

## **Differential Response of Native Arizona Gray Squirrels and Introduced Abert's Squirrels to a Mosaic of Burn Severities**

Author(s): Shari L. Ketcham, John L. Koprowski and Donald A. Falk

Source: Mammal Study, 42(4):247-258.

Published By: Mammal Society of Japan

<https://doi.org/10.3106/041.042.0407>

URL: <http://www.bioone.org/doi/full/10.3106/041.042.0407>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

## Differential response of native Arizona gray squirrels and introduced Abert's squirrels to a mosaic of burn severities

Shari L. Ketcham\*, John L. Koprowski and Donald A. Falk

School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA

**Abstract.** Disturbance events can alter habitat properties, leading to species displacement, isolation, and/or local extinction. Therefore, understanding the interactions of potential ecological drivers on native and introduced wildlife species post-fire is critical to understand influences on distribution. We studied native Arizona gray squirrels (*Sciurus arizonensis*), which are believed to favor dense riparian habitat, and introduced Abert's squirrels (*S. aberti*), which prefer open ponderosa pine (*Pinus ponderosa*) forests. We examined how uncommon native Arizona gray squirrels and introduced Abert's squirrels used areas previously burned by widespread fires more than a decade prior to our study. To determine how past fire may affect squirrel habitat, we examined squirrel use and occupancy within fire altered habitats and used distance sampling to determine squirrel distribution, feeding, and nest use within a mosaic of burn severities. Occupancy and habitat use indicated that introduced Abert's squirrels readily used post-fire conditions more than native Arizona gray squirrels, likely due to the opening of a dense understory. Arizona gray squirrels remained in unburned riparian areas; therefore, fire affected riparian areas can be directly targeted for management to increase abundance of the native species.

**Key words:** dreys, feeding sign, habitat, occupancy, wildfire effects.

Fire has been a component of many forests for millennia, and resident species are often adapted to natural fire regimes. Low severity surface and ground fires were common in many North American forest types before 1900 (Swetnam et al. 2001; Swetnam and Baisan 2003; Swetnam 2005) and burned in fine grain mosaics often less than 10 ha (Cooper 1960; White 1985) with relatively open understories (Cooper 1960), although often over very large areas. Many wildlife species were likely adapted to historical fire regimes (Lyon et al. 2000). However, recent wildfires in forests have burned an average of 86 560 ha per year in the last decade (National Inter-agency Fire Center 2015) that may affect large areas of wildlife habitat (Ream 1981; DeBano et al. 1998; Lyon et al. 2000; Dale et al. 2001). Forests currently burn in more continuous, coarse mosaics of large and homogenous patches (Dillon et al. 2011), due to a century of fire suppression by land management agencies that has increased fuel loads and tree densities (Allen and Breshears 1998; Falk 2004) in forests.

Disturbance events in forest ecosystems alter habitats

with varying impact on wildlife species (Ream 1981; Dale et al. 2001; Koprowski 2005). In montane forests where pine-oak, ponderosa pine (*Pinus ponderosa*), and mixed-conifer dominate upper vegetative zones, fires can create a mosaic of burn severities across the landscape that improves habitat for a variety of wildlife species (Wright and Bailey 1982; DeBano et al. 1998; Lyon et al. 2000). However, synergistic effects of climatic changes (Swetnam 1990; Westerling et al. 2006), introduced and invasive species (Brooks et al. 2004), and forest fuel accumulation may intensify fire behavior and damage critical wildlife habitat (Dale et al. 2001). These events can affect habitat for species dependent on historical duration, size, intensity, and uniformity of fire (Lyon et al. 2000), especially where novel stand replacement fires result in immediate and direct habitat losses (Kirkpatrick and Mosby 1981; King and Koprowski 2009; Swetnam et al. 2009).

Species that rely on montane forests may respond differentially to ecological and/or structural change (Lindenmayer and Fischer 2006). Tree squirrels are

\*To whom correspondence should be addressed. E-mail: sketcham@email.arizona.edu

reliant upon mature trees (Kirkpatrick and Mosby 1981; Steele and Koprowski 2001) and are therefore potentially sensitive to forest structural change (Prather et al. 2006). Tree squirrels are recognized as exceptional gauges of forest condition and likely serve as indicators of forest health (Carey 2000; Steele and Koprowski 2001; Kremsater et al. 2003). Thus, tree squirrel populations may be influenced by a range of fire effects including post-fire edges, habitat alteration and fragmentation, and resource competition for food and nest sites (Kirkpatrick and Mosby 1981), due to reduced use and increased availability of moderate to high severity burned areas.

Native Arizona gray squirrels (*Sciurus arizonensis*) and introduced Abert's squirrels (*S. aberti*) inhabit the Santa Catalina Mountains of southern Arizona, USA (Lange 1960). These two species may be syntopic (Brown 1984; Best and Riedel 1995; Frey et al. 2008). Each species uses dreys and tree cavities for nests and protection (Brown 1984; Steele and Koprowski 2001) and consume similar foods that include cones and seeds, acorns, staminate flowers, mistletoe, and fungi (Brown 1984). Both species forage throughout the year and do not generally cache food (Brown 1984; Best and Riedel 1995). Abert's squirrels consume pine cambium and leave conspicuous twigs with bark removed behind that permit definitive identification (Brown 1984). Abert's squirrels were introduced to the Santa Catalina Mountains in the 1940's (Davis and Brown 1988) and thought to have contributed to the decline of Arizona gray squirrel populations (Cockrum 1960; Lange 1960; Best and Riedel 1995), but multiple factors are likely involved.

Arizona gray squirrels on the Santa Catalina Mountains are rarely observed and thought to be in decline; however, not a single intensive study has ever been conducted on the status of this species in any portion of their distribution with all concerns because of anecdotal information. Once listed as a candidate species for protection as threatened under the U.S. Endangered Species Act in the Santa Catalina Mountains (Lange 1960; Frey et al. 2008), formal protection did not occur. Recently, modified fire regimes may be contributing to this decline since Arizona gray squirrels appear to use unburned riparian areas with dense understory (Brown 1984).

We hypothesized that habitat fragmentation and species displacement by Abert's squirrels are influencing decline of Arizona gray squirrels. Introduced species are often robust and more capable to endure anthropogenic environmental changes than native species (Tuomainen and Candolin 2011), because they are generalist and pos-

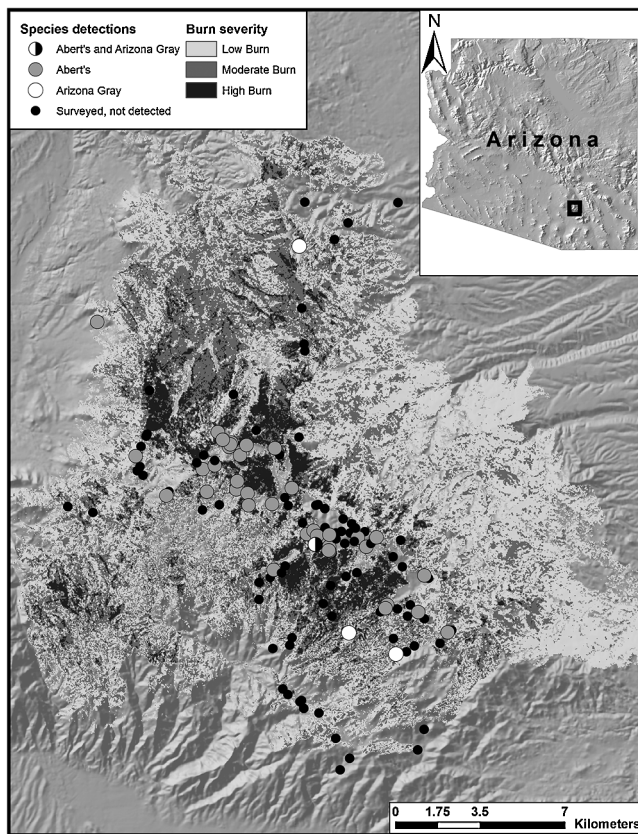
sess increased plasticity of behaviors and life histories. Because Abert's squirrels are generalists and Arizona gray squirrels are specialists, we predicted that Abert's squirrels are well adapted to ecological disturbance whereas Arizona gray squirrels will be impacted by habitat fragmentation and loss. Since limited biological information exists for Arizona gray squirrels, the goal of this study was to determine Arizona gray squirrel habitat use, distribution, and possible interactions with Abert's squirrels in a landscape where fire has caused habitat modification and loss. Particularly, we determined differential use of burn severity and patch sizes for each tree squirrel in a post-fire fragmented landscape.

