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Return of Fire as a Restoration Tool: Long-Term Effects of Burn Severity on Habitat Use by Mexican Fox Squirrels

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Abstract

After decades of suppression, fire is returning to forests of the western United States through wildfires and prescribed burns. These fires may aid restoration of vegetation structure and processes, which could improve conditions for wildlife species and reduce severe wildfire risk. Understanding response of wildlife species to fires is essential to forest restoration 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 long-term effects of burn severity on habitat selection of a native wildlife species. We surveyed burned forest for squirrel feeding sign and related vegetation characteristics to frequency of feeding sign occurrence. We used radio-telemetry within fire-influenced forest to determine home ranges of Mexican fox squirrels, *Sciurus nayaritensis chiricahuae*, and compared vegetation characteristics within home ranges to random areas available to squirrels throughout burned conifer forest. Squirrels fed in forest with open understory and closed canopy cover. Vegetation within home ranges was characterized by lower understory density, consistent with the effects of low-severity fire, and larger trees than random locations. 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. Our study contributes to an understanding of the role and impact of fire in forest ecosystems and the implications for forest restoration as fire returns to the region.

Key words: **Arizona, Chiricahua fox squirrel, prescribed fire, *Sciurus nayaritensis chiricahuae*, severity, wildfire.**

Introduction

Fire has been suppressed in the western United States since approximately 1900, altering species composition and vegetation structure in many ecosystems (Brown & 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 & Smith 2000). Although fire has not been completely excluded, a century of fire suppression has led to dominance of dense undergrowth and "dog-hair thickets" of closely spaced stunted trees (Brown & Smith 2000). Many vertebrate species are sensitive to vegetation structure, specifically those properties related to vertical components and spatial distribution of vegetation (DeWalt et al. 2003; Russell et al. 2010). Long-term fire suppression and accompanying changes to forest structure are implicated in declines of >100 wildlife species in the United States alone (Czech et al. 2000), such as Rocky Mountain bighorn sheep (*Ovis canadensis*, Bentz & Woodard 1988) and red-cockaded woodpeckers (*Picoides borealis*, Wilson et al. 1995).

Fire is returning in the form of wildfires and prescribed burns. Today's wildfires are more likely to burn severely because of climate change and accumulated fuel (Westerling et al. 2006). Not only do severe fires adversely affect many native species by killing 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 & Wilkinson 2005). For example, many forest bird species that forage in tree or shrub foliage respond negatively to severe burns (Smucker et al. 2005). Prescribed burns have been used to reduce accumulated fuels (Brown & Smith 2000; Graham et al. 2004) and are performed in conditions favorable for low-intensity burn. 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 & Koprowski 2010), Abert's squirrels (*Sciurus aberti*, Gwinn 2011), and Rocky Mountain bighorn sheep (*O. canadensis*, Smith et al. 1999).

Restoration of ponderosa pine forests to historical conditions of sparse undergrowth and large, widely spaced trees

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could reduce wildfire risk as well as enhance conditions for native wildlife species (Russell et al. 2010). A better understanding how wildlife species respond to long-term vegetation changes caused by fire can help set restoration goals in fire-adapted forests and measure progress of restoration efforts. The effects of fire on vegetation vary with burn severity (Smucker et al. 2005), and the differences persist over time, especially in dry ponderosa pine forests (Brown & Smith 2000).

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 long-term 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 unburned areas (Pasch & Koprowski 2011), which suggests that low-severity fire may be beneficial to squirrels. Our goal was to relate use by Mexican fox squirrels to vegetation conditions that are modified by fire, and relate those conditions to burn severity, a common index of fire damage. Because much of the forest in the southwestern United States historically sustained frequent, low-severity fire (Swetnam & Baisan 1996), we predicted that Mexican fox squirrels would select structural characteristics associated with low-severity fire.

