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Impacts of fire suppression on space use by Mexican fox squirrels

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Human suppression of fire has resulted in altered species composition and dense forest stands across the western United States. Accumulation of understory shrubs makes forests vulnerable to catastrophic fire and can impact animal use, whereas fire prescription can ameliorate negative impacts of suppression. We used radiotelemetry to determine patterns of habitat use and survival of Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) in fire-suppressed and fire-prescribed areas of the Chiricahua Mountains, Arizona. Core areas of squirrels within fire-suppressed areas were larger and contained more understory shrubs than core areas of squirrels in fire-prescribed areas. Shrub cover and canopy heterogeneity influenced core-area size and distance traveled, and squirrels that were depredated traveled farther than conspecifics that survived, but shrub cover and canopy heterogeneity were not directly associated with squirrel survival. Suppression-induced increases in understory vegetation might force squirrels to travel greater distances to meet energetic requirements and thereby increase predation risk. Retention of mature forested canyons and restoration of natural fire regimes will be important for the persistence of Mexican fox squirrels.

Key words: Arizona, fire suppression, Mexican fox squirrels, *Sciurus nayaritensis chiricahuae*, space use

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Fire plays an integral role in the persistence of many forested ecosystems worldwide (Pyne et al. 1996). Fire facilitates nutrient cycling, prepares seedbeds, and structures forests by influencing successional patterns (DeBano et al. 1998); however, human suppression of fire over the past century has led to degradation of many forested communities in North America (Cooper 1960; Pyne and Cronin 1982). Unnatural fire frequency, severity, and timing create conditions that threaten organisms adapted to historical fire regimes (Noss et al. 1995). Accumulation of understory shrubs and downed logs not only increases the risk of catastrophic fire but also can impact animal movement and habitat use (Carlson et al. 1993; Dees et al. 2001). Structural complexity of understory vegetation can impede locomotion (Schooley et al. 1996), render movement more conspicuous to predators (Brillhart and Kaufman 1991), or increase visual obstruction and thereby reduce likelihood of predator detection, or a combination of these factors (Metcalf 1984; Schooley et al. 1996). Changes in vegetation structure also can correspond with depletion of important food resources and thus represent areas of decreased value to animals.

Current conservation efforts seek to restore historical processes to degraded forests via prescribed fire (Baker 1994; Kauffman 2004). Prescribed fires typically reduce

understory shrub density, decrease hazardous fuel loads, and promote regeneration and sprouting of fire-resistant species (Whelan 1995). Alteration in vegetation structure, nutrient availability, and soil characteristics following prescribed fire affects abundance and diversity of many vertebrate taxa (Briani et al. 2004; Hutto 1995). Postfire succession also affects foraging and space-use patterns of mammals (Carlson et al. 1993; Dees et al. 2001; Vernes and Haydon 2001).

Many tree squirrels (genus *Sciurus*) have evolved (Kiltie 1989) and live in forests that experience frequent ground fires (Brown and Smith 2000; Koprowski 2005). Low-intensity ground fires appear to benefit tree squirrels indirectly by stimulating production of cones and fungi and creating open stands that facilitate terrestrial foraging (Weigl et al. 1989). Conversely, high-intensity crown fires characteristic of fire-suppressed forests negatively impact tree squirrels by destroying nest trees, burning nests, and killing nestlings (Kirkpatrick and Mosby 1981; Koprowski et al. 2006). However, indirect effects of suppression-induced understory



growth on squirrel movement, habitat use, and predation are unknown.

