibility that severely burned areas were included within home ranges solely as an artifact of the process that estimates home ranges from telemetry locations. Since Mexican fox squirrels do not cache most food items (Best, 1995), squirrels likely foraged successfully, but infrequently, in severely burned areas. Isolated ponderosa pines in and at the edge of severely-burned areas produce many seeds (Larson and Schubert, 1970), which may attract squirrels for feeding. Fungi are an important part of Mexican fox squirrel diet (Koprowski and Corse, 2001), and fungal growth on snags and downed logs in severely burned patches may attract squirrels. Cavity nests were used exclusively by females in spring or summer months, likely for rearing young because Mexican fox squirrel females use exclusively cavities for maternity nests (Pasch and Koprowski, 2005; Steele and Koprowski, 2001). The abundance of snags, standing dead trees that are the primary source of cavities in ponderosa pine forest (Scott, 1979), in severely burned areas (Chambers and Mast, 2005) may attract female squirrels during breeding season.

Non-linear responses to burn severity similar to the Mexican fox squirrel have been observed in several bird species, including hermit thrush (*Catharus guttatus*), western tanager (Smucker et al., 2005), Virginia's warbler (*Vermivora virginiae*), Steller's jay (Kotliar et al., 2007), and spotted towhee (Kirkpatrick et al., 2006; Kotliar et al., 2007). Because response to burn severity was not linear, information would have been lost or obscured had any burn severity category been omitted.

Given the ongoing reintroduction of historical fire into forested ecosystems, a better understanding of wildlife responses to the full variety of burn severities can help us most effectively predict and ameliorate effects on wildlife species (Clarke, 2008; Smucker et al., 2005). In fire-adapted ecosystems, native wildlife species may require fire to shape vegetation structure (Hutto et al., 2008; Leonard and Koprowski, 2010), but fire severity effects vary dramatically from harmful to beneficial (Kirkpatrick et al., 2006; Smucker et al., 2005). To conserve forest wildlife species, fire reintroduction may serve as an essential tool, but this tool must be employed carefully to maximize benefits and minimize harmful effects (Driscoll et al., 2010; Tiedemann and Klemmedson, 2000).

Conservation and management implications

To reduce fuels and therefore the threat of catastrophic wildfire, forest managers have adopted thinning and prescription burn policies throughout the western US (Graham et al., 2004; Schoennagel et al., 2004). Consensus is emerging that many native species in fire-adapted forests react favorably to low-severity wildfire and prescribed burns, and that fire-based restoration may be beneficial to native wildlife species (Bock and Bock, 1983; Carlson et al., 1993; Dees et al., 2001; Ivey and Causey, 1984; Pasch and Koprowski, 2011).

Areas of mixed-severity burn likely were present in southwestern ponderosa pine forests historically (Baisan and Swetnam, 1995; Brown and Smith, 2000; Hutto et al., 2008; Swetnam and Baisan, 1996b). Mexican fox squirrels used areas of severe burn for both feeding and nesting, and cavities in these areas appear to be a valuable resource for maternal nests. Further investigation is necessary to determine whether small patches of severe burn should be included in burn prescriptions for ponderosa pine forests in the southwest, and to what degree mixed severity wildfires can be tolerated by wildlife species in these forests. Areas burned at any severity should be managed to retain snags for Mexican fox squirrel females, as well as other cavity-nesting species (Horton and Mannan, 1988; Scott, 1979).

To conserve and manage wildlife species, we must consider fire's effects on vegetation structure and long-term modification of the forest environment (Bradstock et al., 2005; Clarke, 2008). Forest managers must consider ongoing climate change which is predicted to increase wildfire occurrences in the southwestern US (Williams et al., 2010). Species such as the Mexican fox squirrel can serve as indicators for other native wildlife species to help monitor the effects of efforts to reintroduce fire (Driscoll et al., 2010). A return to a natural fire regime should be encouraged when possible to restore the historical forest structure (Bonnicksen and Stone, 1985; Hutto et al., 2008).

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Tables and Figures

Table 1. Squirrels used forest burned at low severity more than fire-suppressed forest or forest severely- or moderately-burned. Pair-wise matrix of estimated log-ratio differences between home ranges of Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) and available areas, Chiricahua Mountains, Cochise Co., Arizona, 2007-2009. Forests were classified as fire-suppressed, low, moderate, or severe burn. Each entry indicates estimated difference and *t*-test *p*-values for the row relative to the column. Rank 1 was used most, rank 4 was used least.

	fire-suppressed		low		moderate		severe		rank
	diff.	*p*	diff.	*p*	diff.	*p*	diff.	*p*	
fire-suppressed			-2.52	0.005	1.24	0.04	0.74	0.25	2
low	2.52	0.005			2.99	<0.000	2.49	<0.000	1
moderate	-1.24	0.04	-2.99	<0.000			-0.50	0.17	4
severe	-0.74	0.25	-2.49	<0.000	0.50	0.17			3

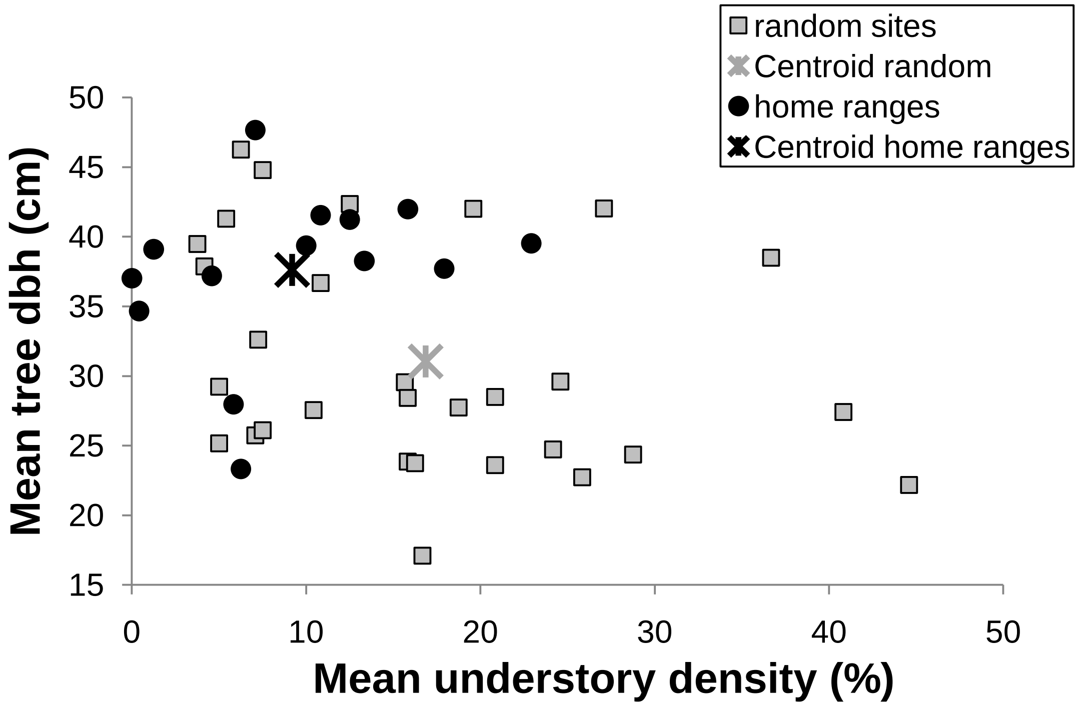

Figure 1. Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) used forest with more open understory and larger trees than random sites, Chiricahua Mountains, Cochise Co., Arizona.