Methods

Study System

The Mexican fox squirrel *(Sciurus nayaritensis)* is a large tree squirrel (approximately 700 g) found throughout the Sierra Madre Occidental of Mexico, northward into the United States 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). Mexican fox squirrels are classified as a sensitive species by the United States Forest Service (USFS, USDA Forest Service 2000) and population densities are among the lowest of any tree squirrel in North America (0.07–0.1/ha, Pasch & Koprowski 2005). The Mexican fox squirrel is the only arboreal squirrel species in the Chiricahuas (Cahalane 1939). The population of squirrels has been isolated in the Chiricahua Mountains 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 United States at least 7000 years ago (Van Devender & 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 & 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 approximately 123,000 ha and range from 1500 to 2795 m in elevation. Historically, forests in the Chiricahua Mountains sustained frequent, low-severity fire (Swetnam & Baisan 1996). 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 & Baisan 1996); 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 selected telemetry study areas in conifer forest because these areas were both used by squirrels and recently burned. We evaluated 10 potential study areas for squirrel activity indicated by feeding sign, live-trapped in 5 areas, and conducted radio-telemetry in 2 study areas. One study area (2600 m elevation) was located 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), which burned at low severity from late 2005 through early 2006. The perimeters were selected so that both fire-suppressed forest and forest burned at other severities were available for use by squirrels and so that we could compare relative use of different burn severities. Because we were interested in long-term effects of fire on vegetation regardless of ignition source or time since fire, we considered all fires that occurred ≤15 years ago. Both study areas experienced only one fire in the past 15 years. Vegetation for all study activities was composed 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*, *Quercus arizonica*, and *Quercus hypoleucoides*), mixed conifer, and riparian forest (deciduous woodland associated with drainages, Sawyer & Kinraide 1980; Gehlbach 1993). Our study was conducted in 2007 through 2009.

Feeding Sign Relative to Vegetation Characteristics

We examined feeding use by the population of Mexican fox squirrels at forest-wide scale relative to vegetation characteristics in burned forest. Forest burned recently (≤15 years) was surveyed on transects ($n = 42$) of 500 m length for signs of squirrels feeding. We located transects randomly relative to vegetation type within perimeters of recent wildfires and prescribed burns. Transects were conducted within a single vegetation type, but may have included multiple burn severities. 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), at the start point and at each 25-m increment along a transect. We surveyed a circular area with radius of 2 m surrounding each survey point and recorded information on current vegetation characteristics. We recorded percent understory density ≤2 m high measured with a cover pole (in increments of 5%, Griffith & Youtie 1988), percent canopy cover measured with spherical densitometer, distance to nearest live tree and nearest burned dead tree or burned downed log. To provide an index of fire damage from fires <15 years ago, we recorded subjective burn severity (fire-suppressed = 0, low severity = 1, moderate severity = 2, and severe burn = 3). Our burn severity classification was similar to Jenness et al. (2004), but incorporated canopy continuity, an important habitat component for tree squirrels (Steele & Koprowski 2001; Pasch & Koprowski 2011). 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. Although forest vegetation changes over time after fire, subjective evaluation of burn severity for a fire up to 15 years ago in dry ponderosa pine forest can be accurate if the severity categories are broad and based on tree mortality. Fifteen years is not sufficient time for large trees to regrow; therefore, severity classifications should be stable for >15 years post-fire.

Frequency of occurrence of feeding sign for a transect was calculated as the proportion of survey points at which feeding sign was found. Frequency of occurrence of feeding sign in conifer forests is strongly correlated to density of a closely related tree squirrel in similar forest habitat (Dodd et al. 1998). To assess squirrel use of burned forest relative to vegetation characteristics, the mean of each vegetation measurement for each transect was related to the frequency of occurrence of feeding sign. We employed stepwise multiple regression analysis to select important vegetation characteristics for squirrel use of burned forest for feeding. Variables were log transformed as necessary to meet assumptions of normality. Models were selected to maximize Akaike's information criterion (AIC).

Determination of Home Ranges

To describe individual squirrel habitat use, we employed radio-telemetry to determine home ranges of squirrels in two study areas burned with varying severities near the perimeters of recent fires (≤15 years, Coronado National Forest Supervisors Office 2006). 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 cloth handling cone (Koprowski 2002) and fitted adults (>550 g) with a radio-collar (Model SOM 2380, Wildlife Materials, Inc., Carbondale, IL, U.S.A.). We used a yagi antenna and receiver (Models F164-165-3FB and TRX-2000S, Wildlife Materials, Inc.) to locate individuals during daylight hours by homing (White & Garrott 1990) and recorded locations with a Global Positioning System unit (eTrex Legend Cx, Garmin International, Inc., Olathe, KS, U.S.A.). We located individuals at ≥120-minute intervals to minimize autocorrelation (White & Garrott 1990) and obtained locations evenly throughout periods of squirrel activity (Koprowski & Corse 2005) during all seasons from May 2007 to November 2008. We applied fixed-kernel methods with least squares cross-validation to set the smoothing parameter (Seaman & Powell 1996; Gitzen & Millspaugh 2003), and used the Animal Movement Analysis extension of ArcView (Hooge & Eichenlaub 2001) to calculate 95% home ranges for squirrels with ≥29 telemetry locations, a point at which accumulation curves generally asymptote (Ranges 6 software, Kenward et al. 2003). We performed a two-factor analysis of variance 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 conducted in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and with approval from 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 USFS.