Mexican fox squirrels (*Sciurus nayaritensis*) inhabit the xeric mountains of northwestern Mexico and extreme southwestern United States. One subspecies, *S. n. chiricahuae*, is a large-bodied (700–800 g) endemic to the Chiricahua Mountains of southeastern Arizona (Best 1995) that has many life-history characteristics associated with vulnerability to extinction, including low densities and large home ranges (Pasch and Koprowski 2005, 2006a, 2006b). Historically, fires were common in the pine–oak forests that *S. n. chiricahuae* inhabits prior to suppression policies begun in the early 1900s (Bahre 1991; Kaib et al. 1996; Swetnam and Baisan 1994, 1996). Reduced fire frequencies appear to have altered plant species composition (Barton 1999; Cooper 1960) and produced dense stands vulnerable to crown fires (Covington and Moore 1994; Fulé et al. 1997; Swetnam et al. 1999), making Mexican fox squirrels a priority for conservation. *S. n. chiricahuae* has been considered an uncommon mammal of the region (Cahalane 1939) and a species of special concern (Drewry 1991) in need of immediate conservation action (Arizona Game and Fish Department 2006).

The aims of our study were to assess the influence of fire suppression on habitat use, movement, and predation of Mexican fox squirrels. We determined patterns of space use within fire-suppressed and fire-prescribed areas and followed the fate of squirrels in both areas. Our findings suggest that continued restoration of historical fire regimes through fire prescription could be an important practice to ensure the persistence of Mexican fox squirrels.

MATERIALS AND METHODS

Study area.—We studied Mexican fox squirrels from May 2002 to September 2003 in Chiricahua National Monument (elevation 1,573–2,228 m), located along the northwestern edge of the Chiricahua Mountains in southeastern Arizona (32°51'N, 109°17'W). The 5,000-ha preserve is dominated by rhyolite pillars and outcroppings covered with chaparral (*Arctostaphylos pungens*, *Quercus toumeyi*, and *Pinus cembroides*). A more detailed description of the study area is provided in Pasch and Koprowski (2006b). Chiricahua National Monument had a mean fire interval of approximately 15 years prior to a recent near century-long fire-suppression policy (Swetnam et al. 1989). Resource managers initiated prescribed fires in 1976 and continue to use fire as a management tool in some areas of the monument. We assigned areas of prescribed fire ($n = 33$, ~260 ha from 1980 to 2001) to one category and did not differentiate among areas that were burned multiple times ($n = 7$). Exemplars of fire-prescribed and fire-suppressed areas are shown in Fig. 1.

Trapping and radiotelemetry.—We captured 43 squirrels (15 females and 28 males) in live traps (model 104; Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanut butter over the course of the study. We assessed sex, age class, reproductive condition, and body mass of all

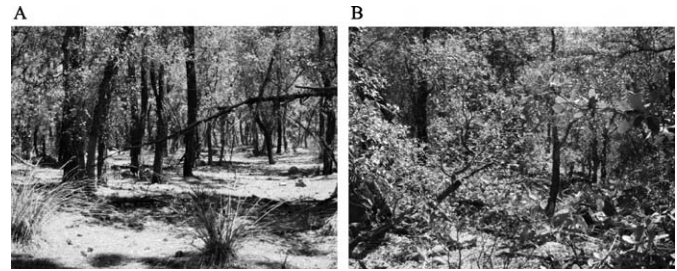


FIG. 1.—Photographs of A) fire-prescribed and B) fire-suppressed areas in Chiricahua National Monument, Arizona, 2002–2003.

squirrels in a cloth handling-cone (Koprowski 2002). We marked squirrels with numbered metal ear tags and colored washers (1-cm model 1005-3 and 1842, respectively; National Band and Tag Co., Newport, Kentucky) and affixed radio-collars (model SOM 2380; Wildlife Materials, Inc., Carbondale, Illinois; <3% of body mass) on adults (>670 g). All procedures followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We mapped (eTrex Vista; Garmin International, Inc., Olathe, Kansas) 189 locations to use as telemetry stations and used the intersection of 2 strong signals (25% of locations—White and Garrott 1990) and homing (75% of locations) to locate squirrels. Squirrel tolerance to human presence (Cahalane 1939; Kneeland et al. 1995) facilitated homing without influencing movement patterns (Kenward 1987). Constancy in radiosignal strength and location indicated immobility and potentially squirrel death. We homed on squirrels that remained immobile for >6 h during normal activity periods to verify their condition. We obtained successive locations at ≥ 120 -min intervals to ensure spatial and temporal independence (White and Garrott 1990) and collected telemetry points throughout the duration of the study. Characterization of seasons (nonbreeding: mid-June through mid-December; breeding: mid-December through mid-June) was determined from data on reproductive condition, mating chases, and emergence of offspring (Pasch and Koprowski 2006a) and controlled for in our analyses because reproductive strategies of males and females influence seasonal movements in this species (Pasch and Koprowski 2006b). Further details on collection of radiotelemetry data and error estimates (mean linear error based on setting collars in known locations = $17.4 \text{ m} \pm 3.1 \text{ SE}$) are presented in Pasch and Koprowski (2006b).