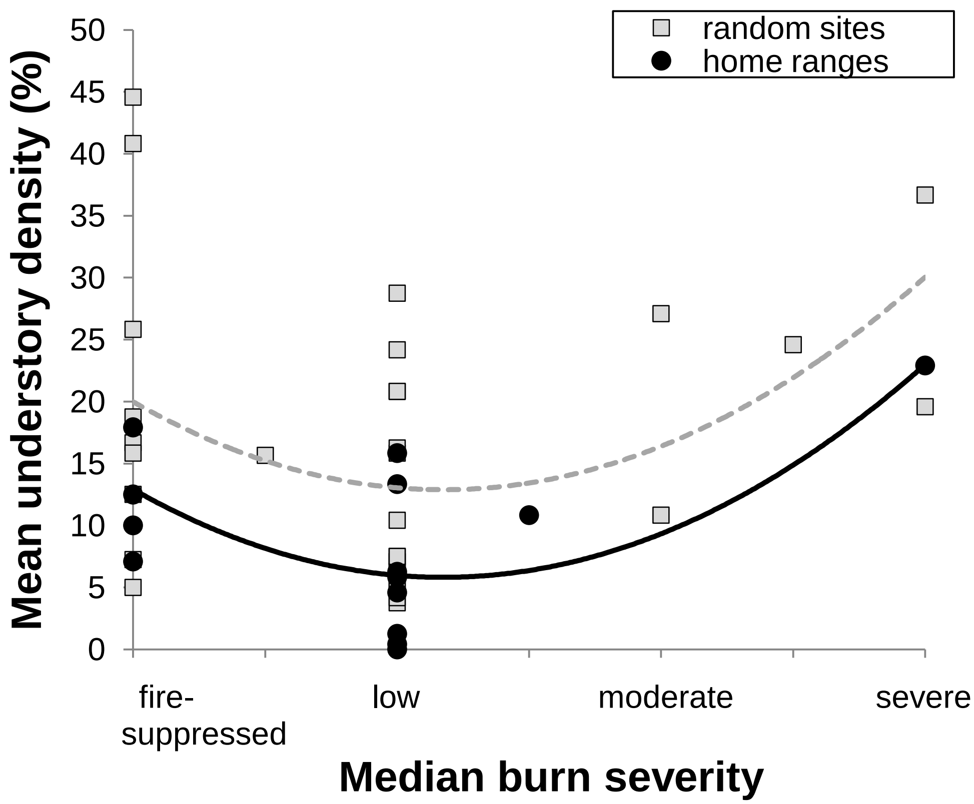

Figure 2. Understory density was lowest at low burn severities. Home ranges of Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) had lower understory density than random sites at all burn severities (solid and dashed lines are best-fit model predictions, mean understory density = 20.0 – (12.1*median burn severity) + (5.1*(median burn severity)^2) – (7.1*random/home range indicator), R^2 = 0.34, p = 0.0009), Chiricahua Mountains, Cochise Co., Arizona.

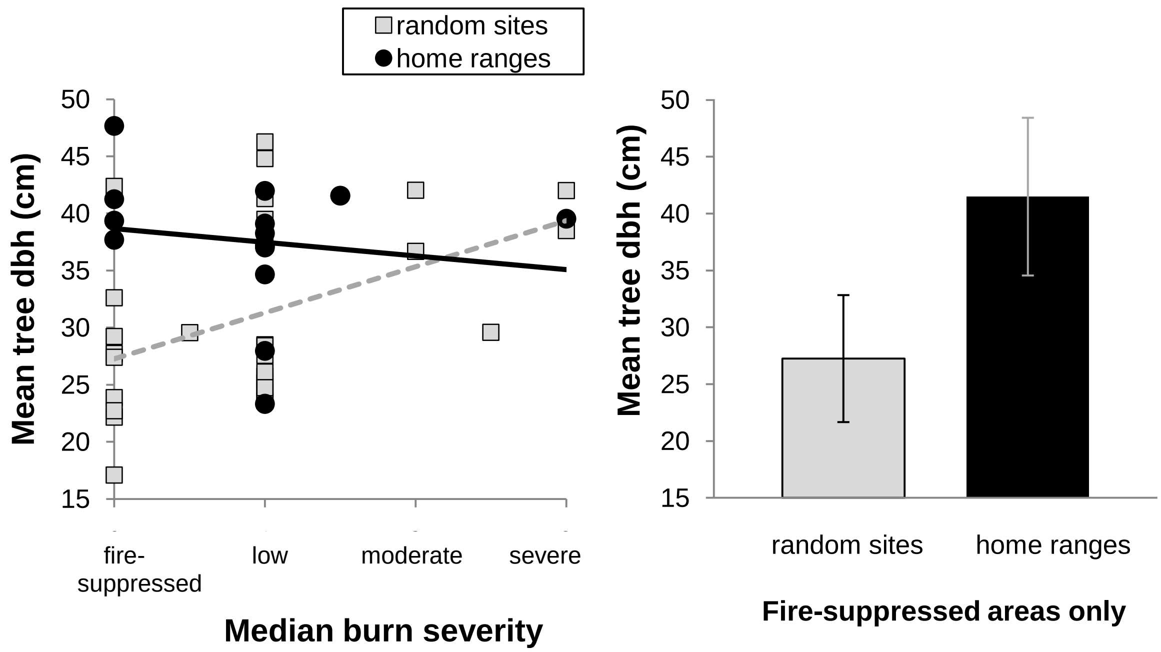

Figure 3. Tree size was largest in fire-suppressed forest in Mexican fox squirrel (*Sciurus nayaritensis chiricahuae*) home ranges and largest at high burn severities in random sites (solid and dashed lines are best-fit model predictions, mean tree dbh = 27.3 + (4.0*median burn severity) + (11.4*random/home range indicator) – (5.2*(median burn severity x random/home range indicator)), $R^2 = 0.28$, $p = 0.004$). In fire-suppressed forest, tree size was larger in home ranges than random sites (error bars are 95%CI, $t_{11} = 3.59$, $p = 0.004$), Chiricahua Mountains, Cochise Co., Arizona.

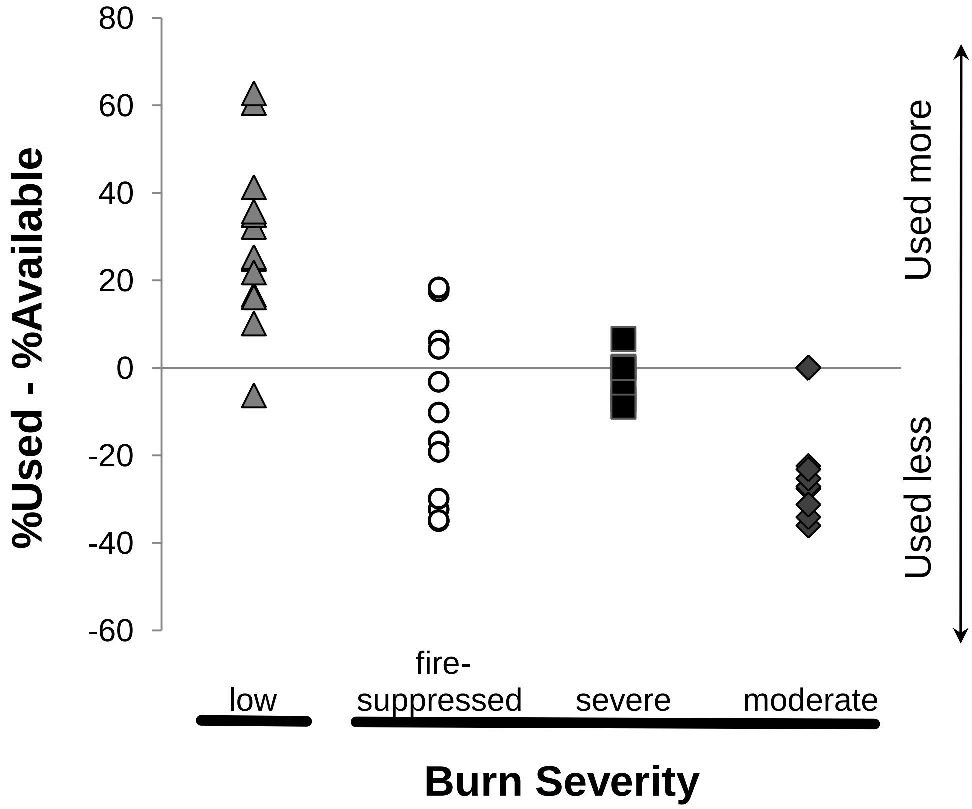

Figure 4. Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) used low-severity burn more than other burn severity categories. Home ranges were compared to available areas in Chiricahua Mountains, Cochise Co., Arizona. Low-severity burn was used more than fire-suppressed forest (*t*-test $p = 0.005$), severely-burned forest ($p < 0.001$), and moderately-burned forest ($p = 0.0000$). Burn severity categories connected by a line on the ordinate indicate categories that are not different (*t*-test *p*-values for fire-suppressed relative to severe $p = 0.25$, for severe relative to moderate $p = 0.17$).

