DIFFERENTIAL RESPONSE OF NATIVE ARIZONA GRAY SQUIRRELS AND
INTRODUCED ABERT'S SQUIRRELS TO A MOSAIC OF BURN SEVERITIES IN THE
SANTA CATALINA MOUNTAINS

by

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ABSTRACT

Disturbance events can alter habitat properties, leading to species displacement, isolation and/or local extinction. In addition, introduced species have been recognized as a threat to biodiversity of native species. Understanding the interacting impacts of fire on native and introduced wildlife species, and the influence on a native species of competition with an introduced species after ecosystem change is critical. Tree squirrels are indicators of forest health; we used two species to determine thresholds and assess behavioral responses to determine adaption to habitat alterations. We studied native Arizona gray squirrels (*Sciurus arizonensis*), which are believed to favor riparian habitat, and introduced Abert's squirrels (*S. aberti*), which prefer open parklike ponderosa pine (*Pinus ponderosa*) in the Santa Catalina Mountains, Arizona, USA. We examined how native but reportedly declining Arizona gray squirrels and introduced Abert's squirrels use areas within widespread fires that burned the study area in 2002-3. Fires burned in a mosaic pattern of unburned, low, moderate, and high burn severity patches. To determine how fire may affect squirrel habitat and behavior, we examined how fire altered habitat use and occupancy, and used distance sampling to determine squirrel abundance, distribution and use within a mosaic of burn severities. Occupancy and habitat use indicate that introduced Abert's squirrels are better adapted to post-fire conditions whereas native Arizona gray squirrels may be adversely impacted by fire disturbance. Our results suggest that Arizona gray squirrel populations may be locally imperiled due to post-fire habitat alteration and loss exacerbated by competition with Abert's squirrels. Abert's squirrels predominantly occupied unburned ponderosa pine and mixed conifer zones with open understories. In contrast, Arizona gray squirrels were documented at only four sites and primarily occupied unburned to low burn riparian areas with dense understories. Abert's squirrels predominately nest and feed in unburned coniferous areas whereas Arizona gray squirrels nest in unburned to low burn non-coniferous areas. Arizona gray squirrels have a reduced distribution and potentially in decline but only remain at lower elevations on the Santa Catalina Mountains. Fire management and restoration efforts should include examination of the differential impacts of fire on native and invasive species.

INTRODUCTION

Fire has been a component of forests of southwestern North America for millennia. Low severity surface and ground fires were common in many forest types before 1900 (Swetnam et al. 2001, Swetnam and Baisan 2003, Swetnam 2005) and burned in smaller 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 western forests have burned an average of 86,560 ha per year in the last decade (National Interagency Fire Center 2015) which 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, coarser mosaics of large, homogenous patches (Dillion et al. 2011), due to a century of fire suppression by land management agencies that has increased fuel loads and tree densities (Allen 1998; Falk 2004). In addition, climatic (Flannigan et al. 2000, Westerling et al. 2006, Zinck et al. 2011) and forest structural changes amplify fire frequency, size, and intensity (Swetnam 1990, Covington and Moore 1994, Sackett et al. 1994, O'Connor et al. 2014), which may further affect wildlife habitat (Ream 1981, DeBano et al. 1998, Lyon et al. 2000).

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 1999). Tree squirrels are 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 patch edges, habitat alteration and fragmentation, and resource competition for food, nest (drey) sites and structures, and tree cavities (Kirkpatrick and Mosby 1981), due to reduced use and increased availability of moderate to high severity areas.

Native Arizona gray squirrels (*Sciurus arizonensis*) and introduced Abert's squirrels (*S. aberti*) inhabit the Santa Catalina Mountains of southern Arizona (Lange 1960). These two species may be syntopic (Brown 1984, Best and Riedel 1995, Frey et al. 2008) and use dreys and tree cavities for nests and protection (Brown 1984, Steele and Koprowski 2001). Both squirrels consume similar foods that include cones and seeds, acorns, staminate flowers, mistletoe, and fungi (Brown 1984). Both species forage throughout the year with only small amounts of scatterhoarding (Brown 1984, Best and Riedel 1995). Abert's squirrels consume pine twig cambium and leave conspicuous stripped twigs behind that permit definitive identification (Brown 1984). Abert's squirrels were introduced to the Santa Catalina Mountains from their

native range in Fort Valley Experimental Forest near Flagstaff in the 1940's to increase hunting opportunities (Davis and Brown 1988). Abert's squirrel introduction and/or habitat loss and fragmentation is 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. They were once listed as a Category 2 species (potentially warranting listing as threatened under the US Endangered Species Act) in the Santa Catalina Mountains (Lange 1960; Frey et al. 2008), but this category was eliminated in 1996 (61 Fed. Reg. 64481: 1996). Recent fire history may be contributing to this decline. Arizona gray squirrels typically use unburned riparian areas with dense understory (Brown 1984); however, just 2% of Arizona gray squirrel suitable habitat remains unburned on the Santa Catalina Mountains following major fires in 2002-2003, which burned over most of the forested area of the mountain range (Maghran 2014), including unburned, dense riparian areas (MTBS 2011). Squirrels may also be affected by climate variability in their native region: within the last 30 years, mean annual temperatures have increased by 0.19° C per decade in the southwest (CLIMAS 2012). In addition, precipitation over the last 50 years has decreased by 5% in Tucson, Arizona (CLIMAS 2012), contributing to extended drought conditions that may affect squirrel populations directly by altering food resources (Dodd et al. 2003) as well as contributing to severe wildfires (Westerling et al. 2006).

