

## Effect of heterogeneity in burn severity on Mexican fox squirrels following the return of fire

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**Abstract.** After decades of suppression, fire has returned to many forested areas of the 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 as historical fires. Recent fires in the Chiricahua Mountains of Arizona provided an opportunity to investigate effects of fire heterogeneity on habitat selection of a native wildlife species. We used radiotelemetry to determine home ranges of Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) within fire-influenced forests. We then applied resource-utilisation 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. Squirrels used small (<0.5 ha) or narrow (<120 m) severely burnt patches, but incorporated only edges of large patches into home ranges. Use of burnt forests by Mexican fox squirrels demonstrates the complexities of fire's effects on wildlife. Our results contribute to an understanding of the role and effect of fire in forest ecosystems and implications for wildlife conservation.

**Additional keywords:** Arizona, Chiricahua fox squirrel, native wildlife, patchiness, prescription burn, *Sciurus nayaritensis chiricahuae*, wildfire.

Received 27 March 2012, accepted 30 July 2012, published online 11 October 2012

### Introduction

In the widespread dry ponderosa pine (*Pinus ponderosa*) forests of the western United States (US), wildfires and prescribed burns have returned to many areas that historically experienced frequent, low-severity fires (Cooper 1960; Swetnam and Baisan 1996b). After nearly a century of suppression, wildfires in recent decades have burnt these forests at increasing frequency, severity and extent (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 are used to reduce fuel loads, which may reduce size and severity of future wildfires (Brown and Smith 2000; Graham *et al.* 2004; Finney *et al.* 2005).

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 effects 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 (Turner *et al.* 1994; Chuvieco 1999). Wildfire burns with a wide range of severities and often heterogeneously, creating a highly variable landscape pattern of unevenly sized patches of different burn severities in close proximity (Baker 1992; Turner *et al.* 1994). However, large severe wildfires can homogenise the landscape by killing most trees in large areas (Chuvieco 1999). Prescribed fires often include prescription of maximum flame lengths (Graham *et al.*

2004), which can result in uniform low severity and 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; Price *et al.* 2005; Parr and Andersen 2006).

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 have been studied extensively (Tews *et al.* 2004), effects of burn heterogeneity on wildlife species have been little studied (Clarke 2008).

Use of burnt forests by wildlife varies with species, habitat requirements and fire characteristics (Stuart-Smith *et al.* 2002; Fisher and Wilkinson 2005; Larsen *et al.* 2007; Vierling *et al.* 2008; Nappi and Drapeau 2009; Russell *et al.* 2010). Use also varies relative to burn severity (Hutto 1995; Smucker *et al.* 2005; Kirkpatrick *et al.* 2006; Kotliar *et al.* 2007; Doumas and Koprowski 2012), 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) nest within severely burnt areas away from edges of unburnt forests (Vierling *et al.* 2008), but reproductive success of black-backed

woodpeckers (*Picoides arcticus*) is higher near edges of unburnt forests (Nappi and Drapeau 2009). The results of a simulation model used to examine the persistence of malleefowl (*Leipoa ocellata*) in Australia suggest 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 to create burns predominately homogeneous relative to burn severity (Knapp and Keeley 2006). 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 (Wilcove *et al.* 1998; Tiedemann and Klemmedson 2000). 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 burnt forests by a conspicuous medium-sized mammal (the Mexican fox squirrel, *Sciurus nayaritensis chiricahuae*) in the Chiricahua Mountains of south-eastern Arizona as a case study to understand the effect of heterogeneity in burn severity on native wildlife species. Because Mexican fox squirrels use small patches of moderate and severe burn within areas burnt at low severity (Dumas and Koprowski 2012), we predicted use by squirrels would increase as heterogeneity of burn severity increases. To allow practical implementation of our findings, we investigated size of severely burnt patches used by squirrels and the level of overall moderate and severe burn tolerated by squirrels.

## Methods

### Study system

The Chiricahua Mountains of south-eastern 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 affected the range (Coronado National Forest Supervisors Office 2006), primarily in conifer forests (ponderosa pine, *Pinus ponderosa* and mixed conifer: Douglas-fir, *Pseudotsuga menziesii*; with white fir, *Abies concolor*; and Engelmann spruce, *Picea engelmannii*). Forests unburnt for nearly a century were rare historically (Swetnam and Baisan 1996a).

We located one study area (2600-m elevation) at the perimeter of a large (>10 000-ha) wildfire that burnt in 1994, in an area with unburnt forest and patches of forest burnt 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 burnt at low severity. The perimeters of fires were selected so that both unburnt and burnt forest were available

for use by squirrels. Vegetation comprised primarily ponderosa pine forest with smaller components of Madrean oak-pine (Chihuahuan and Apache pines, *P. leiophylla* var. *chihuahuana* and *Pinus engelmannii*; with the evergreen oaks *Quercus emoryi*, *Q. arizonica* and *Q. hypoleucoides*), mixed conifer and riparian forest (deciduous woodland associated with drainages, Sawyer and Kinraide 1980; Gehlbach 1993). Our study was conducted in 2007 through 2009.