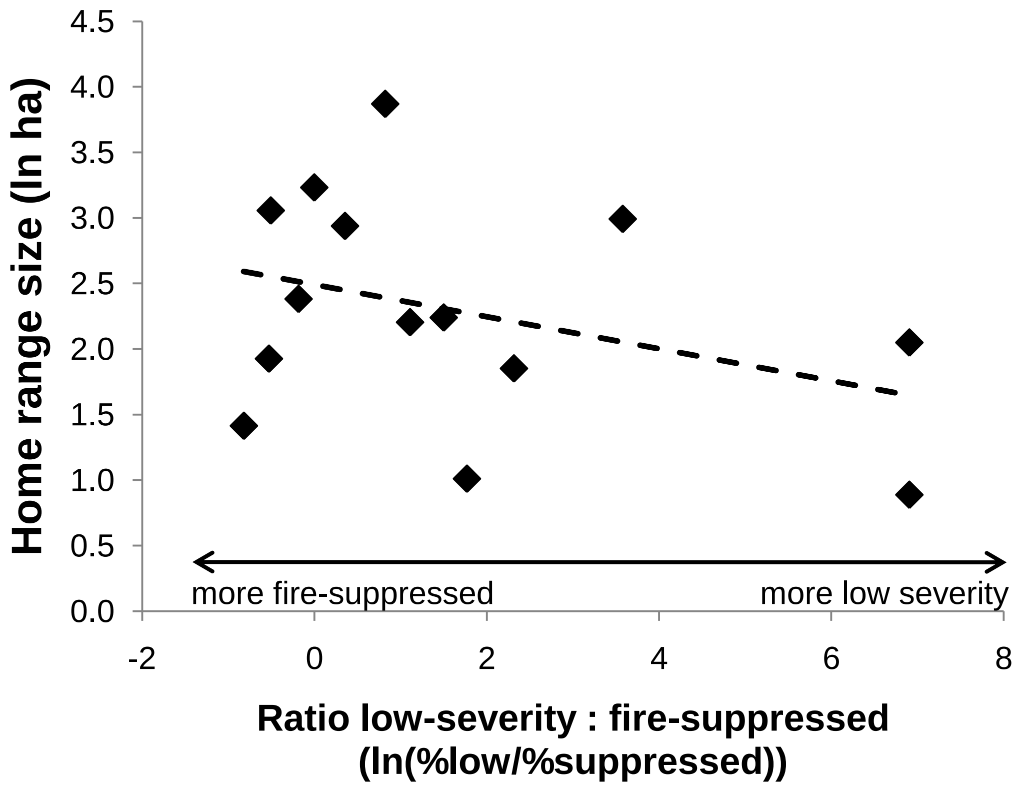

Figure 5. Home range size decreased as the ratio of forest burned at low severity relative to fire-suppressed forest increased within Mexican fox squirrel (*Sciurus nayaritensis chiricahuae*) home ranges, Chiricahua Mountains, Cochise Co., Arizona. Results suggest forest burned at low-severity is of higher quality than fire-suppressed forest (dashed line is best-fit model prediction, ln home range size = 2.49 – (0.12 * ln(%low/%suppressed)), R^2= 0.13, p = 0.21).

APPENDIX B: EFFECT OF HETEROGENEITY IN BURN SEVERITY ON MEXICAN FOX SQUIRRELS FOLLOWING THE RETURN OF HISTORICAL FIRE

Abstract

After decades of suppression, fire is returning to forests of the western United States through wildfires and prescribed burns. Understanding responses of wildlife species to fire is essential to native species conservation because contemporary fires may not have the same effects on forest structure and landscape patterns as historical fires. Recent fires in the Chiricahua Mountains of southeastern Arizona provided an opportunity to investigate effects of fire heterogeneity on habitat selection of a native wildlife species. We used radio-telemetry to determine home ranges of Mexican fox squirrels, *Sciurus nayaritensis chiricahuae*, within fire-influenced forests and applied resource utilization functions to evaluate associations of use intensity within home ranges to heterogeneity of burn severity at two spatial scales. Squirrels used areas with moderate levels of burn heterogeneity at large scale more than areas of low or high heterogeneity and responded more consistently across the population to heterogeneity at large scale than at small scale. Squirrels used small (<0.5 ha) or narrow (<120 m) severely-burned patches, but incorporated only the edges of large patches into home ranges. Mexican fox squirrel use of burned forests demonstrates the complexities of fire impacts on wildlife, and our results contribute to an understanding of the role and impact of fire in forest ecosystems and the implications for wildlife conservation.

Introduction

In the widespread dry ponderosa pine (*Pinus ponderosa*) forests of the western United States (US), wildfires and prescribed burns are returning to a landscape that historically experienced frequent, low-severity fires (Cooper 1960; Swetnam and Baisan 1996b). After nearly a century of suppression, wildfires have burned these forests at increasing frequency, severity, and extent in recent decades (Graham et al. 2004; Westerling et al. 2006). Climate forecasts predict conditions likely to intensify this trend (Brown et al. 2004; Williams et al. 2010). Prescribed burns have been used to reduce fuel loads, which may reduce size and severity of future wildfires (Brown and Smith 2000; Finney et al. 2005; Graham et al. 2004).

To conserve forest wildlife during the reintroduction of fire, we must better understand the effects of fire (Driscoll et al. 2010) and the potentially different impacts of wildfire and prescribed burns. In addition to the direct danger imposed by fire due to extreme heat (Koprowski et al. 2006), landscape pattern is modified by fire (Chuvieco 1999; Turner et al. 1994). Wildfires burn with a wide range of severities and often heterogeneously, creating a highly variable landscape pattern of unevenly-sized patches of different severities in close proximity (Baker 1992; Turner et al. 1994). However, large severe wildfires can homogenize the landscape by killing most trees in large areas (Chuvieco 1999). Prescribed fire often burns uniformly at low-severity which results in little variation of landscape pattern (Conway and Kirkpatrick 2007). Prescribed burns implemented in a mosaic, however, can create fine-grained spatial heterogeneity (Bradstock et al. 2005; Parr and Andersen 2006; Price et al. 2005).

Landscape heterogeneity (size, shape, and distribution of patches of vegetation or structural components within a landscape) is known to affect wildlife species (Tews et al. 2004) directly through vegetative differences (Leopold et al. 1951; Moe and Wegge 1994) and indirectly via mechanisms such as predation (Marzluff et al. 2004). Although effects of landscape heterogeneity resulting from timber extraction, agriculture, and other human activities has been studied extensively (Tews et al. 2004), effects of burn heterogeneity on wildlife species have been little studied (Clarke 2008), and such knowledge is essential for conservation in forest environments where fire is used as a management tool. Improving our understanding of how the spatial heterogeneity of fire affects a small mammal species will broaden our knowledge of the ecosystem effects of fire (Driscoll et al. 2010).

Use of burned forests by wildlife varies with species, habitat requirements, and fire characteristics (Fisher and Wilkinson 2005; Larsen et al. 2007; Nappi and Drapeau 2009; Russell et al. 2010; Stuart-Smith et al. 2002; Vierling et al. 2008). Use also varies relative to burn severity (Appendix A; Hutto 1995; Kirkpatrick et al. 2006; Kotliar et al. 2007; Smucker et al. 2005), but few studies have examined the response of wildlife species to burn patterns on a landscape scale (Clarke 2008; Driscoll et al. 2010). Woodpeckers (family Picidae) nested within severely-burned areas away from edges of unburned forests (Vierling et al. 2008), but reproductive success of black-backed woodpecker (*Picoides arcticus*) was higher near edges of unburned forests (Nappi and Drapeau 2009). The results of a simulation model used to examine the persistence of malleefowl (*Leipoa occellata*) in Australia suggested sensitivity to spatial pattern of fire (Bradstock et al. 2005). Despite the paucity of information concerning the effects of fire heterogeneity on wildlife species, the principles of patch mosaic burning have been adopted by some Australian and South African conservation management agencies to promote biodiversity (Parr and Andersen 2006). In the US, to reduce risk of fire escape and air-quality degradations from smoke, prescriptions for fuel-reduction fires include short flame lengths likely to keep burn severity uniformly low (Graham et al. 2004) and create homogenous burns. The focus of prescribed burns as a fuel-reduction tool while ignoring the effects on wildlife species may pose risks to forest wildlife because we lack knowledge of harmful effects and mitigation strategies (Tiedemann and Klemmedson 2000).