We hypothesized that habitat fragmentation and loss in addition to possible competition with Abert's squirrels are influencing decline of Arizona gray squirrel populations. The goal of this study was to determine responses of native Arizona gray squirrels and introduced Abert's squirrels in a landscape where fire has caused habitat modification and loss. Particularly, our objectives were to determine what burn severity types each species of tree squirrel tends to use

post-fire, and whether habitat fragmentation and loss caused by fires and possible competition with an introduced squirrel might be a contributing factor to the potential decline of Arizona gray squirrels.

STUDY AREAS

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 1975). 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 1975). 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 vegetative zones where upper 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 the top of the Santa Catalina Mountains from montane forest down to upland desert areas (Maghran 2014). As a result, one-third of trees, including canopy trees, were killed in areas that experience high severity burns (Swetnam 2007). Vegetative communities were affected differentially by fire severities (Maghran 2014). Mixed conifer had 0% unburned, 7.1% low, 42.9% moderate, and 50% high severity. Ponderosa pine experienced 17.7% unburned, 29.4% low, 17.7% moderate, and 35.3% high severity. Madrean

pine oak severity was 14.3% unburned, 7.1% low, 14.3% moderate, and 64.3% high severity.

Madrean/Oak/Conifer/Manzanita had 25% unburned, 16.7% low, 25% moderate, and 33.3%

high severity. Oak/Pinyon/Juniper experienced 0% unburned, 9.1% low, 0% moderate, and

73.7% high severity.

METHODS

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 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 at elevations in all vegetation types 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) and did not find presence of either species of squirrel, any associated feeding sign, or dreys. We subsequently replaced high burn severity points with additional randomly generated points distributed among unburned, low and moderate burn severity areas for a total of 201 points (Fig. 1).

 We used trail cameras (Nomad Infrared Digital 5.0, Stealth Cam, LLC., Grand Prairie, TX) and hair tubes (Gurnell et al. 2004) to measure occupancy at each randomly selected point. Hair tubes were placed at the base of trees and trail cameras were attached to tree trunks facing hair tubes. Only a hair tube was deployed at locations where a tree was not available to attach a trail camera, or areas in close proximity to residences and heavy recreation (24 points). Hair tubes were constructed from PVC pipe measuring 30 cm in length and 6.5 cm in diameter

(Gurnell et al. 2004). We baited each hair tube with a peanut butter and oatmeal mixture placed

at the center of the tube. 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

before being moved to the next randomly selected point until the remaining points were sampled.

Tape was removed from the hair tubes and placed into zippered sandwich bags coated with

talcum powder and transported to the laboratory and maintained at 22°C until sampled.

Reference hair samples from the dorsal and posterior body and dorsal tail for Arizona

gray squirrels and Abert's squirrels 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 analyzed hair samples with a compound microscope

(AmScope Model M10FL) at 10x and 40x 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).

Distance sampling: Of 201 points sampled for occupancy, 50 points were randomly

selected for distance sampling (Anderson et al. 1979, Buckland et al. 2001) to search for

presence of squirrels, feeding sign, and dreys. Transects extended 500 m from a sample point in

a random direction, often passing through legacies of various fire severities. Burn severities

were classified on the ground 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. We traversed 200 km of

transects and spent approximately 1500 h to document presence of Arizona gray and Abert's squirrels, and locate feeding sign and dreys.

Each transect was sampled on two passes. On the first pass, we located Abert's squirrels and Arizona gray squirrels by sight and sound. A compass and range finder 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. Each transect was walked again to locate feeding sign and squirrel dreys. We stopped every 10 m to record presence of feeding sign and dreys. Feeding sign located within 2.5 m to each side of the transect line was removed and included clipped pine boughs, cone cores, cone scales, and cambium stripped pine twigs.

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, recorded vegetation type, and determined status as either active or inactive. Dreys were classified into one of three categories: 1) Inactive-poor condition and in disrepair, noticeable holes, not able to be occupied without significant renovation; 2) Potentially active-nest in mild disrepair with old leaves, structure not robust, could be occupied with minimal or no repair; and 3) 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 feeding sign 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. In March after snowmelt, all 50 transects were re-visited to assess feeding sign.