Mexican fox squirrels are large tree squirrels (~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 subspecies, known as the Chiricahua fox squirrel (Best 1995), which is classified as a sensitive species by the United States Forest Service (USFS, USDA Forest Service 2000). The Chiricahua fox squirrel is the only arboreal squirrel species in the Chiricahuas (Cahalane 1939). The population has been isolated in the Chiricahua Mountains since formation at least 7000 years ago of the 'sky island' landscape in north-western Mexico and south-western US, characterised by insular forests at high elevations separated from other mountains by arid lowlands (Gehlbach 1993), (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 habitat use by squirrels, we employed radiotelemetry to determine home ranges in areas burnt with varying severities near the perimeters of recent fires ( $\leq 15$  years, Coronado National Forest Supervisors Office 2006). Although squirrels also use riparian forest, we restricted trapping areas to conifer forests (ponderosa pine and mixed conifer) because these areas were recently burnt. We evaluated 10 potential live-trapping areas for squirrel activity indicated by feeding sign and live trapped in five areas. We were able to calculate home ranges in two 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 radiocollar (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.) 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, KS). We located individuals at  $\geq 120$ -min intervals to minimise 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 (Seaman and Powell

**Table 1. Burn severity classifications**

Burn severity	dNBR values	Ground assessment criteria
Unburnt	Outside USFS perimeter	No burn scars
Low	<0.15	Burn scars on tree trunks but intact canopy
Moderate	0.15–0.32	Tree mortality and interrupted canopy
Severe	>0.32	Complete or nearly complete tree mortality such that remaining live trees were isolated from each other and branches did not overlap

**Table 2. Definitions of spatial scales**

Dimensions, shape and area of moving window over which heterogeneity was assessed, and biological correspondence for Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*), Chiricahua Mountains, Cochise County, Arizona

Spatial scale	Moving window		Biological correspondence
	Dimensions shape	Area	
small	90 × 90-m square	0.81 ha	Immediate needs, such as food sources, view of predators, escape routes and rest locations
large	240-m-diameter circle	4.41 ha	long-term needs, such as water sources, nesting sites, food quantity and variety and shelter from extreme weather and predators

1996; Gitzen and Millsbaugh 2003), and used the 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  $\pm$  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 the USFS.

#### Map of burn severity

We used a supervised classification of the differenced Normalised Burn Ratio (dNBR, Key and Benson 2005) to construct a 30-m-resolution map of burn severity from pre- and post-fire Landsat Thematic Mapper (TM) images. We categorised burn severity into three classes (low, moderate, severe) based on dNBR values (Table 1), and classified areas outside USFS burn perimeters (Coronado National Forest Supervisors Office 2006) as unburnt. We used ground assessments at 344 points generated for vegetation assessment (Doumas and Koprowski 2012) to supervise the classification process. Our ground-assessment classification system (Table 1) consisted of broad categories generally defined by survival of mature trees and canopy continuity because mature trees and canopy are important habitat considerations for Mexican fox squirrels (Pasch and Koprowski 2011). Fifteen years is not sufficient time for large trees to regrow; therefore, severity classifications should be stable for >15 years post fire. We classified continuous dNBR values into burn severity classes in order to use patch-based metrics as measures of heterogeneity (Hayes and Robeson 2011). We used ERDAS IMAGINE (ERDAS, Atlanta GA) for image processing, ArcMap 9.3 (ESRI, Redlands, CA) for GIS

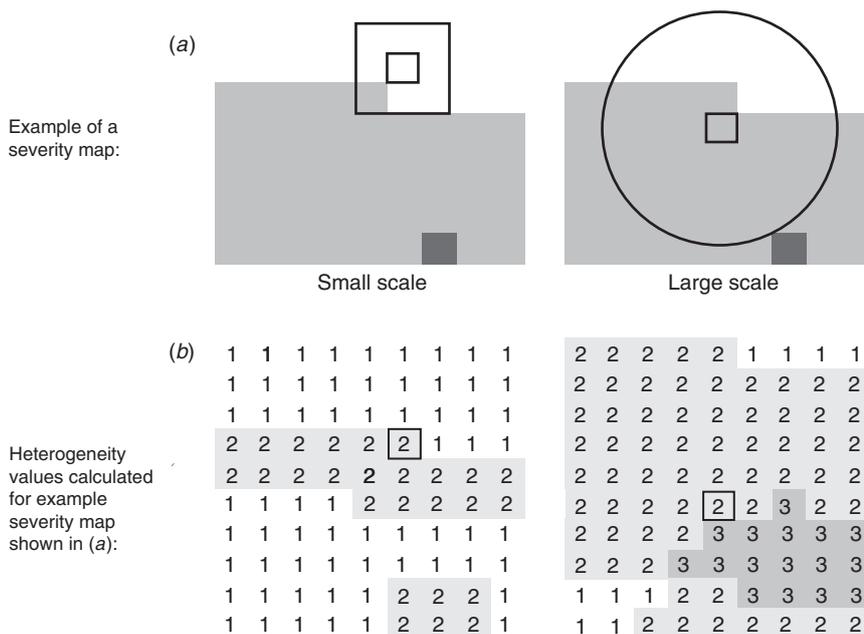
processing, and obtained Landsat TM images from Arizona Regional Image Archive (ARIA Support Team 2008).