The history of suppression and recent reintroduction of fire brings a unique management and conservation challenge as the response of wildlife species is considered in addition to wildfire risk (Tiedemann and Klemmedson 2000; Wilcove et al. 1998). Understanding effects of fire on wildlife species is of utmost importance in informing decisions to return fire to the landscape (Allen et al. 2002; Hutto et al. 2008).

We examined use of burned forests by a conspicuous medium-sized mammal (Mexican fox squirrels, *Sciurus nayaritensis chiricahuae*) in the Chiricahua Mountains of southeastern Arizona as a case study to understand the effect of heterogeneity in burn severity on native wildlife species. Mexican fox squirrels use areas burned at low-severity more than unburned areas and areas of more severe burn, but also infrequently use small patches of severe burn (Appendix A), which led us to investigate effects of burn heterogeneity on squirrels. We studied habitat use relative to burn heterogeneity to better understand response of wildlife species to fire.

Methods

Study System

The Chiricahua Mountains of southeastern Arizona encompass 37 000 ha and range from 1500 m to 2795 m in elevation. Historically, forests in the Chiricahua Mountains sustained frequent, low-severity fire (Swetnam and Baisan 1996a). After nearly 100 years of fire suppression, fires have recently heavily impacted the range (Coronado National Forest Supervisors Office 2006), primarily in conifer forests (ponderosa pine and mixed conifer, Douglas-fir, *Pseudotsuga menziesii*, with white fir, *Abies concolor*, and Engelman spruce, *Picea engelmannii*). Forests unburned for nearly a century were rare historically (Swetnam and Baisan 1996a); unburned areas are herein labeled as “fire-suppressed”.

We located one study area (2600 m elevation) at the perimeter of a large (>10 000 ha) wildfire that burned in 1994, in an area with fire-suppressed forest and patches of forest burned severely, moderately, and at low severity nearby. We located a second study area at the perimeter of a prescribed burn (>2800 ha) from 2005-06, which burned at low severity. The perimeter was selected so that both fire-suppressed forest and forest burned at low severity were available for use by squirrels. Because we were interested in long-term effects of fire regardless of ignition source, we considered all fires that occurred ≤15 years ago equivalent. Vegetation was comprised primarily of ponderosa pine forest with smaller components of Madrean oak-pine (Chihuahuan and Apache pines, *Pinus leiophylla* var. *chihuahuana* and *P. engelmannii*, with evergreen oaks, *Quercus emoryi*, *Q. arizonica*, and *Q. hypoleucoides*), mixed conifer, and riparian forest (deciduous woodland associated with drainages, Gehlbach 1993; Sawyer and Kinraide 1980). Our study was conducted in 2007 through 2009.

The Mexican fox squirrel *(Sciurus nayaritensis)* is a large tree squirrel (~700 g) found throughout the Sierra Madre Occidental of Mexico, northward into the US only in the Chiricahua Mountains (Best 1995). This northernmost population is a unique subspecies *(S. n. chiricahuae)* known as the Chiricahua fox squirrel (Best 1995), and is classified as a sensitive species by the United States Forest Service (USFS, USDA Forest Service 2000). The Mexican fox squirrel is the only arboreal squirrel species in the Chiricahuas (Cahalane 1939), and the population has been isolated in the mountain range since the “sky island” landscape, characterized by insular forests at high elevations separated from other mountains by arid lowlands (Gehlbach 1993), formed in northwestern Mexico and southwestern US at least 7000 years ago (Van Devender and Spaulding 1979). The endemic subspecies appears well adapted to the forest characteristics associated with the natural fire regime and able to serve as a model for other native wildlife species that respond to similar vegetation characteristics. Tree squirrels require mature trees for food and shelter and serve as reliable indicators of forest condition (Gurnell 1987; Steele and Koprowski 2001). Mexican fox squirrels use all forested vegetation types in the Chiricahuas, but are most often associated with riparian and conifer forests (Cahalane 1939).

Determination of home ranges

To describe squirrel habitat use, we employed radio-telemetry to determine home ranges of squirrels in areas burned with varying severities near the perimeters of recent fires (≤15 years, Coronado National Forest Supervisors Office 2006). We selected trapping areas in conifer forests (ponderosa pine and mixed conifer) because these areas were both used by squirrels and recently burned. We evaluated 10 potential trapping areas for squirrel activity indicated by feeding sign and trapped in 5 areas. We were able to calculate home ranges for squirrels in 2 study areas.

We distributed Tomahawk live traps baited with peanuts and peanut butter throughout trapping areas at the base of large trees and at water sources. We transferred captures to a handling cone (Koprowski 2002) and fitted adults (>550 g) with a radio-collar (Model SOM 2380, Wildlife Materials, Inc., Carbondale, IL). We used a Yagi antenna and receiver (Models F164-165-3FB and TRX-2000S, Wildlife Materials, Inc., Carbondale, IL) to locate individuals during daylight hours by homing (White and Garrott 1990) and recorded locations with a Global Positioning System (GPS) unit (eTrex Legend Cx, Garmin International, Inc., Olathe, Kansas).

We located individuals at ≥120-min. intervals to minimize autocorrelation (White and Garrott 1990) and obtained locations evenly throughout periods of squirrel activity (Koprowski and Corse 2005) during all seasons from May 2007 through November 2008. We applied fixed-kernel methods with least squares cross-validation to set the smoothing parameter (Gitzen and Millspaugh 2003; Seaman and Powell 1996), and used Animal Movement Analysis extension of ArcView (Hooge and Eichenlaub 2001) to calculate 95% and 99% home ranges for squirrels with 29 or more telemetry locations, a point at which accumulation curves generally asymptote (Ranges 6 software, Kenward et al. 2003). We performed a 2-factor ANOVA to evaluate effects of sex and study area on home range size (95% kernel). Parameter estimates are shown ± half-width 95% confidence interval unless otherwise noted. Trapping and handling were approved by The University of Arizona Institutional Animal Care and Use Committee (protocols 01-056 and 07-077) with permits from Arizona Game and Fish Department and United States Forest Service (USFS).

Map of Burn Severity

We used a supervised classification of the differenced Normalized Burn Ratio (dNBR, Key and Benson 2005) to construct a map of fire severity from pre- and post-fire Landsat Thematic Mapper images. We categorized burn severity into 3 classes (low, moderate, severe) based on dNBR values (low: <0.15, moderate: 0.15-0.32, severe: >0.32), and classified areas outside USFS burn perimeters (Coronado National Forest Supervisors Office 2006) as fire-suppressed. We used ground assessments at 344 points generated for vegetation assessment (Appendix A) to supervise the classification process. Fifteen years is not sufficient time for large trees to regrow; therefore, severity classifications should be stable for >15 years post-fire. We used ERDAS Imagine (ERDAS 2008) for image processing, ESRI ArcMap (ESRI 2008) for GIS processing, and obtained Landsat TM images from Arizona Regional Image Archive (ARIA support team 2008).

Habitat use relative to burn heterogeneity

We overlaid 99% home ranges onto a 30 m-resolution fire severity map to assess habitat associations relative to burn heterogeneity. Because many measures of heterogeneity are correlated with area size (Kie et al. 2002; Li and Reynolds 1995; Li and Reynolds 1994), which can lead to bias in comparisons of large to small areas, we selected methods that compared equally-sized areas. Because wildlife species may respond differently to various scales (Brose 2003; Schiegg 2000), we calculated heterogeneity of burn severity for each pixel of our burn severity map at two spatial scales: small (90 m x 90 m square surrounding each pixel = 0.81 ha) and large (240 m-diameter circle surrounding each pixel = 4.41 ha). The small scale corresponds to a scale over which squirrels likely evaluate surroundings to meet immediate needs, such as food sources, view of predators, escape routes, and rest locations. The large scale corresponds to a scale over which squirrels likely evaluate surroundings to meet long-term needs, such as water sources, nesting sites, food quantity and variety, and shelter from extreme weather and predators. We selected these scales based on body size (Best 1995), vagility (Koprowski and Corse 2005), home range size (Appendix A; Pasch and Koprowski 2006, 2011), and observations during telemetry activities.