Habitat Use Relative to Vegetation Characteristics and Burn Severity

We examined use by individual 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 & 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 × 4 m plots randomly within each home range and random site. We recorded information on current 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 measured with a cover pole (in increments of 5%, Griffith and Youtie 1988), number of trees ≥10 cm DBH, tree density (m^2 ha^{-1}, measured with variable plot method accounting for slope), percent canopy cover measured with spherical densitometer at plot center, and burn scar height on live tree closest to plot center. To provide an index of fire damage from fires <15 years ago, we also recorded subjective burn severity.

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. Models were selected to maximize AIC.

To relate the selected 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 second-order polynomial fit to discern whether characteristics varied across burn severity in nonlinear 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.

Results

Feeding Sign Relative to Vegetation Characteristics

Feeding sign was found on 20 of 42 transects, with frequency of occurrence as high as 0.71 ($\bar{x} = 0.08 \pm 0.05$). Frequency of occurrence was associated (multiple regression, whole model $F_{[2,39]} = 5.27$, $p = 0.009$) with open understory (effect likelihood ratio test, $F_{[1,39]} = 5.70$, $p = 0.022$, Fig. 1a) and closed canopy (effect likelihood ratio test, $F_{[1,39]} = 5.09$, $p = 0.030$, Fig. 1b).

Determination of Home Ranges

We radio-collared 19 adult squirrels (11 females and 8 males) and located squirrels 575 times ($\bar{x} = 30.3 \pm 8.2$ locations per individual). We calculated home ranges for 14 squirrels (nine female and five male) with $\geq$29 telemetry locations ($\bar{x} = 39.8 \pm 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 and Burn Severity

Home ranges had more open understory (effect likelihood ratio test, $\chi^2 = 3.76, df = 1$, $p = 0.053$) and larger trees ($\chi^2 = 4.54, df = 1$, $p = 0.033$) than random sites (logistic regression, whole model $\chi^2 = 10.87, df = 2$, $p = 0.004$, Fig. 2). The most open understory was found in areas burned at low severity, with minimum understory density at median burn severity = 1.17 (SE = 0.59–2.21) where 1 = low-severity burn and 2 = moderate-severity burn (multiple regression, second-order polynomial, $r^2 = 0.34$, $F_{[3,40]} = 6.72$, $p \leq 0.001$, Fig. 3). 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 $\geq$65%, whereas 60% of all random sites had $\geq$1 plots with understory density $\geq$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, $r^2 = 0.28$, $F_{[3,40]} = 5.31$, $p = 0.004$, Fig. 4a). 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 ($t_{11} = 3.59$, $p = 0.004$, Fig. 4b).

Discussion

Mexican fox squirrels fed more in burned forest with more open understory, and home ranges had more open understory