#### Habitat use relative to burn heterogeneity

We overlaid 99% home ranges onto our burn severity map to assess habitat associations relative to heterogeneity of burn severity. All study animals had home ranges positioned entirely or partially within burnt areas; we investigated level of use within home ranges relative to burn pattern to discern if squirrel use was associated with burn heterogeneity at the home range scale. Because many measures of heterogeneity are correlated with area (Li and Reynolds 1994, 1995; Kie *et al.* 2002), which can lead to bias in comparisons of large to small areas, we selected a moving-window method that compared equal-sized areas (Hayes and Robeson 2011). Because wildlife species may respond differently to various scales (Schiegg 2000; Brose 2003), we calculated heterogeneity of burn severity for each pixel of our burn severity map at two spatial scales: small and large (Table 2). We selected these scales based on body size (Best 1995), vagility (Koprowski and Corse 2005), home-range size (Pasch and Koprowski 2006, 2011; Doumas and Koprowski 2012) 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. The number of patches within a moving window representing the scale was tabulated for the centre pixel of the moving window (Fig. 1).

A heterogeneity value of 1 was calculated when all surrounding pixels were the same burn severity. A heterogeneity value of 2 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



**Fig. 1.** Demonstration of heterogeneity values at small and large scale. An example of a burn severity map is shown in (a), with different severities shown in grey shading. The centre pixel and moving window for each scale are outlined. Heterogeneity values for each pixel are shown in (b). The centre pixel corresponding to (a) is outlined in (b).

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 (Fig. 1).

We used resource-utilisation functions (RUFs, Marzluff *et al.* 2004) to relate squirrel habitat use within home ranges to burn heterogeneity (3rd-order selection, Johnson 1980). The RUF approach is based on multiple linear regression adjusted for spatial autocorrelation. The kernelling process 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  $30 \times 30$ -m map pixel within the 99% kernel home range was used as the response variable of RUF regression and the corresponding small- and large-scale heterogeneity values for the same map pixel were used as the explanatory variables. A separate regression was run for each animal, which made individual squirrels the sampling unit. We used R (R Development Core Team 2009) and the RUF library (Marzluff *et al.* 2004) for statistical analysis. 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 standardised 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 easy interpretation of non-linear effects, we divided heterogeneity values at each scale into five categories. We categorised small-scale heterogeneity into 1, 2, 3, 4 or  $\geq 5$  patches within the moving window representing small scale, and large-scale heterogeneity into 1, 2, 3–5, 6–8 or  $\geq 9$  patches within the moving window representing large scale. We entered categories as explanatory variables of the RUF regression as indicator variables relative to the reference level of one patch, which equals 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 homogeneous areas, and negative coefficient indicated the converse.

We characterised habitat use relative to burn heterogeneity at two 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 significantly 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 centred on 0 (Marzluff *et al.* 2004).

To summarise individual 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.

**Table 3. Estimates of standardised RUF coefficients for Mexican fox squirrels**

Habitat use by Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) in the Chiricahua Mountains, Cochise County, Arizona was most strongly associated with areas of moderate levels of burn heterogeneity at large scale. Mean standardised coefficients, 95% confidence interval (CI) half-widths and *P* values include all sources of variation

Burn heterogeneity		Mean standardised coefficient	95% CI half-width	<i>P</i>	Number of squirrels with individual use significantly associated with number of patches		Sign test <i>P</i>
					+	-	
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

We compared the total number of each sign combination to the expected even distribution across the four sign combinations using Chi-square goodness-of-fit test (Neu *et al.* 1974).

#### Patch-size use

Patch size and heterogeneity are negatively correlated. To translate our findings on habitat use relative to burn heterogeneity into patch-size recommendations, we assessed use by squirrels 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 burnt patches, we compared the area of each patch size used (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 that squirrels can tolerate at home-range scale, we calculated percentage of area burnt moderately or severely for our study area burnt 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 burnt portions of home ranges, excluding unburnt areas.

## Results

### Determination of home ranges

We examined space use of 14 adult squirrels (nine female, five male) with ≥29 telemetry locations ( $\bar{x} = 39.8 \pm 3.0$ ).

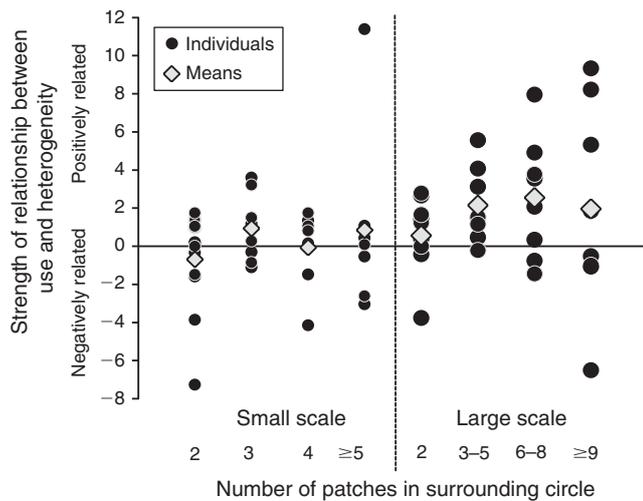
Home-range (95% kernel) sizes did not differ between males and females ( $F_{1,11} = 2.45$ ,  $P = 0.15$ ) or between study areas ( $F_{1,11} = 0.39$ ,  $P = 0.55$ ).