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 and trees or shrubs with canopies that intercepted a vertical projection of the quadrat,

and counted stems of shrubs within each quadrat.

     Riparian surveys: In an attempt to increase our sample size for uncommon Arizona gray

squirrels, we walked additional riparian transects (90 h) and placed trail cameras and hair tubes

every 500-m located within oak vegetation in pre-fire locations where our sampling did not

occur; primarily in upper Sabino Canyon.

     Occupancy data analysis: We analyzed occupancy data using the routing *unmarked*

(Fiske and Chandler 2011) in Program R (R Core Team 2013). Occupancy by the two squirrel

species was modeled separately to permit interspecific comparison. We ran dynamic occupancy

models with and without covariates and additive and multiplicative models with covariates

(Fiske and Chandler 2011) to determine factors that were important for squirrel use. Site

covariates analyzed included burn severity, burn patch size, habitat, elevation, and number of

shrub stems. Burn patch sizes were measured in ArcGIS by drawing polygons around each patch

using the classified dNBR layers. Habitat was determined by specifying particular habitat types

at random and occupied areas and shrub stem density through use of vegetation quadrat. We

selected top models by lowest Akaike Information Criterion (AIC) values, ΔAIC <2, relative

likelihood, and computed Akaike weights (Burnham and Anderson 2002). We backtransformed

models from mean log values to better fit data assumptions, and used a parametric bootstrap

procedure (MacKenzie and Bailey 2004) to assess goodness-of-fit for models to determine which

site covariates had influenced squirrel populations (Table 1).

     Distance sampling data analysis: We used program DISTANCE (Thomas et al. 2006) in

R to estimate density of feeding sign and dreys across a mosaic of burn severities. We pooled

two data sets; one for combined drey data that included distance from transect, nest activity, area

severity, area vegetation type, drey tree severity, and drey tree species and one for combined

feeding sign data that included distance from transect within a 5-m width, type of feeding sign,

and area severity. We stratified eight data sets that included habitat and overall severities within

a 10-m diameter circular plot centered on located dreys, drey tree type, severity of the drey tree,

severities within a 5-m diameter of clippings, cones, and twigs, and overall severities within a

10-m diameter of feeding sign locations. Analysis included four key functions (Half-normal,

Hazard Rate, Negative Exponential, and Uniform) for both pooled and stratified data. We

selected top models by lowest AICc values, ΔAICc <2, relative likelihood, and computed Akaike

weights (Burnham and Anderson 2002). We calculated chi-square values and used Bonferroni's

approach to determine if burn severities at drey and feeding 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, which was calculated as the number of times feeding

sign was found at 10-m intervals on each transect (Dodd et al. 1998). We used forward stepwise

linear regression to determine if severity, habitat type, or shrub stem density were important

factors of squirrel feeding areas and selected models to maximize AIC (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 permit #SP690895, #SP770782, and #SP587510, and U.S. Forest Service permit

#SAN0296.

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 sizes used by Abert's squirrels in unburned areas were 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 (Fig. 3). Unburned and low burn patches were larger than moderate burn patches ($F_{2,42}$ = 5.85, P = 0.006; R^2 =0.22; ANOVA: Single Factor, Tukey HSD comparison). 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 larger in low severity burn (501.24 ha, SE = 424.04, n = 2) but did not differ significantly likely due to small sample size ($F_{1,2}$ = 1.35, P = 0.37; R^2 =0.40; ANOVA: Single Factor, Tukey HSD comparison; Fig. 3). Abert's squirrel occupied locations had a mean of 18 shrub stems (SE = 6.24, n = 24); Arizona gray squirrel occupied locations had more shrub stems ($\bar{x}$ = 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) as predicted, whereas Arizona gray squirrels were found predominantly in 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 habitat covariates. A high proportion of sites occupied by Abert's squirrels were within conifer vegetation (0.84 ± 0.03; P = 0.01). Abert's squirrels had a high detection probability in mixed conifer with open understories (0.83 ± 0.03; P = 0.01). Detection probability and occupancy of Abert's squirrels seemed to be associated with elevation (0.50 ± 1.06; P = 0.05), although model fit was not strong. Abert's squirrels occupied elevations were higher than random elevations (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 pre-fire elevations ($\bar{x}$ = 2359, SE = 69, n = 4; t_{47} = -0.15, $P \leq 0.88$). Burn patch sizes,

burn severity, and shrub stem density did not affect Abert's squirrel occupancy.