We used the number of patches of different burn severities surrounding each pixel as the measure of heterogeneity at each spatial scale. Patches are aggregations of pixels of the same burn severity class, and we treated patches that met only at pixel corners as separate patches. We assigned the number of patches within a 0.81 ha square as the value of the center pixel of the square for its small-scale heterogeneity value, and the number of patches within a 4.41 ha circle as the value of the center pixel of the circle for its large-scale heterogeneity value (Figure 1). The number of patches within a moving window representing the scale was tabulated for the center pixel of the moving window.

A heterogeneity value of 1 was calculated when all surrounding pixels were the same burn severity. A heterogeneity value of 2 patches was calculated near the perimeter of a large patch or in an area of low severity burn with a single patch of moderate or severe burn. Higher levels of heterogeneity occurred in areas with more than a single patch of moderate or severe burn inset within an area of low-severity burn. Squirrels did not incorporate other configurations of burn severity, such as large areas of severe burn with small inset patches of low-severity burn, within home ranges. Large patches resulted in heterogeneity values of 1 for most of the patch and values of 2 for the band of pixels near the perimeter of the patch. This band of pixels with heterogeneity values of 2 was narrow (approximate 2 pixels wide) for small-scale and wide (approximately 8 pixels wide) for large scale (Figure 1).

We used resource utilization functions (RUFs, Marzluff et al. 2004) to relate squirrel habitat use within home ranges to burn heterogeneity. The RUF approach used multiple linear regression adjusted for spatial autocorrelation. The kernelling process we used to create home ranges from telemetry locations resulted in a 3-dimensional plot (x, y, z) where the third dimension (z) was the intensity of use at map coordinate (x, y). The intensity of use for each 30m x 30m map pixel within the 99% kernel home range was used as the response variable of RUF regression (3rd-order selection, Johnson 1980) and the corresponding small and large scale heterogeneity values for the same map pixel was used as the explanatory variables. A separate regression was run for each animal, which made individual squirrels the sampling unit. We used program **R** (R Development Core Team 2009) and the RUF library (Marzluff et al. 2004). The RUF procedure determined maximum likelihood fit based on a Matérn covariance function that accounted for spatial autocorrelation induced by the kernelling process (Marzluff et al. 2004). Because we were interested in comparing responses to different levels and scales of burn heterogeneity, we used standardized coefficients (Marzluff et al. 2004). From exploratory data analysis, we suspected that use would display maximum or minimum values at moderate levels of heterogeneity. To allow for non-linear effects, we divided heterogeneity values at each scale into 5 categories. We categorized small-scale heterogeneity into 1, 2, 3, 4 or ≥5 patches within the 0.81 ha surrounding area, and large-scale heterogeneity into 1, 2, 3-5, 6-8, or ≥9 patches within the 4.41 ha surrounding area. We entered categories as explanatory variables of the RUF regression as indicator variables relative to the reference level of 1 patch = homogeneity. The regression coefficients represented the response of squirrels to heterogeneity, where a positive response corresponded to a positive coefficient, which indicated that an individual squirrel used heterogeneous areas more than homogenous areas, and negative coefficient indicated the converse.

We characterized habitat use relative to burn heterogeneity at 2 scales for individual squirrels, and averaged the regression coefficients across 14 squirrels. We included a regression coefficient of 0 in the calculation of the mean when a level of heterogeneity was available to a squirrel (within the study area) but was not used. We used one-sample *t*-tests to compare mean regression coefficients to 0 (Marzluff et al. 2004); mean regression coefficients that differed from 0 represented consistent response across the study population. To evaluate the effects of scale and level of heterogeneity on intensity of use, we used a 2-factor ANOVA. We tabulated the number of squirrels with individual significant positive and negative coefficients and performed sign tests relative to an expected even distribution centered on 0.

To summarize individual squirrel responses to heterogeneity, we tallied number of positive-positive, positive-negative, negative-positive, negative-negative combinations of small- and large-scale responses for each heterogeneity level for each squirrel. We compared the total number of each sign combination to the expected even distribution across the 4 sign combinations using chi-square goodness-of-fit test (Neu et al. 1974).

Patch Size Use

Patch size and heterogeneity are inversely correlated. To translate our findings on squirrel habitat use relative to burn heterogeneity into patch size recommendations, we assessed squirrel use of various sized patches of severe burn by comparing home ranges to areas available to the study animals (2nd-order selection, Johnson 1980). We merged individual home ranges into one home range perimeter so that patches used by more than one squirrel were counted only once, and used the 95% home range to exclude very lightly used patches at the edges of the 99% kernel home range. To define available area, we used a 784 m buffer (the greatest distance an animal was known to travel from capture point) around trap locations. Considering only severely-burned patches, we compared the area of each patch size used (in ha) to the area available to study squirrels with a chi-square goodness-of-fit test with Yates correction for small expected values.

To determine levels of moderate or severe burn squirrels can tolerate at home-range scale, we calculated percentage of area burned moderately or severely for our study area burned by wildfire. We merged individual home ranges into one home range perimeter and used 95% home range to exclude very lightly used patches at the edges of the 99% kernel home range. We considered both moderate and severe burn because it is unlikely that techniques to include patches of high intensity fire into prescription burns would be able to differentiate moderate and severe burn. We calculated percentages for entire home ranges and for burned portions of home ranges, excluding fire-suppressed areas.

Results

Determination of home ranges

We examined space use of 14 adult squirrels (9 female, 5 male) with ≥29 telemetry locations ($\bar{x}$ = 39.8 ± 3.0). Home-range (95% kernel) sizes did not differ between males and females ($F_{1,11}$ = 2.45, p = 0.15), or between study areas ($F_{1,11}$ = 0.39, p = 0.55).

Habitat use relative to burn heterogeneity

Squirrels in the study area burned by prescribed fire used homogenous fire-suppressed forest, homogenous low-severity burn, and the burn perimeter (Figure 2). Squirrels in the study area burned by wildfire primarily used low-severity burn with small inset patches of moderate and severe burn, but also homogenous fire-suppressed forest, homogenous low-severity burn, and the burn perimeter (Figure 2). Very little area of evenly-distributed burn severities was used by squirrels. Large patches of severe burn were used at edges or in areas where a narrow band extended into low-severity burn (Figure 2).

Association between intensity of use and burn heterogeneity at small-scale was inconsistent across the population (Table 1), indicated by mean regression coefficients not different from 0 (Figure 3). Squirrels used areas with 3 patches of different burn severities at small scale more than areas with lower or higher numbers of patches ($\bar{x}_{3\text{ patches, small scale}} = 0.94$, $t_7 = 1.49$, $p = 0.18$). Squirrels used heavily those areas with moderate levels of burn heterogeneity at large-scale ($\bar{x}_{3\text{-}5\text{ patches, large scale}} = 2.15$, $t_7 = 3.12$, $p = 0.02$ and $\bar{x}_{6\text{-}8\text{ patches, large scale}} = 2.55$, $t_7 = 2.30$, $p = 0.06$. Squirrels responded more positively to heterogeneity at large scale than at small scale ($F_{1,71} = 5.07$, $p = 0.03$), but there was no effect of level of heterogeneity ($F_{3,71} = 1.53$, $p = 0.21$). Distribution of the numbers of squirrels with positive and negative association of use to various levels of small-scale heterogeneity showed similar trends (Table 1).

For our tally of sign combinations of small and large scale responses for each heterogeneity level for individual squirrels, the most numerous combinations were positive response to both small- and large-scale heterogeneity or negative response to small-scale and positive response to large-scale heterogeneity responses ($\chi^2 = 11.00$, *d.f.* = 3, $p = 0.012$, Figure 4). We observed fewer negative responses to both scales than expected if distribution was evenly distributed (Bonferroni *z*-tests, $p < 0.05$, $Z_{0.00625} = -2.50$); only one squirrel responded negatively to heterogeneity at both small and large scales at the same level of heterogeneity.