## Materials and methods

### Study area

The Santa Catalina Mountains, located immediately north of Tucson, Arizona, USA, are found within the Coronado National Forest and span 62 937 ha at elevations ranging from 850 m to 2766 m (Whittaker and Niering 1965). A sequence of vegetative zones including lower desert, upland desert, encinal (evergreen), and montane forest is observed with increasing elevation (Shreve 1915; Whittaker and Niering 1965). Encinal forest includes juniper (*Juniperus* spp.), pinyon pine (*Pinus edulis*), Arizona madrone (*Arbutus arizonica*) and oak (*Quercus* spp.; Lange 1960). Montane forest is dominated by ponderosa pine mixed with southwestern white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and Gambel oak (*Quercus gambelii*; Lange 1960). Riparian areas are located throughout all four vegetation zones: higher elevations contain Arizona alder (*Alnus oblongifolia*) and bigtooth maple (*Acer grandidentatum*) and lower elevations contain Goodding's willow (*Salix gooddingii*), velvet ash (*Fraxinus velutina*), Arizona walnut (*Juglans major*), Arizona sycamore (*Platanus wrightii*), and Fremont cottonwood (*Populus fremontii*; Lange 1960).

Two large wildfires have occurred in the Santa Catalina Mountains since 2000. In 2002, the human-caused Bullock fire burned 12 368 ha over 21 days (Krausman et al. 2004; Maghran 2014). In 2003, the lightning-caused Aspen fire burned 34 323 ha in 29 days (Krausman et al. 2004; Maghran 2014). Both fires burned upper elevations of the Santa Catalina Mountains from montane forest down to upland desert areas with vegetation communities differentially affected by fire severities (Maghran 2014). As a result, 33% of trees, including canopy trees, died



**Fig. 1.** Current Arizona gray squirrel and Abert's squirrel locations in the Santa Catalina Mountains. White circles show Arizona gray squirrel detections, light gray circles show Abert's squirrel detections, half white half black circle is a site with both Arizona gray and Abert's squirrel detections, and black circles are sites where both squirrels were not detected. Fire severities on the landscape are colored light gray for low burn, gray for moderate burn, and dark gray for high burn.

in areas that experienced high severity burns (Swetnam 2007).

#### *Burn severity*

We obtained burn severity spatial layers for the Bullock and Aspen fires from the Monitoring Trends in Burn Severity (MTBS 2011) program. Delta normalized burn ratio (dNBR) is an assessment calculated from pre-fire and post-fire Landsat TM and ETM+ imagery based on reflectance ratios using near-infrared (Landsat band 4) and mid-infrared (Landsat band 7) wavelengths, which are sensitive to reflectance optima in soil and above-ground biomass, and thus can be used to assess changes prior to and post-fire (Parsons et al. 2010; Dillon et al. 2011). Burn severity layers were loaded into a Geographical Information System (GIS) using ArcGIS 10.1 for analysis.

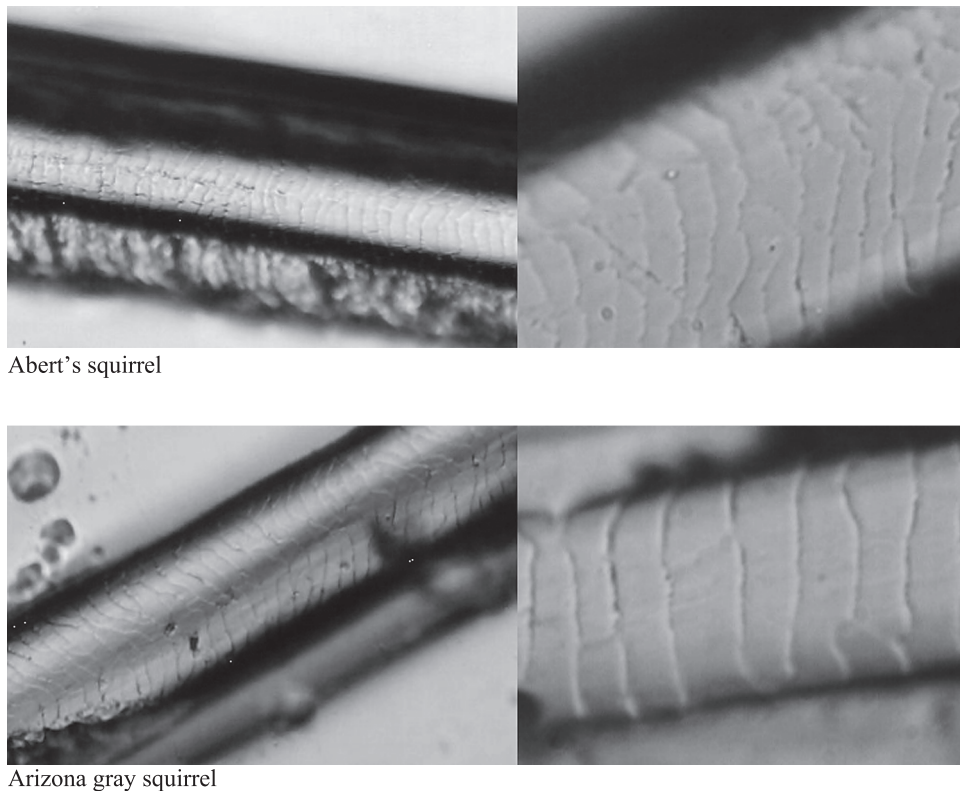
#### *Assessment of occupancy*

We randomly selected 200 points in all vegetation types at elevations above 1066 m, which is the lowest elevation range reported for Arizona gray squirrels (Brown 1984). Points were stratified into unburned, low, moderate, and high burn severity using the uniform allocation method (Hansen et al. 1953). In 2011, we field-surveyed high burn severity areas, which lacked tree canopy cover, without detection of squirrels or any associated feeding or nesting sign. We subsequently replaced high burn severity points with additional randomly generated points uniformly distributed among unburned, low, and moderate burn severity areas for a total of 201 points (Fig. 1).

From 2011–2013, we used either a single hair tube or hair tube (Gurnell et al. 2004)/trail camera (Nomad Infrared Digital 5.0, Stealth Cam, LLC., Grand Prairie, TX) combinations each attached to trees at 201 sites to measure occupancy. Hair tubes were constructed from polyvinylchloride (PVC) pipe measuring 30 cm in length and 6.5 cm in diameter (Gurnell et al. 2004) baited at the center with a peanut butter and oatmeal mixture. We attached double-sided adhesive carpet tape to wood blocks that clipped onto both ends of the hair tube. Hair tube locations were checked once each week and deployed for a total of one month. Hair tube/trail camera combinations were left for one week, where each day was treated as one survey, before being moved to the next randomly selected point until the remaining points were analyzed. Tape was removed from the hair tubes and placed into zippered plastic bags coated with talcum powder and transported to the laboratory and maintained at 22°C until sampled.

We analyzed hair samples from the dorsal and posterior body and dorsal tail for Arizona gray squirrels and Abert's squirrels that were collected from the University of Arizona mammal collection to facilitate hair cuticle scale pattern comparisons (Brunner and Triggs 2002) of known samples to field samples. We examined hair samples with a compound microscope (AmScope Model M10FL) at 10× and 40× magnification (Fig. 2). Abert's squirrel hair cuticle scales are more densely packed and edges are jagged; in contrast, Arizona gray squirrel hair cuticle scales lay farther apart, approximately double the width of Abert's squirrel cuticle scales, and edges are smooth (Gurnell et al. 2004; Fig. 2).