Arizona gray squirrels had site covariates correlated with the null model, habitat, and

burn patch size. Site occupancy by Arizona gray squirrels was greatest within riparian areas

(0.70 ± 0.04; $P \leq 0.001$) than all other vegetative communities. Detection probability for

Arizona gray squirrels was greatest in riparian zones with dense understories (0.70 ± 0.05; $P \leq$

0.001) and within smaller burn patches (0.67 ± 0.02, $P \leq 0.001$). We predicted that Arizona gray

squirrels would be adversely impacted by burn severity and shrub stem density since they are

found in unburned and low burn riparian areas with dense understories; however, burn severity

and shrub stem density were not factors that influenced habitat unlike burn patch sizes that

homogenized riparian areas. Shrub stem densities were greater in locations occupied by Arizona

gray squirrels than shrub stem densities in random locations (t_{52} = 5.42, $P \leq 0.001$). Elevation

did not influence occupancy of Arizona gray squirrels even though they were once found in

higher elevations (Hoffmeister 1986) and are now occupying lower elevations outside Abert's

squirrel ranges. However, Arizona gray squirrel occupied elevations ($\bar{x}$ = 1986 m, SE = 127, n =

4) did not differ from historic elevations ($\bar{x}$ = 2124 m, SE = 162, n = 9; t_{11}=0.53, $P \leq 0.61$).

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.

We summarized our data in totality without stratification for our pooled data sets. Top

models for pooled data were selected for estimation of drey density and estimation of feeding

sign density (Table 2). For our stratified drey data sets, we selected the top model for the

estimation of type of tree in which the drey was found (drey tree types), burn severity of tree where drey was found (drey tree severities), overall burn severity of area surrounding found drey (drey area severity), and overall habitat surrounding found drey (drey habitat type; Table 3). For our stratified feeding sign data sets, we selected the top model for the severity of the nearest tree(s) where pine clippings, eaten cone cobs and stripped twigs were found, and overall severity of surrounding area where feeding sign was found (Table 3).

Dreys: An average of sixteen dreys (SE = 1.92, *n* = 42) were found per 500-m transect in the study area. Unburned ($\bar{x}$ = 0.36/transect, SE = 0.12, *n* = 15) and low burned ($\bar{x}$ = 0.45/transect, 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 ($F_{3,18}$ = 2.67, *P* = 0.08; ANOVA: Single Factor, Tukey HSD comparison). Dreys in unburned (Bonferroni Z-test, 97% confidence intervals: -0.23, 0.21), low burn (Bonferroni Z-test, 97% confidence intervals: -0.24, 0.23), moderate burn (Bonferroni Z-test, 97% confidence intervals: -0.17, 0.21), and high burn (Bonferroni Z-test, 97% confidence intervals: -0.09, 0.10) areas were used in proportion to availability (χ^2= 1.83, df = 41, *P* = 1; Fig. 4). Sixty percent (SE = 0.10, *n* = 25) of dreys were active and 40% (SE = 0.12, *n* = 17) were inactive per transect. Sixty-four percent (SE = 0.09, *n* = 27) of dreys were in ponderosa pine habitat, 24% (SE = 0.14, *n* = 10) in mixed conifer habitat, and 12% (SE = 0.15, *n* = 5) in oak habitat per transect (Fig. 5). Dreys were used in proportion to availability in ponderosa pine (Bonferroni Z-test, 97% confidence intervals: -0.23, 0.14), mixed conifer (Bonferroni Z-test, 97% confidence intervals: -0.19, 0.18) and oak habitats ((Bonferroni Z-test, 97% confidence intervals: -0.13, 0.23; χ^2= 18.99, df = 41, *P* = 0.99). Eighty-six percent of dreys were found in coniferous trees; 62% (SE = 0.10, *n* = 26) in ponderosa pine and 24% (SE = 0.14, *n* = 10) in mixed conifer trees including Douglas-fir, white

fir and Chihuahua pine per transect (Fig. 5). 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. Six of 42 dreys were found in non-coniferous trees; 7% (SE = 0.15, n = 3)

in Fremont cottonwood, 5% (SE = 0.16, n = 2) in Arizona sycamore and 2% (SE = 0.15, n = 1)

in oak per transect (Fig. 5). Dreys in ponderosa pine (Bonferroni Z-test, 97% confidence

intervals: -0.23, 0.23), Douglas-fir (Bonferroni Z-test, 97% confidence intervals: -0.18, 0.18),

white pine (Bonferroni Z-test, 97% confidence intervals: -0.10, 0.10), Chihuahua pine

(Bonferroni Z-test, 97% confidence intervals: -0.10, 0.07), sycamore (Bonferroni Z-test, 97%

confidence intervals: -0.10, 0.10), cottonwood (Bonferroni Z-test, 97% confidence intervals:

-0.12, 0.12), and oak (Bonferroni Z-test, 97% confidence intervals: -0.10, 0.10) trees were used

in proportion to availability (χ^2= 0.02, df = 41, P = 1). Five of six dreys in non-coniferous trees

were identified as Arizona gray squirrel dreys since they were composed of non-coniferous

leaves and twigs and located outside Abert's squirrel ranges. Arizona gray squirrel dreys located

from transects were found at an average of 1524-m. However, while walking to points with

various burn severities and habitat types, we identified other Arizona gray squirrel dreys; three

were at an elevation of 1829-m and one at an elevation of 1341-m that were confirmed with hair

tubes and trail cameras. All dreys that we located were found outside of the coniferous zone

where Abert's squirrels reside.