Patch Size Use

Patches of severe burn ranged in size from 0.09 to 90.27 ha within the available area (Figure 5). Available patches of 0.36 ha, 0.63 ha, and 1.26 ha in size were not used; portions of all other available patch sizes were used by squirrels. The single 90.27 ha patch was used less than available (whole model $\chi^2 = 29.65$, *d.f.* = 11, $p = 0.002$, Bonferroni *z*-tests, $p < 0.05$, $Z_{0.00227} = -2.84$).

Severely-burned patches > 0.45 ha were used only at edges or in areas where a narrow band (<120 m wide) extended into low-severity burn (Figure 2). Squirrels used the largest patches, 62.19 ha and 90.27 ha in size, only at the edges. Squirrel home ranges in wildfire areas were 21.7% burned moderately or severely. If fire-suppressed areas were excluded, squirrels tolerated 30.1% moderate or severe burn.

Discussion

Habitat use by Mexican fox squirrels was associated positively with moderate burn heterogeneity at large scale, which suggests that squirrels selected areas with intermediate levels of burn heterogeneity. Other species respond to burn heterogeneity, although studies have examined only distance-to-edge effects of severely-burned forests. Woodpeckers nested further from edge of burned patches than random, presumably to avoid mammalian predators (Vierling et al. 2008). In contrast, reproductive success of black-backed woodpecker was higher near edges than deep within burned patches (Nappi and Drapeau 2009), as were densities of a favored food of black-backed woodpeckers (Saint-Germain et al. 2004).

Because 2 patches are found predominately at burn perimeters, the pattern of somewhat negative association between habitat use and 2 patches at small scale and mostly positive association between use and 2 patches at large scale suggests that areas immediately adjacent to burn edge were not used as much as areas nearby. Therefore, squirrels were not attracted to burn edges, despite using areas of patchy burn more than homogenous areas. Some species such as red-backed vole (*Clethrionomys gapperi*) are attracted to edges of clearings and forest near openings, whereas deer mice (*Peromyscus maniculatus*) and masked shrews (*Sorex cinereus*) use edge and forest openings differently according to vegetative conditions (Menzel et al. 1999;

Sekgororoane and Dilworth 1995), and sage sparrow (*Amphispiza belli*), California thrasher (*Toxostoma redivivum*), and California towhee (*Pipilo crissalis*) presence has been associated with edge in sage scrub vegetation (Kristan et al. 2003).

Homogenous areas of fire-suppressed forests and low-severity burn were used by squirrels, but homogenous areas of severe burn were not used, suggesting that burn severity plays an important role in squirrel response to fire. Mexican fox squirrels use low-severity burn more than other burn severities and fire-suppressed forest, although squirrels occasionally feed and nest in severely burned areas (Appendix A). Because of the variation in individual squirrel use of heterogeneous burned areas, heterogeneity likely plays a secondary role to burn severity in habitat use of burned forests, but our results indicate burn heterogeneity influences habitat use by Mexican fox squirrels and should not be ignored when assessing response of wildlife species to fire.

Mexican fox squirrel may use heterogeneously-burned forests because resources are distributed across forest patches burned at varying severities. Although forests burned at low-severity are used most heavily by squirrels (Appendix A), small patches of moderately- and severely-burned forest provide abundant seeds in isolated pine trees (Larson and Schubert 1970), fungal growth, an important part of Mexican fox squirrel diet (Koprowski and Corse 2001), on dead wood, and cavities, which female Mexican fox squirrels use exclusively for maternal nests (Pasch and Koprowski 2005; Steele and Koprowski 2001).

Conclusions

In forests inhabited by wildlife species that respond positively to burn heterogeneity, burn prescriptions should include small areas of moderate and severe burn at low proportions. Russell et al. (2010) describe a prescription of high severity patches <1 ha in size that comprise <5% of total burned area. Our results suggest that a configuration of primarily low-severity burn with moderate or severe patches <0.5 ha in size that comprise ≤22% of total area may be tolerated by wildlife species in the coniferous forests of southwestern US, which historical evidence suggests burned at high severities in some cases (Baisan and Swetnam 1995; Conway and Kirkpatrick 2007; Kirkpatrick et al. 2006; Kotliar et al. 2007). Some native wildlife species may be dependent on patches burned at higher severities than are presently prescribed (Hutto et al. 2008). Further studies should examine the effects of a wide range of burn heterogeneity and various fire prescriptions on vegetation structure and wildlife species if the use of prescribed fire is to benefit wildlife species in addition to reducing fuel levels (Tiedemann and Klemmedson 2000). Fuel reduction efforts can also be modified to influence future wildfires to burn in patterns of heterogeneity that are beneficial. Although modification to fire prescriptions may be difficult in the near-term because of high fuel loads, techniques to allow for patchiness of burn severity in the long-term should be developed. A return to a natural fire regime should be encouraged when possible to restore a mosaic in landscape structure (Bonnicksen and Stone 1985; Hutto et al. 2008).

In fire-adapted ecosystems, native wildlife species may require fire to fulfill the essential role as primary driver of landscape heterogeneity (Baker 1994; Bradstock et al. 2005; Parr and Andersen 2006; Price et al. 2005). Fire heterogeneity varies relative to topography, fuel availability, weather and climate conditions (Price et al. 2005; Turner et al. 1994), and the effects on wildlife species can vary as well. Conspicuous species such as the Mexican fox squirrel can serve as indicator species for other native species, and better understanding of how spatial heterogeneity of a single fire affects species can guide efforts to mediate the change of fire regime and its effect on communities and ecosystems (Driscoll et al. 2010).

The return of fire is inevitable, given the fire-prone nature of the ecosystem (Swetnam and Baisan 1996b) and human alternations to the vegetation (Graham et al. 2004) and climate (Brown et al. 2004). It is essential that we determine goals for modifications to the controllable aspects of wildland fires, such as heterogeneity, so that forest vegetation and wildlife species can be conserved.

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Tables and Figures

Table 1: Habitat use by Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) was most strongly associated with areas of moderate levels of burn heterogeneity at large scale, and burn heterogeneity at large scale had stronger positive association with use than burn heterogeneity at small scale, Chiricahua Mountains, Cochise Co., Arizona. Mean standardized coefficients, 95% confidence interval (CI) half-widths, and *p*-values include all sources of variation, *p*-values are given for one-sample *t*-tests that compare each mean regression coefficient to 0. Sign test *p*-value compares numbers of squirrels with individual use significantly associated with each level of heterogeneity to even distribution centered on 0.

Burn Heterogeneity		Mean standardized coefficient	95% CI half-width	*p*	Number of squirrels with individual use significantly associated with number of patches		Sign test *p*
					+	−	
Small scale number of patches	2	-0.70	1.37	0.29	5	6	1.00
	3	0.94	1.48	0.18	5	2	0.45
	4	-0.07	1.61	0.92	5	2	0.45
	≥5	0.85	3.76	0.61	3	3	1.00
Large scale number of patches	2	0.65	1.09	0.22	8	2	0.11
	3-5	2.15	1.63	0.02	7	0	0.02
	6-8	2.55	2.63	0.06	5	2	0.45
	≥9	1.96	4.47	0.34	4	4	1.00