We used ArcMap 10.1 to plot points at which squirrels were detected. Burn severity layers were used to measure the size of unburned, low, moderate, and high severity areas to determine our severity patch sizes for analysis.



**Fig. 2.** Microscopic hair scale patterns at 10 $\times$  and 40 $\times$  magnification of Abert's squirrels and Arizona gray squirrels. Mid-shaft diameters are 80 microns. Photograph by Shari L. Ketcham.

### Occupancy data analysis

We analyzed occupancy data using the package *unmarked* (Fiske and Chandler 2011) in program R (R Development Core Team 2013). Due to lack of detections for Arizona gray squirrels, we could not model single or two-species occupancy analysis that would have included this native species. We could only complete site occupancy models (single season models, with seven surveys per site to accommodate imperfect detection, where presence is specified as one and non-detection is specified as zero) for Abert's squirrels with and without site covariates and additive and multiplicative models with site covariates (Fiske and Chandler 2011). Site covariates included burn severity, burn patch size, vegetation type, elevation, and number of shrub stems to determine factors that were important for squirrel use. Unburned and burn patch sizes were measured in ArcGIS by drawing polygons around each patch using the classified dNBR layers. We used a vegetation quadrat to measure shrub stem density to determine open or dense understory and identified 19 vegetation types with open or dense understory at random and occupied areas. We selected top models by Akaike Information Criterion (AIC) values and computed

Akaike weight (AIC  $\omega$ ) to rank models (Burnham and Anderson 2002). Models  $< 2 \Delta AIC$  were considered top competing models. Models with lowest AIC values were used to estimate parameters (Burnham and Anderson 2002). Goodness-of-fit tests were conducted using a parametric bootstrapping function in *unmarked*.

### Distance sampling

Of 201 points sampled for occupancy, 50 of these points were randomly selected for distance sampling (Anderson et al. 1979; Buckland et al. 1993) to search for observed presence of squirrels and determine tree squirrel distribution regardless of species through feeding sign and drey surveys. Transects extended 500 m from a sample point in a random direction. Because transects passed through segments of various fire severities, GIS generated burn severities were ground-truthed by height of burn scars on trees: unburned  $< 0.3$  m; low severity 0.3–1 m; moderate severity 1–2 m; and high severity  $> 2$  m (Parsons et al. 2010).

Distance sampling was conducted from September 2011–October 2011, March 2012–October 2012 and March 2013–June 2013 to avoid snow that might obscure

feeding sign. Two passes were made on each transect on the same day. On the first pass, we located Abert's squirrels and Arizona gray squirrels by sight and sound. A compass and rangefinder were used to measure distance and angle from the transect and coordinates of each squirrel were recorded with a Global Positioning System (GPS) unit. At locations with detection of squirrels, burn severity and vegetation type (riparian, ponderosa pine, mixed conifer, and pine-oak) were recorded. On the second pass, we located squirrel feeding sign and dreys. We stopped every 10 m to record presence of feeding sign and dreys. Feeding sign (clipped pine boughs, cone cores, cone scales, and cambium stripped pine twigs) located within 2.5 m to each side of the transect line was removed.

For each drey, we identified species of tree, documented GPS coordinates, measured perpendicular distance to transect line, assessed burn severity within a 5 m radius, and recorded vegetation type, and determined status as either active or inactive. Dreys were classified as: 1) Inactive-poor condition and in disrepair, noticeable holes, not able to be occupied without renovation; and 2) Active-nest robust and well maintained, likely in use. Because Arizona gray squirrel and Abert's squirrel dreys are not readily distinguishable in the field in montane areas, we assessed cambium stripped twigs for Abert's squirrel presence and used hand-held squirrel calls (Primos Squirrel Buster Call, Primos Hunting, St. Flora, MS) to determine if the drey was occupied and by which species, if observed. In March after snowmelt, all 50 transects were re-visited totaling two passes along each transect to record observed presence of squirrels, assess feeding sign, and record any missed or newly formed dreys. We traversed 100 km of transects and spent approximately 1500 h to document presence of Arizona gray and Abert's squirrels, and locate feeding sign and dreys to determine distribution.

We assessed vegetation at each of the 50 randomly selected points. Vegetation was analyzed at the random point, then in cardinal directions at 5 m and 10 m (Edelman and Koprowski 2005). We used a 1 m × 1 m vegetation quadrat and tallied all plants that fell within the square, counted stems of shrubs within each quadrat as well as trees or shrubs with canopies that intercepted a vertical projection of the quadrat.

#### *Distance sampling data analysis*

We used program DISTANCE (Thomas et al. 2006) to estimate distribution of dreys and feeding sign across a mosaic of burn severities. We summarized our data in

totality without stratification for our pooled data sets for dreys that included distance from transect, nest activity, area severity, area vegetation type, drey tree severity, and drey tree species and feeding sign that included distance from transect within a 5 m width, type of feeding sign, and area severity (Table 1). Top models for pooled data were selected for estimation of drey density and estimation of feeding sign density.

In addition, we stratified eight data sets, listed below, that included vegetation type and overall severity within a 10 m diameter circular plot centered on located dreys. We selected top models for estimation of drey tree type, drey tree severity, overall area severity surrounding the drey tree, and overall vegetation type surrounding the drey and top models for feeding sign were selected for severity of the nearest tree(s) where pine clippings, eaten cone cobs, and stripped twigs were found, and overall area severity surrounding feed sign (Table 1).

Results were calculated in totality across 17 transects where dreys were found and across 23 transects where feeding sign was found. Analysis included four key functions (Half-normal, Hazard Rate, Negative Exponential, and Uniform) for both pooled and stratified data. The four key functions limits data to four models that allows the user to fit data with specified parameters, then allows model fit using cosine or polynomial adjustments (Buckland et al. 1997). We selected top models by Akaike Information Criterion (AIC) values and computed Akaike weight (AIC  $\omega$ ) to rank models (Burnham and Anderson 2002). Models  $< 2 \Delta AIC$  were considered top competing models. Models with lowest AIC values were used to estimate parameters (Burnham and Anderson 2002). We calculated chi-square values and used a Bonferroni Z-test approach to determine if burn severities at drey and feed sign sites are used in proportion to availability within burn severities (Marcum and Loftsgaarden 1980). In addition, we calculated frequency of occurrence for feeding sign as the number of times that food remains were found at 10 m intervals on each transect (Dodd et al. 1998). We used ONID MINITAB 16 (Minitab 2010) to run ANOVA and Tukey HSD comparisons. Trail camera and hair tube procedures were approved by The University of Arizona Institutional Animal Care and Use Committee (IACUC protocol 08-025), Arizona Game and Fish Department permits #SP690895, #SP770782, and #SP587510, and U.S. Forest Service permit #SAN0296 and conform to the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

**Table 1.** Top pooled distance sampling models and top stratified distance sampling models of drey density and feeding sign density of Abert's squirrels and Arizona gray squirrels in the Santa Catalina Mountains