Feeding sign: Feeding sign was estimated at 59 (SE = 9.31, n =23) locations per transect.

We found feeding sign on 23 of the 50 transects, with frequency of occurrence maximized at

0.34 ($\bar{x}$ = 0.06 ± 0.01). Frequency of occurrence of feeding sign differed for burn severity,

habitat type and shrub stem density ($F_{3,88}$ = 7.02, $P \leq 0.001$; ANOVA: Single Factor); however,

differed only with shrub stems ($F_{1,44}$ = 8.80, P = 0.005; ANOVA: Single Factor, Tukey HSD

comparison). Forty-three percent (SE = 0.06, n = 66) of feeding sign was found in unburned

areas, 23% (SE = 0.07, n = 36) in low burn areas, and 34% (SE = 0.07, n = 52) in moderate burn

areas per transect. Feeding sign (χ^2= 4.11, df = 153, P = 1) was found in unburned (Bonferroni

Z-test, 97% confidence intervals: -0.13, 0.11), low burn (Bonferroni Z-test, 97% confidence

intervals: -0.12, 0.12), and moderate burn (Bonferroni Z-test, 97% confidence intervals: -0.11,

0.12) in proportion to its availability (Fig. 6). Clippings were found in nearly equal proportions;

32% (SE = 0.08, n = 32) in unburned, 32% (SE = 0.08, n = 32) in low burn and 36% (SE = 0.08,

n = 36) in moderate burn. Clippings (χ^2= 0.66, df = 99, P = 1) were in unburned (Bonferroni Z-

test, 97% confidence intervals: -0.15, 0.14), low burn (Bonferroni Z-test, 97% confidence

intervals: -0.14, 0.15), and moderate burn (Bonferroni Z-test, 97% confidence intervals: -0.14,

0.15) in proportion to availability (Fig. 6). Forty-eight percent (SE = 0.09, n = 38) of discarded

cone cobs were found in unburned areas, whereas only 15% (SE = 0.07, n = 12) were in low

burn and 38% (SE = 0.08, n = 30) were in moderate burn areas per transect. However, cones

(χ^2= 6.08, df = 79, P = 1) were found in proportion to availability in unburned (Bonferroni Z-test,

97% confidence intervals: -0.18, 0.15), low burn (Bonferroni Z-test, 97% confidence intervals: -

0.13, 0.16), and moderate burn (Bonferroni Z-test, 97% confidence intervals: -0.17, 0.16) areas

(Fig. 6). Since cone scales were found with cone cobs, we did not analyze scale density.

Stripped twigs were found in 54% (SE = 0.09, n = 23) of unburned areas, 11% (SE = 0.06, n = 5)

of low burn areas, and 35% (SE = 0.08, n = 15) of moderate burn areas. Twigs (χ^2= 6.62, df =

42, P = 1) were discarded in unburned (Bonferroni Z-test, 97% confidence intervals: -0.25, 0.18),

low burn (Bonferroni Z-test, 97% confidence intervals: -0.17, 0.22) and moderate burn

(Bonferroni Z-test, 97% confidence intervals: -0.20, 0.22) areas in proportion to availability (Fig.

 6). We walked additional riparian transects and did not observe or capture pictures of any

Arizona gray squirrels nor did we find any dreys or feeding sign.

DISCUSSION

Arizona gray squirrels were reported to be the rarest animal in Arizona nearly a century and a half ago (Coues 1867). On the Santa Catalina Mountains, Arizona gray squirrels appear to be rare still, as we located only seven individuals. Prior to 1986 individuals were known from eight locations in the Santa Catalina range: Soldier Camp (Doutt 1931, Lange 1960, Hoffmeister 1986), three locations around Summerhaven, two locations in Carter Canyon (Lange 1960, Hoffmeister 1986), three locations on Mt. Bigelow (Lange 1960, Hoffmeister 1986, University of Arizona Mammal Collection), and one location on Butterfly Peak (University of Arizona Mammal Collection), Alder Canyon (Hoffmeister 1986), upper Sabino Canyon (Hoffmeister 1986), and Peppersauce Canyon (Hoffmeister 1986). All documented pre-fire locations were in riparian areas within the conifer zone. In our study, we detected presence of only a single Arizona gray squirrel within the conifer zone. 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 Arizona gray squirrels only remain at lower elevations and may be relegated to smaller burn patches that may indicate displacement by competition with Abert's squirrels. In addition, habitat alteration and loss from wildfires may have restricted dispersal due to 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.

Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) are affected by fire 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, prior to wildfires dreys were found within the conifer zone at General Hitchcock at 1829-m and Mt. Bigelow at 2509-m in elevation (John L. Koprowski, Pers. Comm.). 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 2002-3 fires, and most patches that are left have minimal tree cover and understory, which is poor Arizona gray squirrel habitat (Brown 1984) and likely the reason why we did not find any presence of Arizona gray squirrels within major riparian zones. Dense understory may provide cover and reduce predation on Arizona gray squirrels. However, the 2002-3 Bullock-Aspen wildfires in the Santa Catalina Mountains opened understories and burned approximately 40% of major riparian areas, possibly contributing to further imperilment of Arizona gray squirrel populations.

Home ranges of Abert's squirrels decreased in burned areas (Gwinn 2011) which suggests adaptive capabilities to altered habitats. In our study, Abert's squirrels seem to be more resilient to post-fire conditions than Arizona gray squirrels due to 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. Abert's squirrels nested and were present in every

burn severity located in the conifer zone except high burn severity areas where no tree canopies

remained, similar to findings in the nearby Pinaleño Mountains (Gwinn 2011). 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 evolved to frequent fires and ecosystem change which may explain their

success relative to native Arizona gray squirrels.

Arizona gray squirrels and Abert's squirrels may be syntopic on the Mogollon Rim since

both have evolved together in their native ranges (Frey et al. 2008). Arizona gray squirrels were

observed interacting with Abert's squirrels on the Mogollon Rim (Frey et al. 2008); however,

some populations are thought to have declined due to habitat loss and introduction of Abert's

squirrels in isolated mountain ranges (Best and Riedel 1998). Nonetheless, research has not been

conducted on the Mogollon Rim to determine ecological overlap between the species. 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

sympatic species (Schoener 1974, 1986) can occur post-fire due to vegetation structural changes

(Gill and Catling 2002, Keith et al. 2002b). Competition can force species to specialize within a

particular habitat area in which one species has a competitive advantage over the other and

outcompetes them and pushes the other to competitive exclusion (Hardin 1960, Armstrong and

McGehee 1980, Gurnell et al. 2004). In our study, Abert's squirrels appear to be able to use a

broader range of vegetation types after the fire than native Arizona gray squirrels.   For example,

we found that Abert's squirrels use various burn severities for different resources, which may

explain their ability to respond to severe fire. Conversely, since Arizona gray squirrels are a riparian obligate species (Best and Riedel 1998, Frey et al. 2008) and lower elevations on the Santa Catalina's were not as intensely burned as higher elevations, this may explain why they remain at lower elevations with dense understory in unburned and low burn severities but are no longer found at higher elevations.

Interspecific competition between introduced squirrels and native squirrels is not uncommon. Abert's squirrels were introduced to the Pinaleño Mountains from 1941-1943 (Sanderson and Koprowski 2009) which is believed to have contributed to decline of endangered Mt. Graham red squirrels due to resource competition (Edelman et al. 2009). Resource competition has led to declines of native western gray (*Sciurus griseus*) and Douglas squirrels (*Tamiasciurus douglasii*) due to introductions of eastern fox squirrels (*Sciurus niger*; Ingles 1947, Robinson and McTaggart-Cowan 1954) in Ontario, Canada and throughout the western United States (Flyger and Gates 1982a, Long 2003). Eastern gray squirrels were introduced to Scotland (Gurnell and Pepper 1993), Ireland and Great Britain during the late 19th century and beginning 20th century (Gurnell 1987), and Italy in 1948 (Bertolino and Genovesi 2003). Introductions are responsible for the decline (Gurnell 1987, Gurnell and Pepper 1993, Bertolino and Genovesi 2003) and disappearance of the native red squirrel (*S. vulgaris*; Middleton 1930, Shorten 1946, Lloyd 1962). Red squirrels have reduced reproductive success, juvenile recruitment, and body growth (Wauters et al. 2005a), likely due to increased foraging efficiency of eastern gray squirrels (Williamson 1996) derived from their ability to eat outer cambium from trees (Kenward 1983, Rowe and Gill 1985, Kenward 1989, Dagnall et al. 1998).

Extensive damage to trees and forests have been reported for eastern gray squirrels (Kenward 1983, Rowe and Gill 1985, Kenward 1989, Currado 1998, Dagnall et al. 1998) and

Abert's squirrels (Bailey 1931, Coughlin 1938, Pearson 1950) from excessive tree clipping (Towbridge and Lawson 1942) that expose dead wood and make trees more susceptible to lightning strikes that can increase fire occurrence (Thomas and McAlpine 2010). Southwest forests have a higher occurrence of lightning strikes compared to anywhere else in the western United States (Swetnam and Betancourt 1990). Tree clipping by squirrels can facilitate penetration of fungi and insect infestations that can promote tree degradation (Kenward 1983, Rowe and Gill 1985, Dagnall et al. 1998), which may further exacerbate future fire disturbances by creating ladder fuels that in turn may contribute to stand replacing 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 resulting from increased fuel loads and anthropogenic influences are changing forest fuel mass and distribution, which is amplifying 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, changing nutrient amounts and availability, and increasing erosion and inhibiting 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 the southwest 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 (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).