### Habitat use relative to burn heterogeneity

Squirrels in the study area burnt by prescribed fire used homogeneous unburnt forest, homogeneous low-severity burn and the burn perimeter. Squirrels in the study area burnt by wildfire primarily used low-severity burn with small inset patches of moderate and severe burn, but also homogeneous unburnt forest, homogeneous low-severity burn and the burn perimeter. 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 (maps showing habitat use and burn pattern within study areas are provided as supplementary material, see [http://www.publish.csiro.au/?act=view\\_file&file\\_id=WF12046\\_AC.pdf](http://www.publish.csiro.au/?act=view_file&file_id=WF12046_AC.pdf)).

Association between intensity of use and burn heterogeneity at small scale was inconsistent across the population (Table 3), indicated by mean regression coefficients not different from 0 (Fig. 2). Squirrels used areas with three patches of different burn severities at small scale somewhat 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 ( $\bar{x}_{3-5 \text{ patches, large scale}} = 2.15$ ,  $t_7 = 3.12$ ,  $P = 0.02$ ;  $\bar{x}_{6-8 \text{ patches, large scale}} = 2.55$ ,  $t_7 = 2.30$ ,  $P = 0.06$ ). 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 3).

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 ( $\chi^2 = 11.00$ , d.f. = 3,  $P = 0.012$ , Fig. 3). We observed fewer negative responses at both scales than expected if distribution



**Fig. 2.** Use by Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) in the Chiricahua Mountains, Cochise County, Arizona 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 did small-scale heterogeneity ( $F_{1,71} = 5.07, P = 0.03$ ). Values for individuals shown as solid points, and means, as open diamonds.

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.

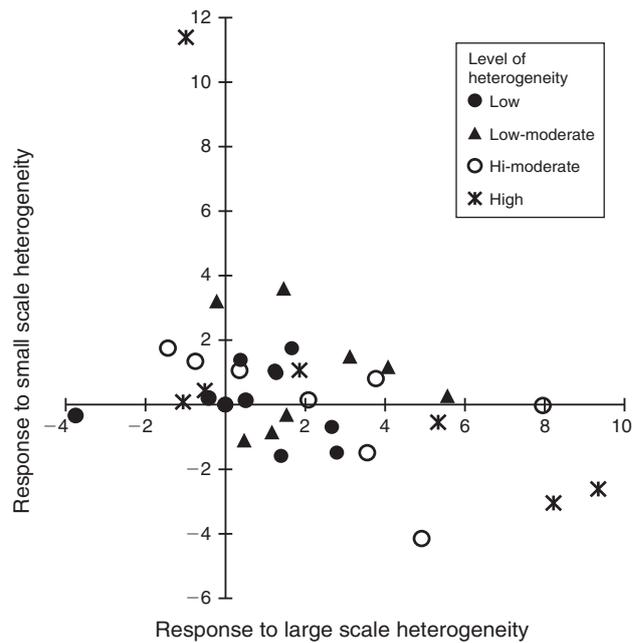
**Patch-size use**

Patches of severe burn ranged in size from 0.09 to 90.27 ha within the available area (Fig. 4). Available patches of 0.36, 0.63 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,  $P < 0.05, Z_{0.00227} = -2.84$ ).

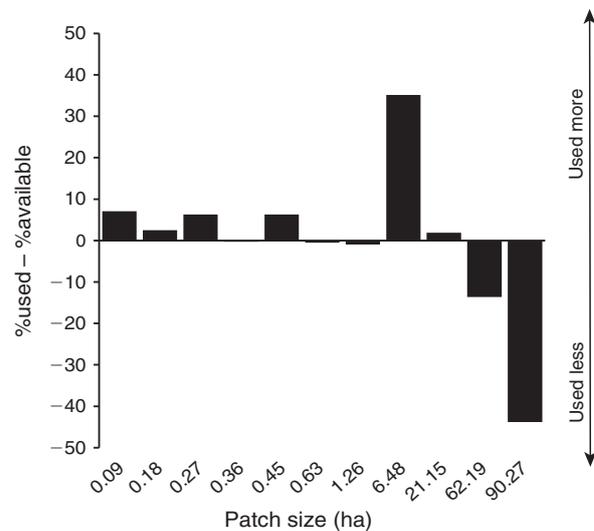
Severely burnt patches  $>0.45$  ha were used only at edges or in areas where a narrow band ( $<120$  m wide) extended into low-severity burn. Squirrels used the largest patches, 62.19 ha and 90.27 ha in size, only at the edges. Home ranges in wildfire areas were 21.7% burnt moderately or severely. If unburnt 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. Our prediction that use would increase as heterogeneity of burn severity increases was correct for low and moderate levels of heterogeneity at large scale, but incorrect for high levels of heterogeneity. Other species respond to burn heterogeneity, although studies have examined only distance-to-edge effects of severely burnt forests. Woodpeckers nest further from edge of burnt patches than random, presumably to avoid mammalian predators (Vierling *et al.* 2008). In contrast, reproductive success of black-backed woodpeckers is higher near edges than it is deep within burnt patches (Nappi and Drapeau 2009), as are densities of a favoured food of black-backed woodpeckers (Saint-Germain *et al.* 2004).