Pooled Data							
Data Analyzed	Key	Adjustment Terms	Parameters	AICc	$\Delta$ AICc	wt	CV
Drey density	Half Normal	Cosine, binned by 3	1	54.77	0.00	0.02	0.12
	Half Normal	No term, binned by 4	1	54.81	0.00	0.02	0.12
Feeding sign density	Hazard Rate	Cosine, 5% truncation	2	142.28	0.00	0.02	0.16
	Uniform	Hermite Polynomial, 5% truncation	2	142.52	0.25	0.02	0.15
	Half Normal	Cosine, 5% truncation	1	143.87	1.60	0.01	0.15
Stratified Data							
Data Analyzed	Key	Adjustment Terms	Parameters	AICc	$\Delta$ AICc	wt	CV
Drey tree type	Hazard Rate	No term, binned by 4	30	36.67	0.00	0.04	28.13
	Uniform	Simple Polynomial, binned by 2	9	37.91	37.91	0.00	19.89
Drey tree severity	Uniform	No term, binned by 2	3	40.21	40.21	0.03	0.16
	Half Normal	No term, binned by 4	22	40.56	0.17	0.00	56.68
Drey area severity	Uniform	No term, binned by 3	6	85.23	0.47	0.03	18.82
	Half Normal	No term, binned by 4	20	86.54	7.19	0.00	0.19
Drey habitat type	Uniform	Simple Polynomial, binned by 3	1	23.71	0.00	0.03	0.18
	Half Normal	No term, binned by 3	1	23.74	0.03	0.02	0.21
Pine clippings	Uniform	No term, 10% truncation	2	72.36	0.00	0.03	0.18
Cones (eaten)	Uniform	No term, 10% truncation	2	37.39	0.00	0.04	0.15
Stripped pine twigs	Half Normal	No term, binned by 3 to 1.31 m	3	89.25	9.06	0.01	0.28
	Half Normal	No term, binned by 3	3	89.38	1.73	0.00	0.23
Feed sign area severity	Uniform	No term, 10% truncation	2	84.84	0.00	0.03	0.14

## Results

### Occupancy and habitat

Of 201 randomly selected sites, we detected Abert's squirrels at 45 sites (22%) and Arizona gray squirrels at four sites (2%) from 2011–2013. Average patch size used by Abert's squirrels in unburned areas was 175.30 ha ( $SE = 36.85$ ,  $n = 22$ ), 204.55 ha ( $SE = 86.08$ ,  $n = 9$ ) in low severity, and 2.20 ha ( $SE = 0.95$ ,  $n = 14$ ) in moderate severity. Unburned and low burn patches used by Abert's squirrels were larger than moderate burn patches ( $ANOVA$ :  $F_{2,42} = 5.85$ ,  $P = 0.006$ ;  $R^2 = 0.22$ ). Whereas, average patch sizes where Abert's squirrels were undetected in unburned areas was 100.97 ha ( $SE = 33.17$ ,  $n = 45$ ), 710.88 ha ( $SE = 664.43$ ,  $n = 58$ ) in low severity, and 27.39 ha ( $SE = 22.84$ ,  $n = 53$ ) in moderate severity.

Arizona gray squirrels used only unburned and low severity areas. Average patch size used by Arizona gray squirrels in unburned areas was 8.25 ha ( $SE = 7.99$ ,  $n = 2$ ), but was 501.24 ha in low severity ( $SE = 424.04$ ,

$n = 2$ ). It did not differ significantly likely due to small sample size ( $ANOVA$ :  $F_{1,2} = 1.35$ ,  $P = 0.37$ ;  $R^2 = 0.40$ ). However, average patch sizes where Arizona gray squirrels were undetected in unburned areas was 128.98 ha ( $SE = 116.79$ ,  $n = 65$ ) and 638.58 ha ( $SE = 1327$ ,  $n = 65$ ) in low severity.

Abert's squirrel occupied locations had 18 shrub stems ( $SE = 6.24$ ,  $n = 24$ ), which was less than Arizona gray squirrel occupied locations ( $\bar{x} = 71$ ,  $SE = 5.54$ ,  $n = 4$ ;  $t_{26} = 3.39$ ,  $P = 0.002$ ). Abert's squirrels were found within mixed conifer elevations ( $\bar{x} = 2374$  m,  $SE = 29$ ,  $n = 45$ ), whereas Arizona gray squirrels were found at lower elevations ( $t_{47} = -3.78$ ,  $P \leq 0.001$ ) outside or on the edge of the conifer zones ( $\bar{x} = 1986$  m,  $SE = 127$ ,  $n = 4$ ).

Abert's squirrel site occupancy was best explained by elevation and vegetation covariates (Table 2). A high proportion of sites occupied by Abert's squirrels were within conifer vegetation ( $\bar{x} \pm SE = 0.84 \pm 0.03$ ;  $P = 0.01$ ). Abert's squirrels had a high detection probability in mixed conifer with open understories ( $0.83 \pm 0.03$ ;  $P =$

**Table 2.** Top competing occupancy models with covariates for Abert's squirrels in the Santa Catalina Mountains

Model	Parameters	AIC	$\Delta$ AIC	AIC wt	Cumulative wt
$\psi(\text{elevation})p(\text{elevation})$	4	688.67	0.00	0.39	0.39
$\psi(\text{habitat})p(\cdot)$	3	689.02	0.35	0.33	0.71

Psi ( $\psi$ ) is the proportion of sites occupied and p is detection probability.

0.01). Detection probability and occupancy of Abert's squirrels seemed to be associated with elevation ( $0.50 \pm 1.06$ ;  $P = 0.05$ ), although model fit was not strong. Abert's squirrel elevations in 45 occupied areas were higher than elevations that were not occupied ( $t_{200} = 6.82$ ,  $P \leq 0.001$ ). Abert's squirrel current occupied elevations ( $\bar{x} = 2374$ ,  $SE = 29$ ,  $n = 45$ ) did not differ from elevations of pre-fire historical detections ( $\bar{x} = 2359$ ,  $SE = 69$ ,  $n = 4$ ;  $t_{47} = -0.15$ ,  $P \leq 0.88$ ). Burn patch sizes, burn severity, and shrub stem density were not significantly related to Abert's squirrel habitat use ( $P > 0.05$ ) and therefore, did not affect Abert's squirrel occupancy.

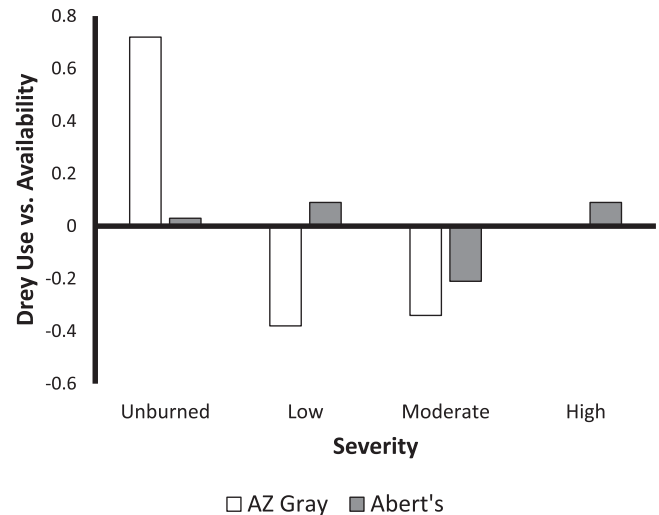
Shrub stem densities were greater in four locations occupied by Arizona gray squirrels ( $\bar{x} = 71$ ,  $SE = 5.54$ ,  $n = 4$ ;  $t_{26} = 3.39$ ,  $P = 0.002$ ) than shrub stem densities in random locations ( $\bar{x} = 13$ ,  $SE = 3$ ,  $n = 50$ ;  $t_{52} = 5.42$ ,  $P \leq 0.001$ ). Arizona gray squirrel occupied elevations ( $\bar{x} = 1986\text{-m}$ ,  $SE = 127$ ,  $n = 4$ ) did not differ from historic elevations ( $\bar{x} = 2124\text{-m}$ ,  $SE = 162$ ,  $n = 9$ ;  $t_{11} = 0.53$ ,  $P \leq 0.61$ ); however, this result may be due to small sample sizes.

#### Distance sampling

We detected only six Abert's squirrels on five of the 50 transects; however, we counted 168 Abert's squirrels while walking to points. We did not observe any Arizona gray squirrels on transects nor while walking to points. Due to small sample sizes, we were unable to estimate abundance of species.