Data analyses included only adult animals with ≥ 30 locations ($\bar{X} = 33.2 \pm 0.52 \text{ SE}$, $n = 11$ males and 9 females) per season because area-observation curves for 95% fixed-kernel home ranges reached an asymptote at 30–35 locations (Kernohan et al. 2001). We included locations of squirrels within leaf nests only once to avoid artificial clustering of fixes, because squirrels often returned to the same nest nightly (Gurnell et al. 2001). We used Animal movement extension (Hooge and Eichenlaub 1997) of ArcView (ESRI 1996) to calculate 50% fixed-kernel estimates (Worton 1989) and selected least-squares cross-validation to create the smoothing parameter (Gitzen and Millsaugh 2003). We used the 50%

TABLE 1.—Vegetation characteristics useful in discriminating between areas of Mexican fox squirrel use and random unused locations within fire-prescribed and fire-suppressed areas of Chiricahua National Monument, Arizona, 2002–2003. D.F. = discriminant function. r = canonical coefficients. Univariate values are means (\pm SEs).

Variable	Multivariate		Univariate		
	r (D.F. 1) ^a	r (D.F. 2) ^b	Squirrel-use	Fire-prescribed	Fire-suppressed
Species diversity (H')	0.46**	0.20	1.52 \pm 0.06	0.54 \pm 0.07	0.55 \pm 0.07**
Basal area (m ²)	0.12*	−0.07	0.10 \pm 0.01	0.04 \pm 0.01	0.04 \pm 0.01*
Understory volume	−0.15	0.85**	0.32 \pm 0.03	0.38 \pm 0.04	0.72 \pm 0.05**
Shrub cover (no./plot)	−0.13	0.68*	3.14 \pm 0.39	2.91 \pm 0.44	8.58 \pm 1.06**
Canopy cover (%) ^c	0.02	−0.26	82.13 \pm 1.04	85.04 \pm 1.35	80.26 \pm 2.63
Species evenness (J)	0.01	0.16	0.45 \pm 0.01	0.37 \pm 0.04	0.41 \pm 0.06
Canopy heterogeneity ^c	0.08	0.13	16.30 \pm 1.59	12.22 \pm 1.46	19.10 \pm 3.18

^a Eigenvalue = 4.55, R -canonical = 0.905, λ = 0.112.

^b Eigenvalue = 0.605, R -canonical = 0.614, λ = 0.623.

^c Log-transformed.

* $P < 0.05$; ** $P < 0.01$.

isopleth to represent the core area (Wray et al. 1992). Core areas represent sections of concentrated resources and are expected to vary with changes in food distribution and abundance (Burt 1943).

We quantified distance traveled by randomly selecting 3 days per season when animals were located 3 times between 0500 and 1100 h. We calculated total linear distance traveled between 3 successive fixes over the 6-h morning period. Average distance traveled over 3 days served as an index of daily movement.