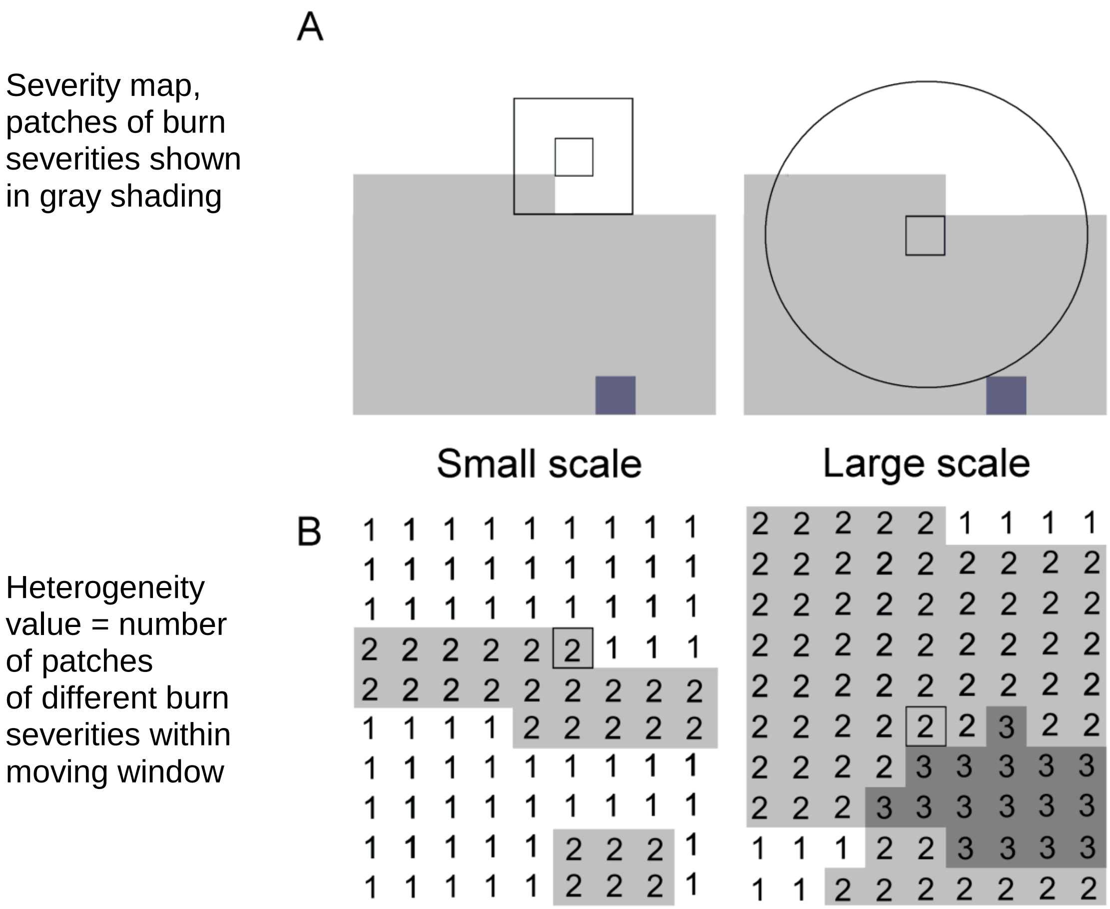

Figure 1: Small- and large-scale heterogeneity values (Figure 1B) were calculated by tallying the number of patches of different burn severities in the 0.81 ha square or 4.41 ha circular moving window, respectively (Figure 1A). Severity map from which the heterogeneity values were derived is shown in Figure 1A with the center pixel, 0.81 ha square, and 4.41 ha circle outlined. The heterogeneity value = number of patches at each scale is shown in Figure 1B, with the center pixel corresponding to Figure 1A outlined. The severity map represents the edge of a large patch, such as a burn perimeter, and a small patch within a large homogenous area.

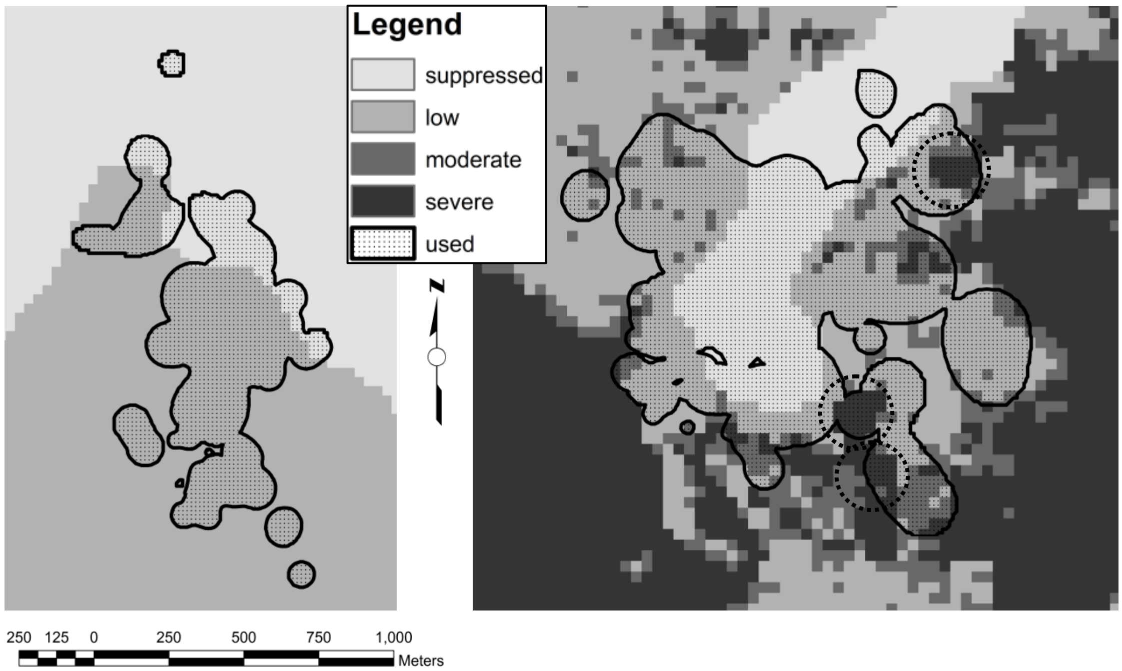

Figure 2: Study area burned by prescribed fire (left) was more homogeneous in burn severity than study area burned by wildfire (right). Home ranges of Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) are outlined (adjacent ranges merged into one shape). Areas used by squirrels in the study area burned by wildfire (right) were comprised of a large patch of fire-suppressed forest and large patches of low-severity burn with small inset patches of moderate and severe burn. Squirrels did not use regions of evenly distributed burn severities (center bottom of study area burned by wildfire at right). Large patches of severe burn were used at edges or in areas where a narrow band extended into low-severity burn (dashed circles), Chiricahua Mountains, Cochise Co., Arizona.

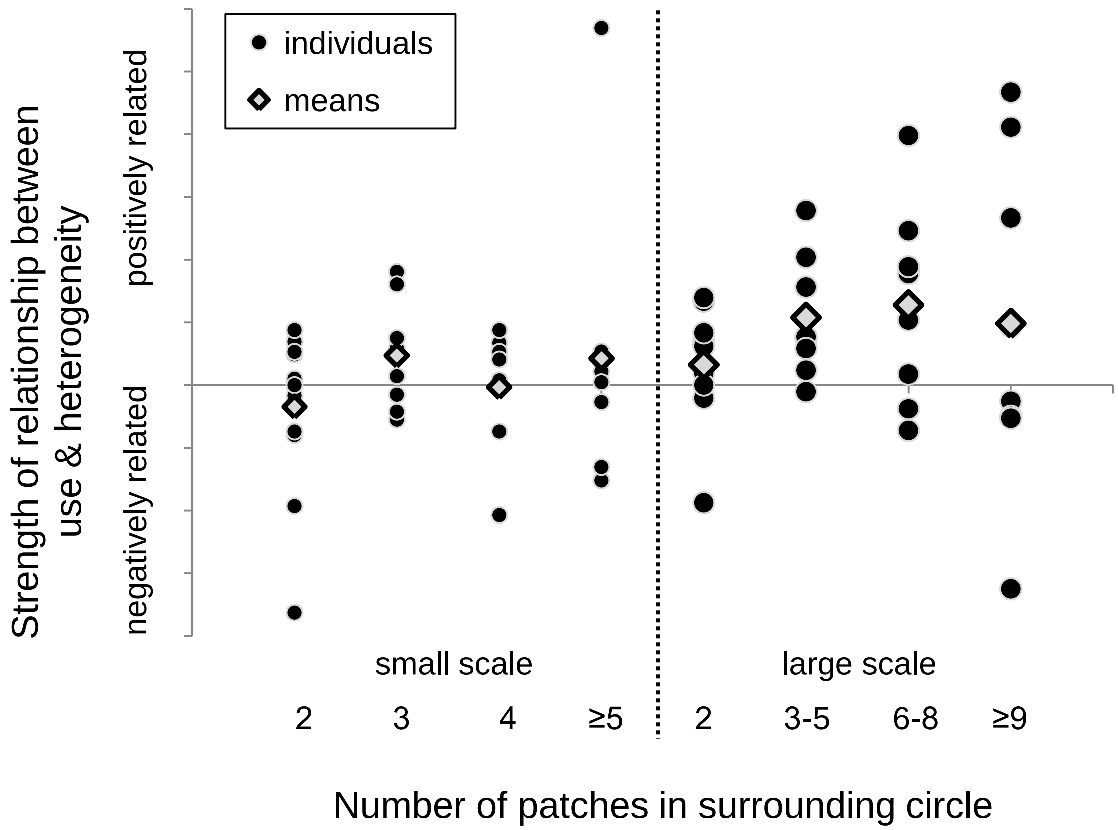

Figure 3: Use by Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) was most strongly associated with areas of moderate levels of burn heterogeneity at large scale, and large-scale heterogeneity had stronger positive association with use than small-scale heterogeneity ($F_{1,71}$ = 5.07, p = 0.03). Standardized RUF coefficients represent the strength of relationship between use and heterogeneity relative to reference level of 1 patch = homogeneity, individuals shown as solid points. Means, shown as open diamonds, were calculated to include all sources of variation, Chiricahua Mountains, Cochise Co., Arizona.