#### Dreys

We found a total of 42 dreys on 17 transects of 50 transects that were walked. Unburned ( $\bar{x} = 0.36$ ,  $SE = 0.12$ ,  $n = 15$ ) and low burned ( $\bar{x} = 0.45$ ,  $SE = 0.11$ ,  $n = 19$ ) areas were primarily used for drey locations. Drey numbers found in unburned, low burn, moderate burn, and high burn did not differ for area severity (*ANOVA*:  $F_{3,18} = 2.67$ ,  $P = 0.08$ ). Dreys in unburned (*Z*-test, 97% confidence intervals:  $-0.23, 0.21$ ), low burn (*Z*-test, 97% confidence intervals:  $-0.24, 0.23$ ), moderate burn (*Z*-test, 97% confidence intervals:  $-0.17, 0.21$ ), and high burn (*Z*-test, 97% confidence intervals:  $-0.09, 0.10$ ) areas



**Fig. 3.** Abert's squirrel and Arizona gray squirrel drey use versus availability of burn severity areas. Abert's squirrels used low burned and high burned areas more than other severities and Arizona gray squirrels used unburned areas more than other severities. Bars above zero indicate those areas are occupied more than their availability; bars below zero indicate areas are used less than proportionately available.

were used in proportion to availability ( $\chi^2 = 1.83$ ,  $df = 41$ ,  $P = 1$ ; Fig. 3). We found more active dreys ( $\bar{x} \pm SE = 0.60 \pm 0.10$ ) than inactive dreys ( $0.40 \pm 0.12$ ). We found dreys in ponderosa pine ( $0.64 \pm 0.09$ ) more frequently than dreys in mixed conifer ( $0.24 \pm 0.14$ ) and oak ( $0.12 \pm 0.15$ ). Dreys were used in proportion to availability ( $\chi^2 = 18.99$ ,  $df = 41$ ,  $P = 0.99$ ) in ponderosa pine (*Z*-test, 97% confidence intervals:  $-0.23, 0.14$ ), mixed conifer (*Z*-test, 97% confidence intervals:  $-0.19, 0.18$ ), and oak (*Z*-test, 97% confidence intervals:  $-0.13, 0.23$ ). Dreys were found predominantly in coniferous trees; ponderosa pine ( $\bar{x} = 0.62 \pm 0.10$ ) and mixed conifer ( $\bar{x} = 0.24 \pm 0.14$ ) that included Douglas-fir, white fir and Chihuahua pine. Six of 42 dreys were found in non-coniferous trees; Fremont cottonwood ( $\bar{x} = 0.07 \pm 0.15$ ), Arizona sycamore ( $\bar{x} = 0.05 \pm 0.16$ ), and oak ( $\bar{x} = 0.02 \pm 0.15$ ). Dreys in ponderosa pine (*Z*-test, 97% confidence intervals:  $-0.23, 0.23$ ), Douglas-fir (*Z*-test, 97% confidence intervals:  $-0.18, 0.18$ ), white pine (*Z*-test, 97% confidence intervals:  $-0.10, 0.10$ ), Chihuahua pine (*Z*-test, 97% confidence intervals:  $-0.10, 0.07$ ), sycamore (*Z*-test, 97% confidence intervals:

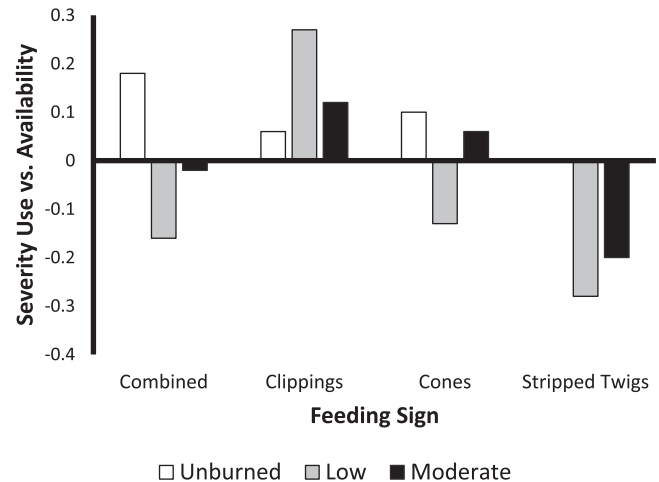


–0.10, 0.10), cottonwood (*Z*-test, 97% confidence intervals: –0.12, 0.12), and oak (*Z*-test, 97% confidence intervals: –0.10, 0.10) trees were used in proportion to availability ( $\chi^2 = 0.02$ ,  $df = 41$ ,  $P = 1$ ).

Of 42 dreys, 32 were confirmed Abert's squirrel dreys from sight and sound, stripped twigs found near drey trees, and dreys composed of pine boughs and needles. Five of six dreys in non-coniferous trees were identified as those of Arizona gray squirrel since they were composed of non-coniferous leaves and twigs and located outside Abert's squirrel elevational ranges. Due to small sample size of Arizona gray squirrel dreys, we could not analyze burn severities of found dreys by species. Arizona gray squirrel dreys located from transects were found at an average elevation of 1524 m. However, while walking to points with various burn severities and vegetation types, we identified other Arizona gray squirrel dreys; three were at an elevation of 1829 m and one at an elevation of 1341 m were confirmed with occupancy. All dreys that we located were found outside of the coniferous zone where Abert's squirrels reside.

#### Feeding sign

We found feeding sign on 23 of the 50 transects ( $SE = 9.31$ ,  $n = 23$ ), with frequency of occurrence maximized at 0.34 ( $\bar{x} \pm SE = 0.06 \pm 0.01$ ). Frequency of occurrence of feeding sign differed across burn severity, vegetation type, and shrub stem density (*ANOVA*:  $F_{3,88} = 7.02$ ,  $P \leq 0.001$ ); however, differed singularly by shrub stem density (*ANOVA*:  $F_{1,44} = 8.80$ ,  $P = 0.005$ ). Feeding sign was found more frequently in unburned areas ( $0.43 \pm 0.06$ ) than low burn ( $0.23 \pm 0.07$ ) and moderate burn ( $0.34 \pm 0.07$ ) areas. Feeding sign was found in unburned (*Z*-test, 97% confidence intervals: –0.13, 0.11), low burn (*Z*-test, 97% confidence intervals: –0.12, 0.12), and moderate burn (*Z*-test, 97% confidence intervals: –0.11, 0.12) in proportion to its availability ( $\chi^2 = 4.11$ ,  $df = 153$ ,  $P = 1$ ) (Fig. 4). Clippings were found in nearly equal proportions in unburned ( $\bar{x} \pm SE = 0.32 \pm 0.08$ ), low burn ( $0.32 \pm 0.08$ ), and moderate burn ( $0.36 \pm 0.08$ ). Clippings were in unburned (*Z*-test, 97% confidence intervals: –0.15, 0.14), low burn (*Z*-test, 97% confidence intervals: –0.14, 0.15), and moderate burn (*Z*-test, 97% confidence intervals: –0.14, 0.15) in proportion to availability ( $\chi^2 = 0.66$ ,  $df = 99$ ,  $P = 1$ ) (Fig. 4). Discarded cone cobs were found more frequently in unburned areas ( $\bar{x} \pm SE = 0.48 \pm 0.09$ ) than low burn ( $0.15 \pm 0.07$ ) and moderate burn ( $0.38 \pm 0.08$ ) areas. However, cones were found in proportion to availability ( $\chi^2 = 6.08$ ,  $df = 79$ ,  $P = 1$ ) in unburned (*Z*-test, 97%



**Fig. 4.** Combined and individual feeding sign use versus availability within burn severities. Combined feeding sign and cones were found in unburned areas more than other severities. Clippings were found in low and moderate burned areas more than other severities. Bars above zero indicate those areas are occupied more than their availability; bars below zero indicate areas are used less than proportionately available.

confidence intervals: –0.18, 0.15), low burn (*Z*-test, 97% confidence intervals: –0.13, 0.16), and moderate burn (*Z*-test, 97% confidence intervals: –0.17, 0.16) areas (Fig. 4). Stripped twigs, a distinct sign of Abert's squirrel feeding activity, were found in unburned areas ( $\bar{x} \pm SE = 0.54 \pm 0.09$ ) more often than low burn ( $0.11 \pm 0.06$ ) and moderate burn ( $0.35 \pm 0.08$ ) areas. Twigs were discarded by squirrels in unburned (*Z*-test, 97% confidence intervals: –0.25, 0.18), low burn (*Z*-test, 97% confidence intervals: –0.17, 0.22), and moderate burn (*Z*-test, 97% confidence intervals: –0.20, 0.22) areas in proportion to availability ( $\chi^2 = 6.62$ ,  $df = 42$ ,  $P = 1$ ) (Fig. 4).