Vegetation measurements.—We overlaid squirrel core areas on a georeferenced map depicting fire-prescribed and fire-suppressed areas as determined by the boundaries of fire prescription. The location and size of core areas did not differ between reproductive and nonreproductive seasons (Pasch and Koprowski 2006b), so we categorized squirrels as fire-prescribed if $\geq 90\%$ of their core area fell within fire-prescribed areas ($n = 12$; 6 males and 6 females), and fire-suppressed if $\geq 90\%$ of their core area fell outside fire-prescribed areas ($n = 8$; 5 males and 3 females). We generated randomly 20 points (Jenness Enterprises 2003) within each squirrel's core area and 40 points in both fire-suppressed and fire-prescribed nonuse areas. The presence of decayed leaf nests indicated that random locations in fire-suppressed and fire-prescribed areas were available but not currently used by squirrels (Pasch and Koprowski 2005). We established 4×10 -m transects at each location to quantify vegetation characteristics. We identified and counted all trees ≥ 10 cm diameter at breast height (DBH) and shrubs $2.5 \leq \text{DBH} \leq 10$ cm, determined canopy cover, and quantified understory density with a cover pole (Griffith and Youtie 1988). We converted tree size and abundance to basal area (m²) and calculated tree species diversity (H') and evenness (J) with Shannon–Wiener's diversity index (Shannon and Weaver 1949). We used the coefficient of variation of canopy cover to estimate canopy heterogeneity.

Data analyses.—We conducted a 3-group discriminant function analysis to identify variables that distinguished areas of squirrel use from unused areas in fire-prescribed and fire-suppressed plots. We then used a 2-group discriminant

function analysis to identify variables that distinguished areas of squirrel use in fire-prescribed and fire-suppressed areas. Three-group discriminant function analysis enabled identification of variables important in habitat use, whereas 2-group discriminant function analysis identified habitat features that differed between fire-prescribed and fire-suppressed areas used by squirrels. We used analysis of variance (ANOVA) and 2-sample t -tests following discriminant function analysis to compare univariate vegetation characteristics.

We used multifactor ANOVAs with sex and season effects to determine how core-area size and distance traveled differed between squirrels in fire-prescribed and fire-suppressed areas. We used multiple linear regression to determine if distribution of core-area size and distance traveled was related to habitat characteristics. To determine if core-area size differed between squirrels that died and those that survived, we used one-tailed Wilcoxon rank-sum (Z) tests with the prediction that increased movement would increase predation risk (Vásquez et al. 2002). Logistic regression was used to determine if squirrel survival was explained by vegetation variables. All statistical analyses were conducted with JMP, Version 5 (2002). We log-transformed core-area size, distance traveled, and canopy cover estimates to meet assumptions of normality and homogeneity of variance (Ramsey and Schafer 2002). We report means (\pm SE) as untransformed values.

RESULTS

Differences in species diversity and basal area (discriminant function 1: $\chi^2_{14} = 205.56$, $P < 0.001$) separated squirrel-use areas from unused areas; squirrels used stands with larger and more diverse trees (Table 1). Differences in shrub cover and understory volume (discriminant function 2: $\chi^2_6 = 44.41$, $P < 0.001$) also separated squirrel-use areas from unused areas. Squirrels used sites with little understory volume and shrub cover, characteristic of fire-prescribed but not fire-suppressed areas (Table 1).

Shrub cover and understory volume explained differences between fire-prescribed and fire-suppressed areas used by squirrels ($\chi^2_7 = 19.43$, $P < 0.007$). Core areas of squirrels

TABLE 2.—Vegetation characteristics useful in discriminating between fire-prescribed and fire-suppressed areas used by Mexican fox squirrels at Chiricahua National Monument, Arizona, 2002–2003. D.F. = discriminant function. r = canonical coefficients. Univariate values are means (\pm SEs).

Variable	Multivariate	Univariate	
	r (D.F. 1) ^a	Fire-prescribed	Fire-suppressed
Shrub cover (no./plot)	0.52**	2.24 \pm 0.38	4.58 \pm 0.47**
Understory volume	0.33*	0.22 \pm 0.03	0.47 \pm 0.04*
Species diversity (H')	-0.27	1.61 \pm 0.07	1.41 \pm 0.08
Canopy cover (%) ^b	-0.21	83.36 \pm 1.30	80.35 \pm 1.60
Species evenness (J)	-0.19	0.46 \pm 0.02	0.32 \pm 0.02
Canopy heterogeneity ^b	0.13	14.66 \pm 2.02	18.84 \pm 2.47
Basal area (m ²)	0.02	0.10 \pm 0.01	0.10 \pm 0.01

^a Eigenvalue = 2.819, R -canonical = 0.859, λ = 0.262.