**Fig. 3.** Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) in the Chiricahua Mountains, Cochise County, Arizona responded positively to heterogeneity at  $\geq 1$  scales, and rarely responded negatively at both small and large scale for the same level of heterogeneity. Each point is an individual squirrel's response to one level of heterogeneity.



**Fig. 4.** Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) in the Chiricahua Mountains, Cochise County, Arizona used patches of severe burn non-randomly relative to patch size ( $\chi^2 = 29.65, d.f. = 11, P = 0.002$ ).

Homogeneous areas of unburnt forests and low-severity burn were used by squirrels, but homogeneous areas of severe burn were not used, suggesting that burn severity plays an important role in response of squirrels to fire. Because of the variation in individual use of heterogeneous burnt areas, heterogeneity likely plays a secondary role to burn severity in habitat use of burnt forests. However, 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.

A heterogeneity level of two patches is found predominately at burn perimeters or edges of large patches, and the band of two patches at the burn edge is narrow (~2 pixels) for small scale and wide (~8 pixels) for large scale (Fig. 1). The pattern of somewhat negative association between habitat use and two patches at small scale, and mostly positive association between use and two 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 they did homogeneous areas. Some species such as red-backed voles (*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 (Sekgororoane and Dilworth 1995; Menzel *et al.* 1999). Presence of sage sparrows (*Amphispiza belli*), California thrashers (*Toxostoma redivivum*) and California towhees (*Pipilo crissalis*) is associated with edge in sage-scrub vegetation (Kristan *et al.* 2003).

Mexican fox squirrels may use heterogeneously burnt forests because resources are distributed across forest patches burnt at varying severities. Although forests burnt at low severity are used most heavily by squirrels (Doumas and Koprowski 2012), small patches of moderately and severely burnt forest provide abundant seeds in isolated pine trees (Larson and Schubert 1970), fungal growth – an important part of the diet of Mexican fox squirrels (Koprowski and Corse 2001) – on dead wood, and cavities, which female Mexican fox squirrels use exclusively for maternity nests (Steele and Koprowski 2001; Pasch and Koprowski 2005).

## 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 burnt 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 south-western US, which are suggested by historical evidence to burn at high severities in some cases (Baisan and Swetnam 1995; Kirkpatrick *et al.* 2006; Conway and Kirkpatrick 2007; Kotliar *et al.* 2007). Some native wildlife species may be dependent on patches burnt 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.

Following a period of fire suppression, forests with a historical fire regime of frequent, low-severity fire will likely require multiple fires or other restoration measures to re-establish

historical landscape patterns (Baker 1994). Heterogeneity in vegetative conditions can be created over time using a variety of techniques (Allen *et al.* 2002; Bradstock *et al.* 2005). 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). Mexican fox squirrels respond positively to single episodes of fire (Doumas and Koprowski 2012), suggesting a fire-based restoration process may improve habitat.

In fire-adapted ecosystems, native wildlife species may require fire to fulfil the essential role as primary driver of landscape heterogeneity (Baker 1994; Bradstock *et al.* 2005; Price *et al.* 2005; Parr and Andersen 2006). Fire heterogeneity varies relative to topography, fuel availability, weather and climate conditions (Turner *et al.* 1994; Price *et al.* 2005), and the effects on wildlife species can vary as well. Conspicuous species such as Mexican fox squirrels 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).

In 2011, 2 years after this study, nearly all of the forested portions of Chiricahua Mountains were burnt by an uncontrolled wildfire. Intensity and heterogeneity varied widely. The entire population of Mexican fox squirrels in the US, as well as many other species in the Chiricahuas, will be subject over the next 15 years to similar conditions to those examined in this study. Such fires demonstrate that the return of fire is inevitable, given the fire-prone nature of the ecosystem (Swetnam and Baisan 1996b) and human alterations 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.

## Acknowledgements

Special thanks to K. Makansi, T. Skinner and R. LeFevre of the Coronado National Forest, USFS, who generously provided assistance and GIS maps. We thank N. Tautfest, L. Baker, A. Goetz, G. Dean, A. Kozuch, Dax, A. Doumas, G. Yenni and C. Holmgren for field assistance, and B. Kertson and A. Johnston for statistical advice. Arizona Game and Fish Department Heritage Fund, School of Natural Resources and the Environment, The University of Arizona, Arizona Agricultural Experiment Station and Chiricahua National Park graciously provided funding. Research was conducted under permit from the Arizona Game and Fish Department, USFS and University of Arizona Institutional Animal Care and Use Committee. We thank M. Wilch for accommodations in Paradise.