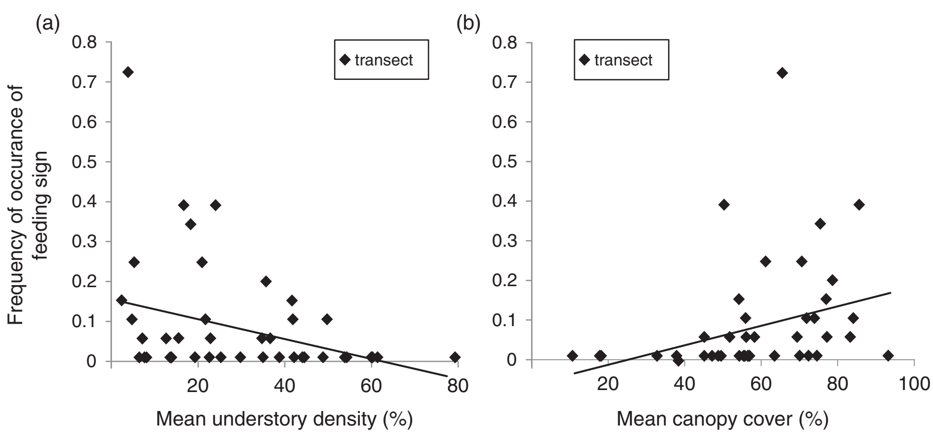

Figure 1. Frequency of occurrence (proportion of 21 transect points) of feeding sign showed (a) negative association to understory density and (b) positive association to canopy cover in forest areas recently burned ($\leq$15 years, solid lines are best-fit model predictions, frequency of occurrence of feeding sign = 0.009 − (0.003 × mean understory density) + (0.003 × mean canopy cover), $r^2 = 0.21$, $p = 0.009$), Chiricahua Mountains, Cochise Co., Arizona.

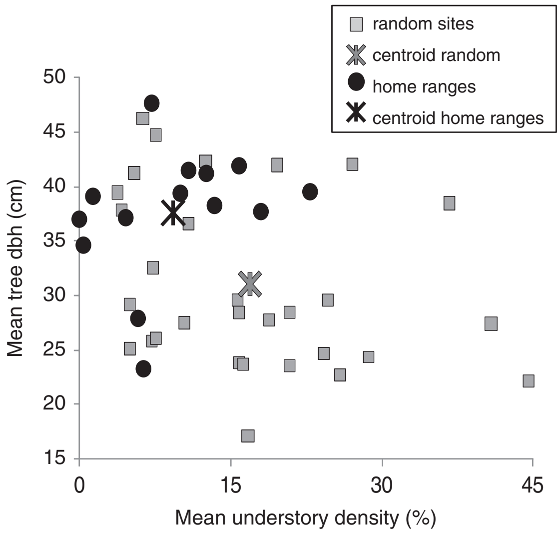

Figure 2. Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) used forest with more open understory and larger trees than random sites, Chiricahua Mountains, Cochise Co., Arizona.

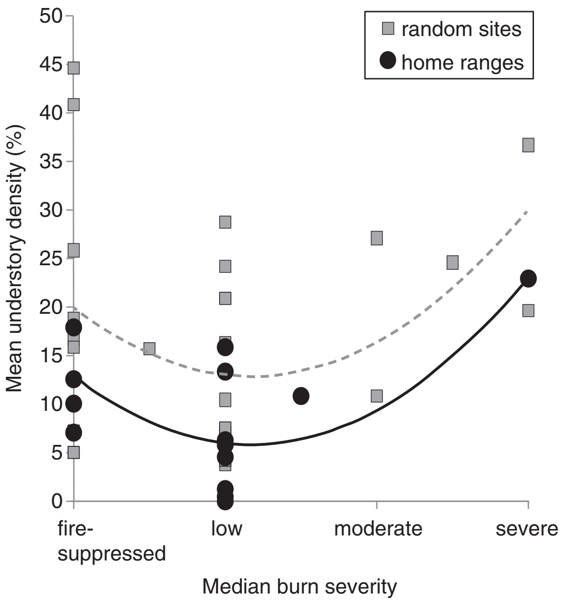

Figure 3. Understory density was lowest at low burn severities. Home ranges of Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) had lower understory density than random sites at all burn severities (solid and dashed lines are best-fit model predictions, mean understory density = 20.0 − (12.1 × 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.

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 (Swetnam & Baisan 1996; Brown & Smith 2000; Pasch & Koprowski 2011). Many wildlife species respond to forest structural components that are modified by fire (DeWalt et al. 2003). 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 (*Cyanocitta stelleri*), respond positively to low-severity fire (Kotliar et al. 2007), whereas species that prefer dense understory 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 fed more in forest with more continuous canopy and placed home ranges in areas with larger trees than random sites. Continuous canopy is a characteristic of large, mature trees, and repeated frequent, low-severity fire increases average tree size relative to fire-suppressed areas by killing the smallest and youngest trees (Regelbrugge & 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 (Smucker et al. 2005; Schmidt et al. 2006).