^b Log-transformed.

* $P < 0.05$; ** $P < 0.01$.

within fire-prescribed areas had fewer shrubs and less understory volume than those of squirrels in fire-suppressed areas (Table 2).

Squirrels within fire-suppressed areas had larger core areas than animals in fire-prescribed areas, after accounting for sex and season (fire-suppressed: 6.6 \pm 1.2 ha; fire-prescribed: 2.9 \pm 1.0 ha; $F_{1,29} = 7.68$, $P = 0.01$; Fig. 2). Examination of our data also suggested that squirrels in fire-suppressed areas traveled greater distances each day (fire-suppressed: 335.7 \pm 41.8 m; fire-prescribed: 212.3 \pm 38.8 m; $F_{1,34} = 2.91$, $P = 0.09$; Fig. 2). Shrub cover and canopy heterogeneity explained differences in core-area size (shrub cover: $\hat{\beta} = 0.3$, $SE = 0.1$, $t_{16} = 2.61$, $P = 0.02$; canopy heterogeneity: $\hat{\beta} = 1.1$, $SE = 0.5$, $t_{16} = 2.32$, $P = 0.03$) and distance traveled (shrub cover: $\hat{\beta} = 0.3$, $SE = 0.05$, $t_{15} = 3.61$, $P = 0.003$; canopy heterogeneity: $\hat{\beta} = 2.0$, $SE = 0.5$, $t_{15} = 3.73$, $P = 0.002$). Median core-area size increased by a factor of 0.3 (95% confidence interval [95% CI] = 0.1 to 0.8) and median distance traveled increased by a factor of 0.12 (95% CI = 0.11–0.14) for every shrub added. A doubling of canopy heterogeneity increased median core-area size by a factor of 0.12 (95% CI = 0.10–0.14) and median distance traveled by a factor of 0.4 (95% CI = 0.2–0.9).

We located remains of 9 radiocollared squirrels. Eight animals appeared healthy <3 days prior to locating clipped tails or stripped bones or both next to collars in the forest understory, signs characteristic of avian predators (Goheen and Swihart 2005; Lema 2001). We found an ear tag of another squirrel in gray fox (*Urocyon cinereoargenteus*) scat 3 weeks after losing her signal. We discovered all remains within the individual's core area and assumed squirrels were depredated nearby. Core-area size was similar between squirrels that were killed by predators (2.8 \pm 1.6 ha) and conspecifics that survived (4.7 \pm 1.1 ha; $Z = -0.26$, $n = 20$, $P = 0.397$). However, squirrels that were depredated traveled farther (371.3 \pm 43.6 m) than conspecifics that survived (195.3 \pm 37.7 m; $Z = 2.15$, $n = 20$, $P = 0.016$). Squirrel survival was not directly associated with vegetation charac-