#### Discussion

Arizona gray squirrels were reported to be the rarest animal in Arizona nearly a century and a half ago (Coues 1867). Restricted primarily to upland environments, the distribution of the species is naturally fragmented in the Sonoran and Chihuahuan deserts (Hoffmeister 1986). However, historically Arizona gray squirrels appear to have been reasonably common and widespread on the Santa Catalina Mountains. Prior to 1986, individuals were known from 13 locations on the Santa Catalina range (Doutt 1931; Lange 1960; Hoffmeister 1986; University of Arizona Mammal Collection). All documented pre-fire locations were in riparian areas within the high elevation conifer zone. In our study, we detected presence

of only a single Arizona gray squirrel within the conifer zone; however, this area was next to a steep riparian corridor that dropped quickly in elevation. All other Arizona gray squirrel locations were below the conifer zone at lower elevations in dense, unburned riparian areas. With this result, we attempted to increase our sample size for Arizona gray squirrels and walked an additional 36.4 km of riparian transects (90 h) outside of Abert's squirrels elevation range and placed trail camera/hair tube combinations every 500 m at locations known to harbor Arizona gray squirrels prior to fire and where our previously described sampling did not occur. Unfortunately, we did not observe or capture pictures of any Arizona gray squirrels nor did we find any dreys or feeding sign. Therefore, we concluded that Arizona gray squirrels appear to be rare, as we located only seven individuals; three camera locations detected pairs of squirrels and one camera location had a single squirrel. This outcome is important because historically Arizona gray squirrels occupied dense riparian zones (Brown 1984) from oak vegetation communities to conifer communities (Hoffmeister 1986) ranging from 1066 m to 2286 m (Brown 1984) with most locations in upper elevations (Lange 1960; Hoffmeister 1986).

In contrast, we determined that Arizona gray squirrels only remain at lower elevations and may be relegated to smaller burn patches that may indicate displacement by Abert's squirrels. In addition, habitat alteration and loss from wildfires may have restricted dispersal as a result of the larger, more homogenous intensely burned mountain tops where Arizona gray squirrels resided before severe wildfires occurred on the Santa Catalina Mountains. In a concurrent study (Doumas and Koprowski 2013), Chiricahua fox squirrels (*S. nayaritensis chiricahuae*), a close relative of Arizona gray squirrels, did not use homogenous high severity areas but instead used heterogeneous unburned and low severity areas with open understory. Fire impacts Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) through direct mortality and loss of middens and drey trees (Koprowski et al. 2006; Leonard and Koprowski 2010; Blount and Koprowski 2012). We found Arizona gray squirrel dreys in unburned areas outside of the conifer zone at approximately 1524 m, whereas, immediately prior to wildfires, dreys were found within the conifer zone at 1829 m (General Hitchcock Campground) and Mt. Bigelow at 2509 m in elevation (John L. Koprowski, personal communication). All other Arizona gray squirrel dreys were found within the oak vegetation zone within unburned,

dense riparian areas. Arizona gray squirrel dreys in the nearby Huachuca (Cudworth and Koprowski 2011) and Rincon Mountains were also found in unburned, dense riparian areas (Western National Parks Association 2006). Arizona gray squirrels used riparian areas with numerous shrub stems, which may indicate preference for dense understories over open understories. Our surveys showed that riparian habitats still have not fully recovered since the 2002–2003 fires, and most patches that remain have minimal tree cover and understory, which is poor Arizona gray squirrel habitat (Brown 1984) and likely the reason why we did not find this species within major riparian zones. However, the 2002–2003 Bullock-Aspen wildfires in the Santa Catalina Mountains opened understories and burned approximately 40% of major riparian corridors including those unsuitable for gray squirrels, possibly contributing to further imperilment of Arizona gray squirrel populations.

Conversely, Abert's squirrels seem to be more resilient to post-fire conditions than Arizona gray squirrels perhaps due to a high dispersal ability in mature forests (Davis and Brown 1988). In addition, Abert's squirrels prefer areas with more open understory (Dodd et al. 1998) than Arizona gray squirrels, which is indicative of their ability to remain common in post-fire communities. Home ranges of Abert's squirrels remained unchanged in burned areas (Gwinn and Koprowski 2017) likely due to opening forest understory that increased food resources, which suggests the ability of the introduced species to adjust to altered habitats. In our study, Abert's squirrels nested and were present in every burn severity located in the conifer zone except high burn severity areas where no tree canopy remained, similar to findings in the nearby Pinaleno Mountains (Gwinn and Koprowski 2017). Since Abert's squirrels predominantly used unburned and moderate burn areas and were not affected by burn patch sizes, burn severity type, and shrub stem density, these factors may imply that introduced Abert's squirrels have adapted to environments with frequent fires and ecosystem change due to high plasticity that may explain their success relative to native Arizona gray squirrels.

Since Abert's squirrels have slightly larger litter sizes (average 3.4; Nash and Seaman 1977) than Arizona gray squirrels (average 3.1; Cudworth and Koprowski 2013), Abert's squirrels may have a demographic advantage over Arizona gray squirrels. In addition, niche partitioning by sympatric species (Schoener 1974, 1986) can occur post-fire due to vegetation structural changes (Gill and Catling 2002; Keith et al. 2002). In our study, Abert's

squirrels appear to use a broader range of vegetation types after fire than native Arizona gray squirrels. Conversely, Arizona gray squirrels are a riparian obligate species (Best and Riedel 1995; Frey et al. 2008) and lower elevations on the Santa Catalina Mountains were not as intensely burned as higher elevations. This may explain why the native species remains at lower elevations with dense understory in unburned and low burn severities but are no longer found at higher elevations. This result may also be competitive exclusion of Arizona gray squirrels by Abert's squirrels (Hardin 1960; Armstrong and McGehee 1980; Gurnell et al. 2004), since Abert's squirrels seem to be well adapted to large, homogenous fires.

Historically, large stand replacing fires in ponderosa pine forests were relatively rare prior to fire suppression (Brown and Smith 2000; Friederici 2003). Forest structural changes that result from increased fuel loads and anthropogenic influences have changed forest fuel mass and distribution, which amplifies fire frequency, size, and intensity (Swetnam 1990; Covington and Moore 1994; Sackett et al. 1994). When fire results in moderate to high burn severity, heat exposure alters soil structure and chemistry, changes nutrient amounts and availability, increases erosion, and inhibits plant reestablishment (Neary et al. 1999). Extensive changes in forest ecosystems can alter habitats drastically, especially after stand replacing fires that can create large, homogeneous patches (Chuvieco 1999; Savage and Mast 2005), which may either benefit or adversely impact resident wildlife species depending on habitat preference. Many wildlife species in arid forests may be adapted to the historic frequent, low severity fire regime (Kiltie 1989; Brown and Smith 2000; Lyon et al. 2000). Stand replacing burned areas are generally avoided by small mammals (Ream 1981) likely due to loss of habitat structure (Lyon et al. 2000). Habitat alteration and loss will likely favor species that have evolved in habitats with less frequent higher-severity fires, like Abert's squirrels, and potentially cause decline or local extinction of species that are not adapted to recurrent, intense fires (DeBano et al. 1998; Ketcham and Koprowski 2013). Fire and forest management will thus be key to maintaining both forests and wildlife (Noss et al. 2006) during a period of rapid climate change and intensifying fire regimes.

Our findings indicate that Arizona gray squirrels are rare on the Santa Catalina Mountains likely due to intensely burned riparian areas that lack dense understory in addition to potential displacement by an introduced species. Restoration of riparian vegetation at locations

where Arizona gray squirrels currently reside and riparian corridors that would create habitat connectivity between occupied sites is recommended. Prescribed fire should be used judiciously in riparian areas so that dense understories are maintained where Arizona gray squirrels can persist since Abert's squirrels appear to thrive in more open forests.