## References

- Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, Stacey PB, Morgan P, Hoffman M, Klingel JT (2002) Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* **12**, 1418–1433. doi:10.1890/1051-0761(2002)012[1418:EROSPP]2.0.CO;2
- ARIA Support Team (2008) Arizona Regional Image Archive. (Arizona Remote Sensing Center, University of Arizona) Available at <http://aria.arid.arizona.edu/> [Verified 30 September 2008]
- Baisan CH, Swetnam TW (1995) Historical fire occurrence in remote mountains of southwestern New Mexico and northern Mexico. In 'Proceedings of the Symposium on Fire in Wilderness and Park Management', 30 March–1 April 1993, Missoula, MT. (Eds JK Brown, RW Mutch, CW Spoon, RH Wakimoto) USDA Forest Service,

- Intermountain Forest and Range Experiment Station, General Technical Report INT-GTR-320, pp. 153–156. (Ogden, UT)
- Baker WL (1992) Effects of settlement and fire suppression on landscape structure. *Ecology* **73**, 1879–1887. doi:10.2307/1940039
- Baker WL (1994) Restoration of landscape structure altered by fire suppression. *Conservation Biology* **8**, 763–769. doi:10.1046/J.1523-1739.1994.08030763.X
- Best TL (1995) *Sciurus nayaritensis*. *Mammalian Species* **492**, 1–5.
- Bonnicksen TM, Stone EC (1985) Restoring naturalness to national parks. *Environmental Management* **9**, 479–485. doi:10.1007/BF01867322
- Bradstock RA, Bedward M, Gill AM, Cohn JS (2005) Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* **32**, 409–423. doi:10.1071/WR02114
- Brose U (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia* **135**, 407–413.
- Brown JK, Smith JK (Eds) (2000) 'Wildland Fire in Ecosystems: Effects of Fire on Flora.' USDA Forest Service, Rocky Mountain Research Station. (Fort Collins, CO)
- Brown TJ, Hall BL, Westerling AL (2004) The impact of twenty-first century climate change on wildland fire danger in the western United States: an applications perspective. *Climatic Change* **62**, 365–388. doi:10.1023/B:CLIM.0000013680.07783.DE
- Cahalane VH (1939) Mammals of the Chiricahua Mountains, Cochise County, Arizona. *Journal of Mammalogy* **20**, 418–440. doi:10.2307/1374590
- Chuvieco E (1999) Measuring changes in landscape pattern from satellite images: short-term effects of fire on spatial diversity. *International Journal of Remote Sensing* **20**, 2331–2346. doi:10.1080/014311699212056
- Clarke MF (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* **35**, 385–394. doi:10.1071/WR07137
- Conway CJ, Kirkpatrick C (2007) Effect of forest fire suppression on buff-breasted flycatchers. *The Journal of Wildlife Management* **71**, 445–457. doi:10.2193/2005-755
- Cooper CF (1960) Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs* **30**, 129–164. doi:10.2307/1948549
- Coronado National Forest Supervisors Office (2006) 'Fires in Chiricahua Mountains Since 1950 GIS Shape Files.' (USDA Forest Service: Tucson, AZ)
- Dumas SL, Koprowski JL (2012) Return of fire as a restoration tool: long-term effects of burn severity on habitat use by Mexican fox squirrels. *Restoration Ecology*. [Published online early 7 June 2012] doi:10.1111/J.1526-100X.2012.00864.X
- Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF, Dexter N, Fensham R, Friend G, Gill M, James S, Kay G, Keith DA, MacGregor C, Russell-Smith J, Salt D, Watson JEM, Williams RJ, York A (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* **143**, 1928–1939. doi:10.1016/J.BIOCON.2010.05.026
- Finney MA, McHugh CW, Grenfell IC (2005) Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. *Canadian Journal of Forest Research* **35**, 1714–1722. doi:10.1139/X05-090