Other species adapted to vegetation types that historically experienced frequent, low-severity fires may also benefit from reintroduction of low-severity fire or treatments that mimic low-severity burn, including Mount Graham red squirrels (Leonard & Koprowski 2010), Abert's squirrels (Gwinn 2011), Florida panthers (*Puma concolor coryi*, Dees et al. 2001), Rocky Mountain bighorn sheep (Smith et al. 1999), several songbird species and deer mice (*Peromyscus maniculatus*, Bock & 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.

In 2011, 2 years after this study, nearly all of the forested portions of Chiricahua Mountains were burned by an uncontrolled wildfire. Intensity varied widely, with some areas burned severely. The entire population of Mexican fox squirrels in the United States, as well as many other species in the Chiricahuas, will be subject over the next 15 years to the vegetative conditions examined in this study. Many other forested areas in the western United States must undergo fuels-reduction treatments (prescribed burns or thinning, Graham et al. 2004; Schoennagel et al. 2004) in the near future; if fuels are not reduced, severe wildfires are likely due to the excessive buildup of fuel combined with the predicted drier and hotter weather conditions (Williams et al. 2010). To conserve and manage wildlife species, we must better understand relative use by wildlife of different burn severities and consider fire's effects on vegetation structure (Bradstock et al. 2005; Clarke 2008). 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 & Bock 1983; Carlson et al. 1993; Dees et al. 2001; Pasch & Koprowski 2011). Species such as the Mexican fox squirrel, sensitive to vegetative conditions that were historically common, can serve as indicators for other native wildlife species to help monitor the effects of efforts to reintroduce fire (Driscoll et al. 2010).

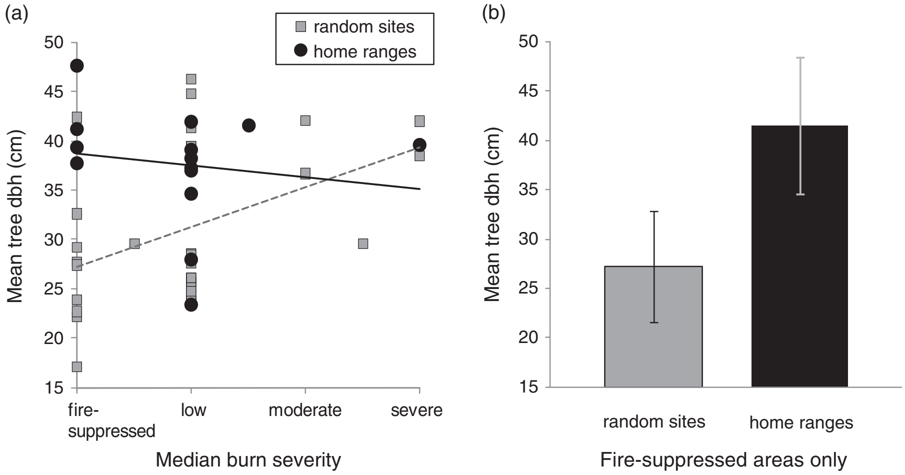

Figure 4. (a) Tree size was largest in fire-suppressed forest in Mexican fox squirrel (*Sciurus nayaritensis chiricahuae*) home ranges and largest at high burn severities in random sites (solid and dashed lines are best-fit model predictions, mean tree diameter at breast height (DBH) = 27.3 + (4.0 × median burn severity) + (11.4 × random/home range indicator) − (5.2 × [median burn severity × random/home range indicator]), $r^2 = 0.28$, $p = 0.004$). (b) In fire-suppressed forest, tree size was larger in home ranges than random sites (error bars are 95% confidence interval, $t_{11} = 3.59$, $p = 0.004$), Chiricahua Mountains, Cochise Co., Arizona.

Implications for Practice

- For benefit of native wildlife, low-severity fire should be re-introduced to forests that historically experienced such fires frequently.
- Because benefits of low-severity fire appear to arise from pruning of undergrowth while allowing large trees to survive, treatments producing similar vegetative conditions may also benefit native wildlife.
- Research should investigate effects of varying understory openness and tree size on native wildlife and how fuel-reduction treatments can best mimic low-severity fire's effects on vegetation.
- Aspects of fire other than severity, such as heterogeneity, frequency, and size, should be studied for effects on native wildlife.
- Native wildlife species that are sensitive to vegetative conditions modified by fire may serve as indicators of restoration progress in fire-impacted forests.

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