Climate change combined with increasing wildfires may increase vulnerability of wildlife

species due to reduced habitats and possible competition with other species, especially since

some plant and wildlife species are showing a trend of moving upwards in elevation (Brusca et

al. 2013). Areas of greatest ecological risk include biome transition zones and high topographic

relief locations (Allen et al. 1998, Julius et al. 2008). If future wildfires continue to increase in

frequency and intensity, and create larger, homogenous high-severity patches (Dillion et al.

2011, Dennison et al. 2014), the result may exacerbate resource competition among wildlife

species within smaller mosaic patches (Swetnam 1990, Covington and Moore 1994, Sackett et al.

1994). 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.

MANAGEMENT IMPLICATIONS

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. We suggest that a habitat conservation plan be implemented for restoration of riparian vegetation at locations where Arizona gray squirrels reside currently. 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. Managers should determine if Arizona gray squirrels and Abert's squirrel exhibit syntopy in native areas of sympatry as well as areas where Abert's squirrels have been introduced. In addition, research can be conducted on other isolated mountains to determine if fire or introduction of Abert's squirrels are contributing factors to the decline of Arizona gray squirrels. Comparisons could be made between our study and the Rincon Mountains where stand-replacing fires have not occurred throughout most of the 20th century but where Abert's squirrels occur. Studies could also encompass other mountain ranges, such as the Gila, Huachucha, Patagonia, and Santa Rita Mountains where Abert's squirrels are absent. Such research will allow further clarification of the relative roles of fire-induced habitat change and interspecific competitive exclusion.

APPENDIX A FIGURES

Figure 1. Current and historic Arizona gray squirrel and Abert's squirrel locations in the Santa Catalina Mountains. White stars show Arizona gray squirrel detections, black stars show historic sites, gray circles with black dot show Abert's squirrel detections, white triangles with black triangle show historical sites, black square is a site with both Arizona gray and Abert's squirrel detections, and small light gray circles are all surveyed sites in this study.
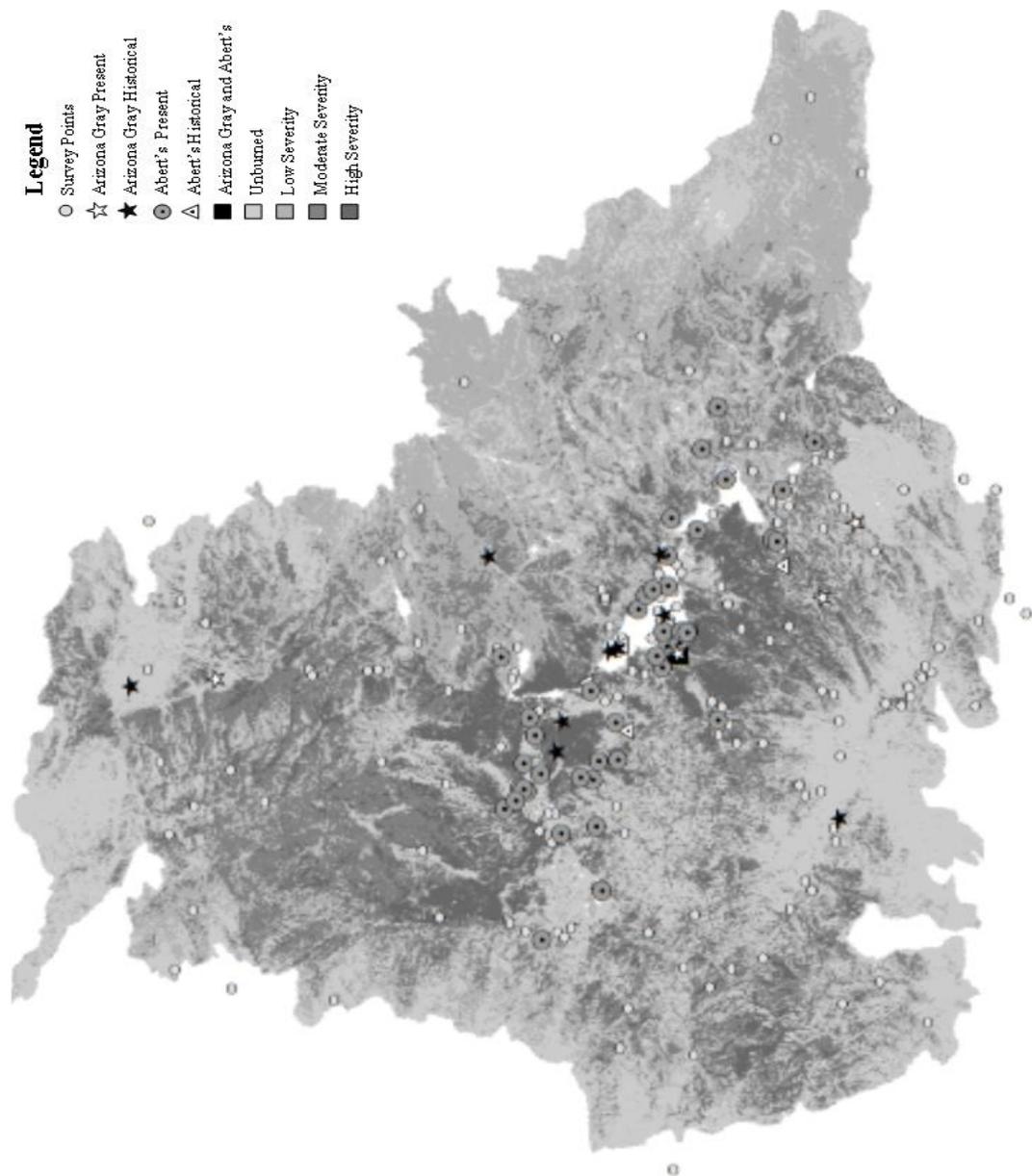
Figure 2. Microscopic hair scale patterns at 10x and 40x magnification of Abert's squirrels and