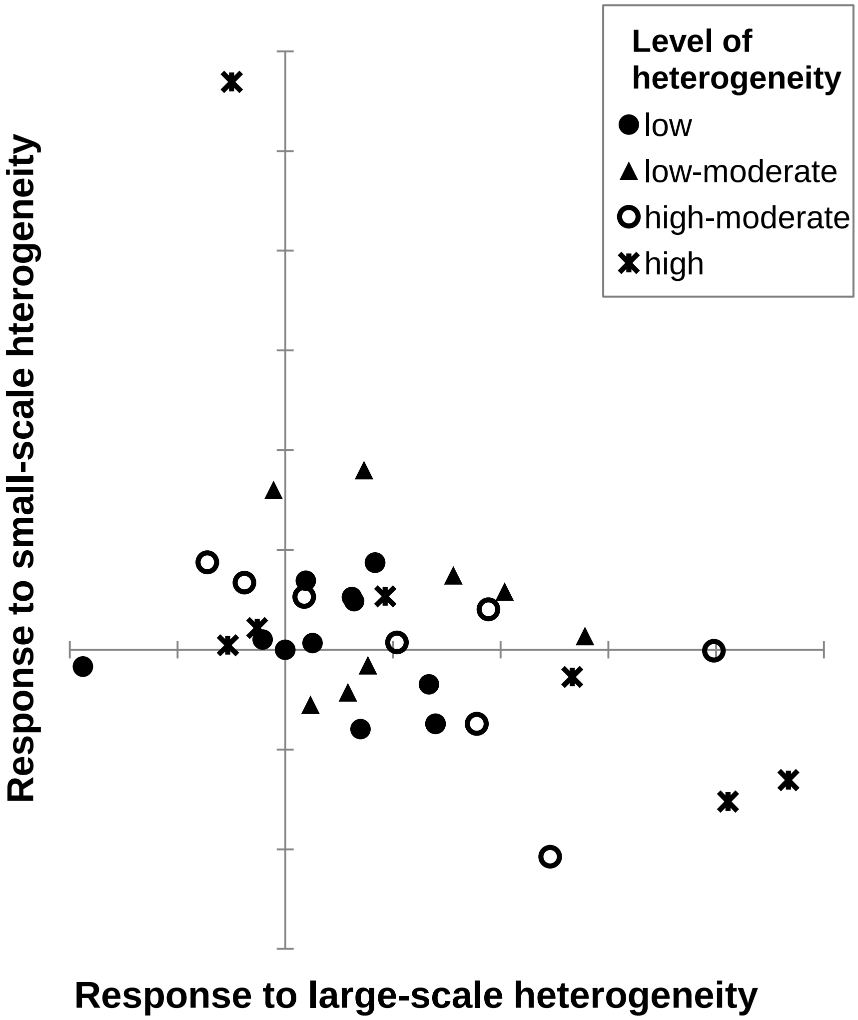

Figure 4: Mexican fox squirrels responded positively to heterogeneity at ≥1 scales ($\chi^2 = 11.00$, *d.f.* = 3, $p = 0.012$), and rarely responded negatively at both small and large scale for the same level of heterogeneity (Bonferroni *z*-tests, $p < 0.05$, $Z_{0.00625} = -2.50$). Each point is an individual squirrel's small- and large-scale response to one level of heterogeneity, Chiricahua Mountains, Cochise Co., Arizona.

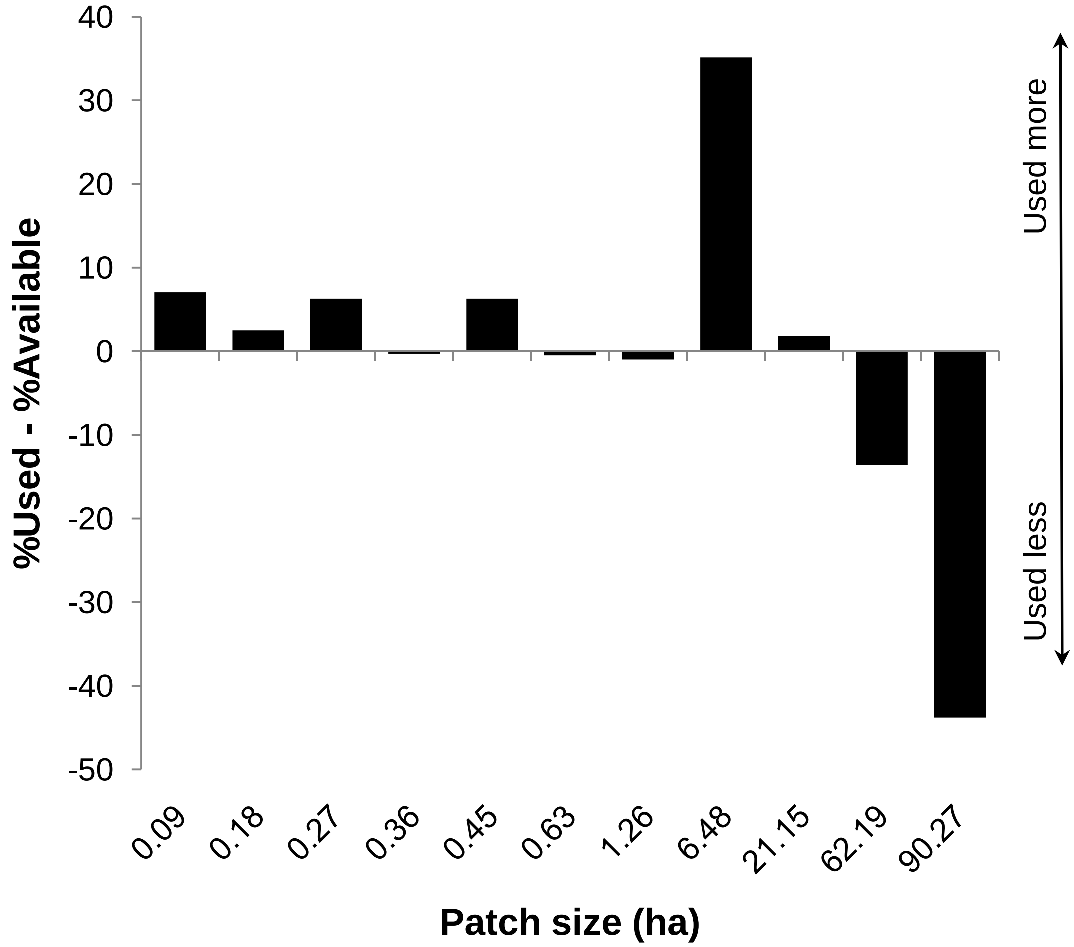

Figure 5: Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) used patches of severe burn non-randomly relative to patch size ($\chi^2 = 29.65$, *d.f.* = 11, $p = 0.002$). The single patch 90.27 ha in size was used less than available (Bonferroni *z*-tests, $p < 0.05$, $Z_{0.00227} = -2.84$). Used areas were defined as within home ranges, and patches used by more than one squirrel were counted only once. Areas available to study squirrels were defined by 784 m buffer around all trap locations, Chiricahua Mountains, Cochise Co., Arizona.