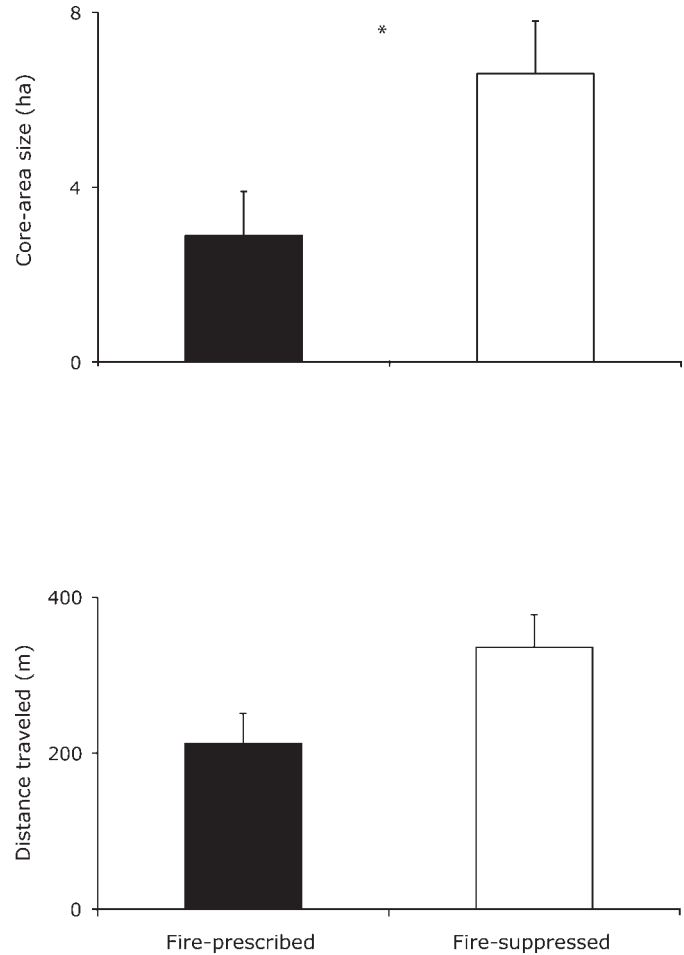


FIG. 2.—Mean (\pm SE) core-area size (top) and distance traveled (bottom) by Mexican fox squirrels within fire-prescribed ($n = 12$) and fire-suppressed ($n = 8$) areas of Chiricahua National Monument, Arizona, 2002–2003. * $P < 0.05$.

teristics, including shrub cover and canopy heterogeneity (Table 3).

DISCUSSION

Use of mature and diverse forest stands in both fire-suppressed and fire-prescribed areas suggests that tree size and diversity might be important habitat features for Mexican fox squirrels. In general, tree squirrels are dependent on mature forests that produce abundant mast (Gurnell 1987), and population sizes fluctuate with annual tree seed productivity (Steele and Koprowski 2001). Squirrels also appear to construct leaf nests in large trees with interconnected branches to decrease predation risk (Salsbury et al. 2004; Steele and Koprowski 2001). The broad diet of Mexican fox squirrels (>22 food items—Koprowski and Corse 2001) corresponds to use of diverse tree stands. Such dietary diversity likely enables squirrels to forage on a variety of mast species without relying on a single food source in drought-prone forests.

For tree squirrels core-area size is negatively correlated with food abundance and distribution. Large core areas are

TABLE 3.—Vegetation factors that explained survival of Mexican fox squirrels in Chiricahua National Monument, Arizona, 2002–2003. Wald's chi-square values and *P*-values from logistic regression. $\chi^2_6 = 12.92$, $n = 20$ squirrels, $P = 0.07$, $R^2 = 0.52$.

Variable	Surviving squirrels		Depredated squirrels		χ^2	<i>P</i>
	\bar{X}	<i>SE</i>	\bar{X}	<i>SE</i>		
Canopy cover	81.62	1.31	84.04	1.62	0.60	0.44
Canopy heterogeneity	18.10	2.22	12.34	1.72	0.59	0.45
Basal area	0.06	0.003	0.06	0.01	0.62	0.43
Shrub cover	2.70	0.41	3.79	0.82	0.05	0.82
Visual obscurity	0.27	0.03	0.36	0.06	0.41	0.52
Species diversity	1.55	0.09	1.62	0.06	1.61	0.20
Species evenness	0.43	0.02	0.40	0.02	1.81	0.18

indicative of resource-poor environments, whereas small core areas are characteristic of resource-abundant areas (Gurnell 1987; Lurz et al. 2000). In our study squirrels living in fire-suppressed areas had larger core areas and showed a slight trend toward traveling greater distances than animals in areas with prescribed burns. Differences in space use could be related to understory density and canopy heterogeneity, the 2 vegetation characteristics that differed between the areas. In general, fox squirrels prefer open forests with a continuous canopy and rarely inhabit stands with dense understory (Steele and Koprowski 2001). Increased understory vegetation of fire-suppressed areas can impede terrestrial foraging (Weigl et al. 1989) and thereby influence animals to move far to find open patches of forest.