- Fisher JT, Wilkinson L (2005) The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* **35**, 51–81. doi:10.1111/J.1365-2907.2005.00053.X
- Gehlbach F (1993) 'Mountain Islands and Desert Seas.' (Texas A&M Press: College Station, TX)
- Gitzen RA, Millspaugh JJ (2003) Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. *Wildlife Society Bulletin* **31**, 823–831.
- Graham RT, McCaffrey S, Jain TB (2004) Science basis for changing forest structure to modify wildfire behavior and severity. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-120. (Fort Collins, CO)
- Gurnell J (1987) 'The Natural History of Squirrels.' (Facts on File: New York)
- Hayes JJ, Robeson SM (2011) Relationships between fire severity and post-fire landscape pattern following a large mixed-severity fire in the Valle Vidal, New Mexico, USA. *Forest Ecology and Management* **261**, 1392–1400. doi:10.1016/J.FORECO.2011.01.023
- Hooge PN, Eichenlaub B (2001) 'Animal Movement Extension to ArcView.' (USGS Alaska Biological Science Center: Anchorage, AK)
- Hutto RL (1995) Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* **9**, 1041–1058. doi:10.1046/J.1523-1739.1995.9051033.X-I1
- Hutto RL, Conway CJ, Saab VA, Walters JR (2008) What constitutes a natural fire regime? Insight from the ecology and distribution of coniferous forest birds in North America. *Fire Ecology* **4**, 115–132. doi:10.4996/FIRECOLOGY.0402115
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71. doi:10.2307/1937156
- Kenward R, South A, Walls S (2003) 'Ranges 6 1.208.' (Anatrack Ltd.: Wareham, UK)
- Key CH, Benson NC (2005) Landscape assessment: ground measure of severity, the composite burn index; and remote sensing of severity, the normalized burn ratio. In 'FIREMON: Fire Effects Monitoring and Inventory System.' (Eds DC Lutes, RE Keane, JF Caratti, CH Key, NC Benson, LJ Gangi) USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-164-CD, pp. LA1–LA51. (Ogden, UT)
- Kie JG, Bowyer RT, Nicholson MC, Boroski BB, Loft ER (2002) Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* **83**, 530–544. doi:10.1890/0012-9658(2002)083[0530:LHADSE]2.0.CO;2
- Kirkpatrick C, Conway CJ, Jones PB (2006) Distribution and relative abundance of forest birds in relation to burn severity in southeastern Arizona. *The Journal of Wildlife Management* **70**, 1005–1012. doi:10.2193/0022-541X(2006)70[1005:DARAOF]2.0.CO;2
- Knapp EE, Keeley JE (2006) Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. *International Journal of Wildland Fire* **15**, 37–45. doi:10.1071/WF04068
- Koprowski JL (2002) Handling tree squirrels with a safe and efficient restraint. *Wildlife Society Bulletin* **30**, 101–103.
- Koprowski JL, Corse MC (2001) Food habits of the Chiricahua fox squirrel (*Sciurus nayaritensis chiricahuae*). *The Southwestern Naturalist* **46**, 62–65. doi:10.2307/3672374
- Koprowski JL, Corse MC (2005) Time budgets, activity periods, and behavior of Mexican fox squirrels. *Journal of Mammalogy* **86**, 947–952. doi:10.1644/1545-1542(2005)86[947:TBAPAB]2.0.CO;2
- Koprowski JL, Leonard KM, Zugmeyer CA, Jolley JL (2006) Direct effects of fire on endangered Mount Graham red squirrels. *The Southwestern Naturalist* **51**, 59–63. doi:10.1894/0038-4909(2006)51[59:DEOFOE]2.0.CO;2
- Kotliar NB, Kennedy PL, Ferree K (2007) Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. *Ecological Applications* **17**, 491–507. doi:10.1890/06-0253
- Kristan WB, III, Lynam AJ, Price MV, Rotenberry JT (2003) Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub. *Ecography* **26**, 29–44. doi:10.1034/J.1600-0587.2003.03341.X