**Acknowledgments:** We thank C. Ketcham, C. Reynoso, B. Kelley, K. Arnold, M. Mazzella, K. Schmidt, B. Klink, and H. Rissi for assistance with field work. We thank J. Taiz and D. Swann for sharing information associated with our study. We thank Arizona Game and Fish Department Heritage Grant No. I12024, T & E Inc. Grant for Conservation Biology Research, Institute of the Environment Travel Grant, Graduate and Professional Student Council Travel Grant, and Deer Breeder's Corporation Scholarship for graciously providing funding. We thank C. Schwalbe, M. Merrick, T. Jessen, J. Derbridge, M. Mazzella, A. Kilanowski, M. Altemus, K. Fulgham, and anonymous reviewers for comments that improved the paper.

## References

- Allen, C. D. and Breshears, D. D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences* 95: 14839–14842.
- Anderson, D. R., Laake, J. L., Crain, B. R. and Burnham, K. P. 1979. Guidelines for line transect sampling of biological populations. *Journal of Wildlife Management* 43: 70–78.
- Armstrong, R. A. and McGehee, R. 1980. Competitive exclusion. *American Naturalist* 115: 151–170.
- Best, T. L. and Riedel, S. 1995. *Sciurus arizonensis*. *Mammalian Species* 496: 1–5.
- Blount, S. J. and Koprowski, J. L. 2012. Response of the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) to postfire conditions. *Southwestern Association of Naturalists* 57: 8–15.
- Brooks, M. L., D'antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., Hobbs, R. J., Pellant, M. and Pyke, D. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677–688.
- Brown, D. E. 1984. Arizona's Tree Squirrels. Arizona Game and Fish Department, Phoenix, 114 pp.
- Brown, J. K. and Smith, J. K. 2000. Wildland fire in ecosystems: effects of fire on flora. U. S. Forest Service, General Technical Report RMRS-GTR 42: 1–257.
- Brunner, H. and Triggs, B. 2002. Hair ID: An Interactive Tool for Identifying Australian Mammalian Hair. CSIRO Publishing, Collingwood, Victoria, Australia (CD-ROM).
- Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London, 446 pp.

- Buckland, S. T., Burnham, K. P. and Augustin, N. H. 1997. Model selection: an integral part of inference. *International Biometric Society* 53: 603–618.
- Burnham, K. P. and Anderson, D. R. 2002. *Model Selection and Multi-model Inference: A Practical Information-theoretic Approach*. Springer, New York, 488 pp.
- Carey, A. B. 2000. Effects of new forest management strategies on squirrel populations. *Ecological Applications* 10: 248–257.
- 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.
- Cockrum, E. L. 1960. *The Recent Mammals of Arizona: Their Taxonomy and Distribution*. University of Arizona Press, Tucson, Arizona, 276 pp.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of ponderosa pine forests since white settlement. *Ecological Monographs* 30: 129–164.
- Coues, E. 1867. The quadrupeds of Arizona. *American Naturalist* 1: 351–363.
- Covington, W. W. and Moore, M. M. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *Journal of Forestry* 92: 39–47.
- Cudworth, N. L. and Koprowski, J. L. 2011. Importance of scale in nest-site selection by Arizona gray squirrels. *Journal of Wildlife Management* 75: 1668–1674.
- Cudworth, N. L. and Koprowski, J. L. 2013. Foraging and reproductive behavior of Arizona gray squirrels (*Sciurus arizonensis*): impacts of climatic variation. *Journal of Mammalogy* 94: 683–690.
- Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., et al. 2001. Climate and forest disturbances. *BioScience* 51: 723–734.
- Davis, R. and Brown, D. E. 1988. Documentation of the transplanting of Abert's squirrels. *Southwestern Naturalist* 33: 490–492.
- DeBano, L. F., Neary, D. G. and Ffolliott, P. F. 1998. *Fire's Effects on Ecosystems*. John Wiley and Sons, New York, 352 pp.
- Dillon, G. K., Holden, Z. A., Morgan, P., Crimmins, M. A., Heyerdahl, E. K. and Luce, C. H. 2011. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. *Ecosphere* 2: 130.
- Dodd, N. L., Rosenstock, S. S., Miller, C. R. and Schweinsburg, R. E. 1998. *Tassel-eared Squirrel Population Dynamics in Arizona: Index Techniques and Relationships to Habitat Condition*. Arizona Game and Fish Department Technical Report 27. Phoenix, Arizona, 49 pp.
- Doumas, S. L. and Koprowski, J. L. 2013. Effect of heterogeneity in burn severity on Mexican fox squirrels following the return of fire. *International Journal of Wildland Fire* 22: 405–413.
- Doutt, J. K. 1931. A new subspecies of the Arizona gray squirrel (*Sciurus arizonensis* Coues). *Annals Carnegie Museum* 20: 271–273.
- Edelman, A. J. and Koprowski, J. L. 2005. Selection of drey sites by Abert's squirrels in an introduced population. *Journal of Mammalogy* 86: 1220–1226.
- Falk, D. A. 2004. *Scaling Rules for Fire Regimes*. Ph. D. Dissertation, University of Arizona, Tucson, 304 pp.
- Fiske, I. and Chandler, R. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43: 1–23.
- Frey, J. K., Hill, M. T., Christman, B. L., Truett, J. C. and Macdonald, S. O. 2008. Distribution and habitat of the Arizona gray squirrel (*Sciurus arizonensis*) in New Mexico. *The Southwestern Naturalist* 53: 248–255.
- Friederici, P. 2003. *Ecological Restoration of Southwestern Ponderosa Pine Forests*. Island Press, Washington, 541 pp.
- Gill, A. M. and Catling, P. 2002. Fire regimes and biodiversity of forested landscapes of southern Australia. In (Bradstock, R. A., Williams, J. E. and Gill, M. A., eds.) *Flammable Australia: The Fire Regimes and Biodiversity of Continent*, pp. 351–369. Cambridge University Press, Cambridge.
- Gurnell, J., Lurz, P., Shirley, M., Cartmel, S., Garson, P., Magris, L. and Steele, J. 2004. Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain. *Mammal Review* 34: 51–74.
- Gwinn, R. N. and Koprowski, J. L. 2017. Differential response to fire by an exotic and an endemic species complicates endangered species conservation. *Hystrix, Italian Journal of Mammalogy* 27. DOI: 10.4404/hystrix-27.2-11447.
- Hansen, M. H., Hurwitz, W. N. and Madow, W. G. 1953. *Sample Survey Methods and Theory*. John Wiley and Sons, New York, 332 pp.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131: 1292–1297.
- Hoffmeister, D. F. 1986. *Mammals of Arizona*. University of Arizona Press, Tucson, 602 pp.
- Keith, D. A., Williams, J. E. and Woinarski, J. C. Z. 2002. Fire management and biodiversity conservation: key approaches and principles. In (Bradstock, R. A., Williams, J. E. and Gill, A. M., eds.) *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*, pp. 1928–1939. Cambridge University Press, Cambridge.
- Ketcham, S. L. and Koprowski, J. L. 2013. Impacts of wildfire on wildlife in Arizona: a synthesis. In (Gottfried, G. J., Gebow, B. S. and Eskew, L. G., eds.) *Biodiversity and Management of the Madrean Archipelago III*, pp. 345–350. U. S. Forest Service, General Technical Report RMRS-P 67, Fort Collins.
- Kiltie, R. A. 1989. Wildfire and the evolution of dorsal melanism in fox squirrels, *Sciurus niger*. *Journal of Mammalogy* 70: 726–739.
- King, S. R. B. and Koprowski, J. L. 2009. Effect of human and non-human disturbance on Mt. Graham red squirrels. In (Sanderson, H. R. and Koprowski, J. L., eds.) *The Last Refuge of the Mt. Graham Red Squirrel: Ecology and Endangerment*, pp. 301–317. University of Arizona Press, Tucson.
- Kirkpatrick, R. L. and Mosby, H. S. 1981. Effect of prescribed burning on tree squirrels. In (Wood, G. W., ed.) *Prescribed Fire and Wildlife in Southern Forests*, pp. 99–101. Belle Baruch Forest Science Institute of Clemson University, Clemson.
- Koprowski, J. L. 2005. The response of tree squirrels to fragmentation: a review and synthesis. *Animal Conservation* 8: 369–376.
- Koprowski, J. L., Leonard, K. M., Zugmeyer, C. A. and Jolley, J. L. 2006. Direct effects of fire on endangered Mount Graham red squirrels. *The Southwestern Naturalist* 51: 59–63.
- Krausman, P. R., Cain III, J. W. and Johnson, H. E. 2004. Impact of the Bullock and Aspen Fires on Desert Bighorn Sheep Habitat in the Santa Catalina Mountains, Arizona. Final Report in Fulfillment of Contract #41-8197-3-0107. U. S. Forest Service, Tucson, 15 pp.
- Kremsater, L., Bunnell, F., Huggard, D. and Dunsworth, G. 2003. Indicators to assess biological diversity: Weyerhaeuser's coastal British Columbia forest project. *Forestry Chronicle* 79: 590–601.
- Lange, K. I. 1960. Mammals of the Santa Catalina Mountains, Arizona. *The American Midland Naturalist* 64: 436–458.
- Leonard, K. M. and Koprowski, J. L. 2010. Effect of fire on endangered Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*): responses of individuals with known fates. *Southwestern Naturalist* 55: 217–224.
- Lindenmayer, D. B. and Fischer, J. 2006. *Habitat Fragmentation and*