High canopy heterogeneity indicates discontinuous mature tree stands, which may represent resource-poor areas for squirrels. Furthermore, lack of fire and high shrub cover can inhibit growth of hypogeous fungi, an important food item for Mexican fox squirrels (Koprowski and Corse 2001; Pasch and Koprowski 2006a) and other tree squirrels of western North America (Brown 1984; Carey et al. 2002; Dodd et al. 2003). Fungi are typically abundant in areas that experience frequent ground fires (Fujimura et al. 2005; Pilz et al. 2004) and are known to influence mammalian space-use patterns (Vernes and Haydon 2001). Thus, suppression-induced increases in understory vegetation might force squirrels to range over larger areas to acquire sufficient food items. As a result, activity budgets of squirrels could be altered to include more time spent traveling to locate food.

Although the mechanism to explain why squirrels may travel farther in fire-suppressed areas is uncertain, examination of our data indicates that animals that traveled greater daily distances experienced higher risk of predation. If activity budgets in fire-suppressed areas are modified to increase traveling time, squirrels have proportionally less time to rest or be vigilant. Red squirrels (*Tamiasciurus hudsonicus*) that spent less time resting or being vigilant, or both (Stuart-Smith and Boutin 1995), and individuals in poor body condition (Wirsing et al. 2002), were more likely to be depredated. Furthermore, moving animals are easier targets for predators,

especially raptors (Curio 1976; Martel and Dill 1995; Schoener 1971). Potential predators of Mexican fox squirrels include gray hawks (*Asturina nitida*—Kneeland et al. 1995), northern goshawks (*Accipiter gentilis*—S. Jacobs, Sky Island Alliance, pers. comm.), and other raptors (e.g., *Buteo jamaicensis*—Brown 1984) that commonly prey upon Arizona's tree squirrels. Predation risk also can be linked directly to vegetation characteristics (Lima 1990; Sharpe and Van Horne 1998). For example, increased shrub cover is correlated with short predator-detection distances and can increase predation risk by impeding mobility and thereby decreasing ability to escape from predators (Schooley et al. 1996).

The century-long suppression of fire has had significant effects on the structure of forests (Barton 1999; Cooper 1960); however, the indirect consequences of such changes for fire-adapted wildlife are more subtle but potentially important. Species diversity of wildlife in fire-suppressed areas might remain similar in the short-term, but increased movements and reduced survival could alter species composition over the long-term. Thus, space-use patterns can be an important indicator of long-term persistence in degraded ecosystems and used to monitor the efficacy of fire restoration.

Conservation implications.—Fire suppression negatively impacts tree squirrels by promoting catastrophic fires that lead to direct mortality (Koprowski et al. 2006) and destruction of habitat (Weigl et al. 1989). Our study suggests that suppression-induced accumulation of understory vegetation also reduces use of such areas by squirrels and can increase predation risk. The larger core areas found in fire-suppressed areas suggest lower densities of tree squirrels as well. A larger-scale sampling effort throughout the species range would provide a useful test of these predictions. We recommend continued use of prescribed fire to restore open pine-oak forests previously maintained by frequent, low-intensity fires and increase the available habitat to squirrels. Prescribed fires are valuable in habitat maintenance for threatened Big Cypress fox squirrels (*Sciurus niger avicennia*—Humphrey and Jodice 1992) and endangered Delmarva fox squirrels (*S. n. cinereus*—Taylor 1974) and likely will benefit Mexican fox squirrels. Concurrent monitoring of food and predator abundance and squirrel demography will help clarify mechanisms by which prescribed fire affects populations of Mexican fox squirrels. Restoration of natural fire regimes, especially in canyons with mature forests, will help maintain habitat quality for Mexican fox squirrels and other regional endemics that depend on fire (e.g., montane rattlesnakes—Smith et al. 2001).

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