- Larsen KW, Adams IT, Haughland DL (2007) Small mammal communities in a pyrogenic habitat mosaic. *International Journal of Wildland Fire* **16**, 728–740. doi:10.1071/WF05106
- Larson MM, Schubert GH (1970) Cone crops of ponderosa pine in central Arizona, including the influence of Abert squirrels. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Paper RM-58. (Fort Collins, CO)
- Leopold AS, Riney T, McCain R, Tevis L, Jr (1951) The Jawbone deer herd. *California Fish and Game Bulletin* **4**, 1–139.
- Li H, Reynolds JF (1994) A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* **75**, 2446–2455. doi:10.2307/1940898
- Li H, Reynolds JF (1995) On definition and quantification of heterogeneity. *Oikos* **73**, 280–284. doi:10.2307/3545921
- Marzluff JM, Millsbaugh JJ, Hurvitz P, Hancock MS (2004) Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* **85**, 1411–1427. doi:10.1890/03-0114
- Menzel MA, Ford WM, Laerm J, Krishon D (1999) Forest to wildlife opening: habitat gradient analysis among small mammals in the southern Appalachians. *Forest Ecology and Management* **114**, 227–232. doi:10.1016/S0378-1127(98)00353-3
- Moe SR, Wegge P (1994) Spacing behaviour and habitat use of axis deer (*Axis axis*) in lowland Nepal. *Canadian Journal of Zoology* **72**, 1735–1744. doi:10.1139/Z94-234
- Nappi A, Drapeau P (2009) Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? *Biological Conservation* **142**, 1381–1391. doi:10.1016/j.biocon.2009.01.022
- Neu CW, Byers CR, Peek JM (1974) A technique for analysis of utilization-availability data. *The Journal of Wildlife Management* **38**, 541–545. doi:10.2307/3800887
- Parr CL, Andersen AN (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* **20**, 1610–1619. doi:10.1111/j.1523-1739.2006.00492.x
- Pasch BS, Koprowski JL (2005) Correlates of vulnerability in Chiricahua fox squirrels. In 'Connecting Mountain Islands and Desert Seas: Biodiversity and Management of the Madrean Archipelago II', 11–15 May 2004, Tucson, AZ. (Eds GJ Gottfried, BS Gebow, LG Eskew, CB Edminster) USDA Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-36, pp. 426–428. (Fort Collins, CO)
- Pasch BS, Koprowski JL (2006) Sex differences in space use of Chiricahua fox squirrels. *Journal of Mammalogy* **87**, 380–386. doi:10.1644/05-MAMM-A-121R1.1
- Pasch BS, Koprowski JL (2011) Impacts of fire suppression on space use by Mexican fox squirrels. *Journal of Mammalogy* **92**, 227–234. doi:10.1644/10-MAMM-A-133.1
- Price O, Edwards A, Connors G, Woinarski J, Ryan G, Turner A, Russell-Smith J (2005) Fire heterogeneity in Kakadu National Park, 1980–2000. *Wildlife Research* **32**, 425–433. doi:10.1071/WR03043
- R Development Core Team (2009) R: a language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna, Austria) Available at [www.R-project.org](http://www.R-project.org) [Verified 19 September 2009]
- Russell RE, Lehmkuhl JF, Buckland ST, Saab VA (2010) Short-term responses of red squirrels to prescribed burning in the interior Pacific Northwest, USA. *The Journal of Wildlife Management* **74**, 12–17. doi:10.2193/2008-342
- Saint-Germain M, Drapeau P, Hebert C (2004) Landscape-scale habitat selection patterns of *Monochamus scutellatus* (Coleoptera: Cerambycidae) in a recently burned black spruce forest. *Environmental Entomology* **33**, 1703–1710. doi:10.1603/0046-225X-33.6.1703
- Sawyer DA, Kinraide TB (1980) The forest vegetation at higher altitudes in the Chiricahua Mountains, Arizona. *American Midland Naturalist* **104**, 224–241. doi:10.2307/2424862
- Schiegg K (2000) Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience* **7**, 290–298.
- Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**, 2075–2085. doi:10.2307/2265701
- Sekgororoane GB, Dilworth TG (1995) Relative abundance, richness, and diversity of small mammals at induced forest edges. *Canadian Journal of Zoology* **73**, 1432–1437. doi:10.1139/Z95-168
- Smucker KM, Hutto RL, Steele BM (2005) Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* **15**, 1535–1549. doi:10.1890/04-1353
- Steele MA, Koprowski JL (2001) 'North American Tree Squirrels.' (Smithsonian Institution Press: Washington)
- Stuart-Smith K, Adams IT, Larsen KW (2002) Songbird communities in a pyrogenic habitat mosaic. *International Journal of Wildland Fire* **11**, 75–84. doi:10.1071/WF01050
- Swetnam TW, Baisan CH (1996a) Fire histories of montane forests in the Madrean borderlands. In 'Effects of Fire on Madrean Province Ecosystems: a Symposium Proceedings.' (Eds PF Pfalliott, LF DeBano, MB Baker, GJ Gottfried, G Solis-Garza, CB Edminster, DG Neary, LS Allen, RH Hamre) USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-289, pp. 15–36. (Fort Collins, CO)
- Swetnam TW, Baisan CH (1996b) Historical fire regime patterns in the southwestern United States since AD 1700. In 'Fire effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium', 29–31 March 1994, Los Alamos, NM. (Ed. CD Allen) USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-286, pp. 11–32. (Fort Collins, CO)
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92. doi:10.1046/j.0305-0270.2003.00994.x
- Tiedemann AR, Klemmedson O (2000) Solution of forest health problems with prescribed fire: are forest productivity and wildlife at risk? *Forest Ecology and Management* **127**, 1–18. doi:10.1016/S0378-1127(99)00114-0
- Turner MG, Hargrove WW, Gardner RH, Romme WH (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* **5**, 731–742. doi:10.2307/3235886
- USDA Forest Service (2000) Summary of sensitive species. (USDA Forest Service, Washington DC) Available at [http://fs.usda.gov/Internet/FSE\\_DOCUMENTS/fsm8\\_035767.pdf](http://fs.usda.gov/Internet/FSE_DOCUMENTS/fsm8_035767.pdf) [Verified 24 July 2010]
- Van Devender TR, Spaulding WG (1979) Development of vegetation and climate in the southwestern United States. *Science* **204**, 701–710. doi:10.1126/SCIENCE.204.4394.701
- Vierling KT, Lentile LB, Nielsen-Pincus N (2008) Preburn characteristics and woodpecker use of burned coniferous forests. *The Journal of Wildlife Management* **72**, 422–427. doi:10.2193/2006-212
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western US forest wildfire activity. *Science* **313**, 940–943. doi:10.1126/SCIENCE.1128834
- White GC, Garrott RA (1990) 'Analysis of Wildlife Radio-tracking Data.' (Academic Press: San Diego, CA)
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *Bioscience* **48**, 607–615. doi:10.2307/1313420
- Williams AP, Allen CD, Millar CI, Swetnam TW, Michaelsen J, Still CJ, Leavitt SW (2010) Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 21289–21294. doi:10.1073/PNAS.0914211107