- Landscape Change: An Ecological and Conservation Synthesis. Island Press, Washington, D.C., 352 pp.
- Lyons, L. J., Telfer, E. S. and Schreiner, D. S. 2000. Direct effects of fire and animal responses. In (Smith, J. K., ed.) *Wildland Fire in Ecosystems: Effects of Fire on Fauna*, pp. 17–23. U. S. Forest Service, General Technical Report RMRS-GTR 42, Fort Collins.
- Maghran, L. A. 2014. Recovery and Changes of Plant Communities from Two Large Fires in the Santa Catalina Mountains, Arizona, USA. M.S. Thesis, University of Arizona, Tucson, 120 pp.
- Marcum, C. L. and Loftsgaarden, D. O. 1980. A nonmapping technique for studying habitat preferences. *Journal of Wildlife Management* 44: 963–968.
- MTBS [Monitoring Trends In Burn Severities]. 2011. MTBS homepage. Available at <http://www.mtbs.gov>. (Accessed 9 March 2011).
- Nash, D. J. and Seaman, R. N. 1977. *Sciurus aberti*. *Mammalian Species* 80: 1–5.
- National Interagency Fire Center. 2015. NIFC homepage. Available at <https://www.nifc.gov/>. (Accessed 4 August 2015).
- Nearby, D. G., Klopatek, C. C., DeBano, L. F. and Ffolliott, P. F. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51–71.
- Noss, R. F., Beier, P., Wallace Covington, W., Edward Grumbine, R., Lindenmayer, D. B., Prather, J. W., Schmiegelow, F., Sisk, T. D. and Vosick, D. J. 2006. Recommendations for integrating restoration ecology and conservation biology in ponderosa pine forests of the southwestern United States. *Restoration Ecology* 14: 4–10.
- Parsons, A., Robichaud, P. R., Lewis, S. A., Napper, C. and Clark, J. T. 2010. Field guide for mapping post-fire soil burn severity. U. S. Forest Service, General Technical Report RMRS-GTR 243: 1–49.
- Prather, J. W., Dodd, N. L., Dickson, B. G., Hampton, H. M., Xu, Y., Aumack, E. N. and Sisk, T. D. 2006. Landscape models to predict the influence of forest structure on tassel-eared squirrel populations. *Journal of Wildlife Management* 70: 723–731.
- R Development Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. Available at <http://www.R-project.org/> (Accessed 5 October 2013)
- Ream, C. H. 1981. The effects of fire and other disturbances on small mammals and their predators: an annotated bibliography. U. S. Forest Service, General Technical Report INT 106: 1–55.
- Sackett, S. S., Haase, S. and Harington, M. G. 1994. Restoration of southwestern ponderosa pine ecosystems with fire. In (Covington, W. W. and DeBano, L. F., eds.) *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, pp. 115–121. U. S. Forest Service, General Technical Report RM 247, Fort Collins.
- Savage, M. and Mast, J. N. 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research* 35: 967–977.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185: 27–39.
- Schoener, T. W. 1986. Resource partitioning. In (Kikkawa, J. and Anderson, D. J., eds.) *Community Ecology: Pattern and Process*, pp. 91–126. Blackwell Scientific Publications, Melbourne.
- Shreve, F. 1915. The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors, Publication 217, pp. 1–112. Carnegie Institution of Washington Press, Washington, D.C.
- Sikes, R. S., Gannon, W. L. and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92: 235–253.
- Steele, M. A. and Koprowski, J. L. 2001. North American Tree Squirrels. Smithsonian Institution Press, Washington, D.C., 224 pp.
- Swetnam, T. W. 1990. Fire history and climate in the southwestern United States. In (Krammes, J. S., ed.) *Effects of Fire in Management of Southwestern Natural Resources: A Symposium Proceeding*, pp. 6–17, U. S. Forest Service, General Technical Report RM-GTR 191, Fort Collins.
- Swetnam, T. W. 2005. Fire histories from pine-dominant forests. In (Gottfried, G. J., Gebow, B. S., Eskew, L. G. and Edminster, C. B., eds.) *Biodiversity and Management of the Madrean Archipelago II: Connecting Mountain Islands and Desert Seas*, pp. 35–43. U. S. Forest Service, General Technical Report RMRS-P 36, Fort Collins.
- Swetnam, T. W. 2007. Climate and the changing landscape. *Restoring Connections* 10: 4–5.
- Swetnam, T. W. and Baisan, C. H. 2003. Tree-ring reconstructions of fire and climate history in the Sierra Nevada and southwestern United States. In (Veblen, T. T., Baker, W., Montenegro, G. and Swetnam, T. W., eds.) *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*, pp. 158–195. Springer, New York.
- Swetnam, T. W., Baisan, C. H. and Grissino-Mayer, H. D. 2009. Tree-ring perspectives on fire regimes and forest dynamics in mixed conifer and spruce-fir forests on Mt. Graham. In (Sanderson, H. R. and Koprowski, J. L., eds.) *The Last Refuge of the Mt. Graham Red Squirrel: Ecology of Endangerment*, pp. 55–67. University of Arizona Press, Tucson.
- Swetnam, T. W., Baisan, C. H. and Kaib, J. M. 2001. Forest fire histories in the sky islands of La Frontera. In (Webster, G. L. and Bahre, C. J., eds.) *Changing Plant Life of La Frontera: Observations on Vegetation in the United States/Mexico Borderlands*, pp. 95–119. University of New Mexico Press, Albuquerque.
- Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Hedley, S. L., Pollard, J. H., et al. 2006. Distance 5.0. Release 1. University of Saint Andrews, Fife, Scotland, United Kingdom.
- Tuomainen, U. and Candolin, U. 2011. Behavioural responses to human-induced environmental change. *Biological Reviews* 86: 640–657.
- Westerling, A. L., Hidalgo, H. G., Cayan, D. R. and Swetnam, T. W. 2006. Warming and earlier spring increase western United States fire activity. *Science* 313: 940–943.
- Western National Parks Association. 2006. *Ecology of Introduced Abert's Squirrels*. Saguaro National Park, Tucson, 47 pp.
- White, A. S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66: 589–594.
- Whittaker, R. H. and Niering, W. A. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. *Ecology* 46: 429–452.
- Wright, H. A. and Bailey, A. W. 1982. *Fire Ecology, United States and Southern Canada*. John Wiley and Sons, New York, 528 pp.

Received 29 April 2017. Accepted 28 October 2017.

Editor was Noriko Tamura.