Arizona gray squirrels. Photography by Shari L. Ketcham**.**
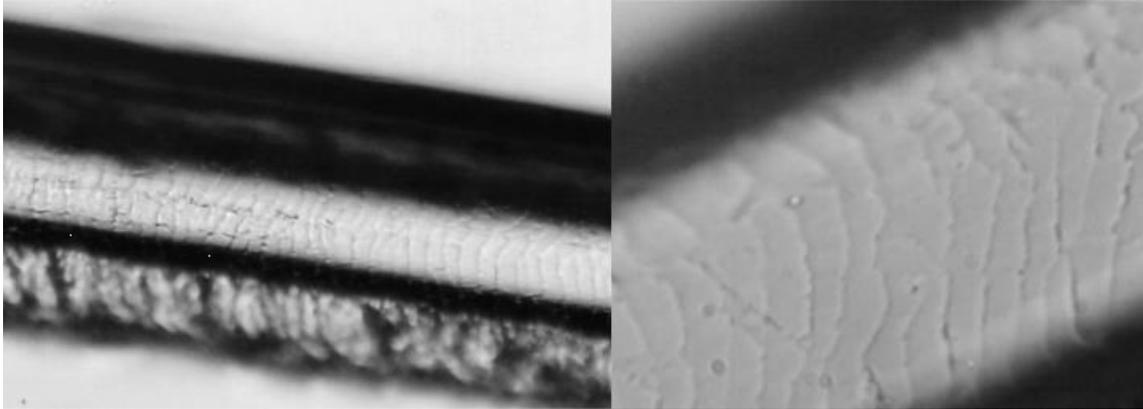
Abert's squirrel
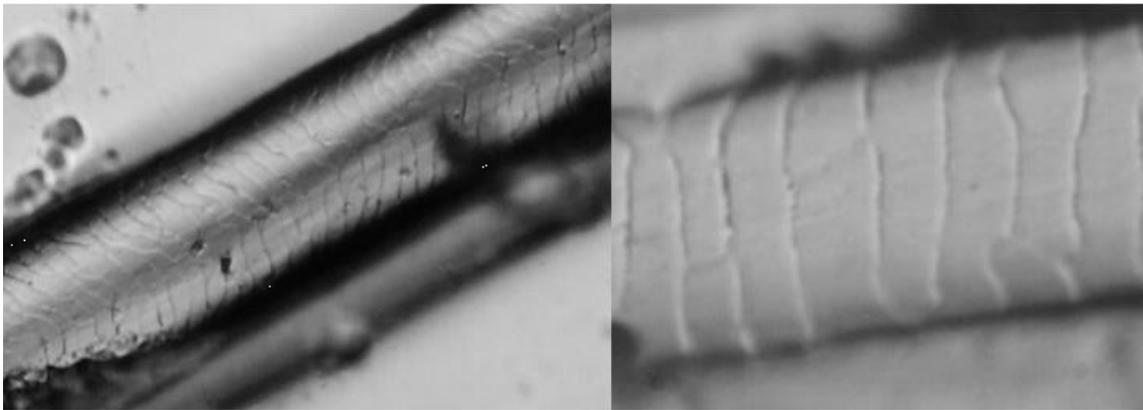
Arizona gray squirrel

Figure 3. Abert's squirrel and Arizona gray squirrel occupancy within burn severity areas versus availability of burn severity areas. Abert's squirrels 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.

Figure 4. 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.
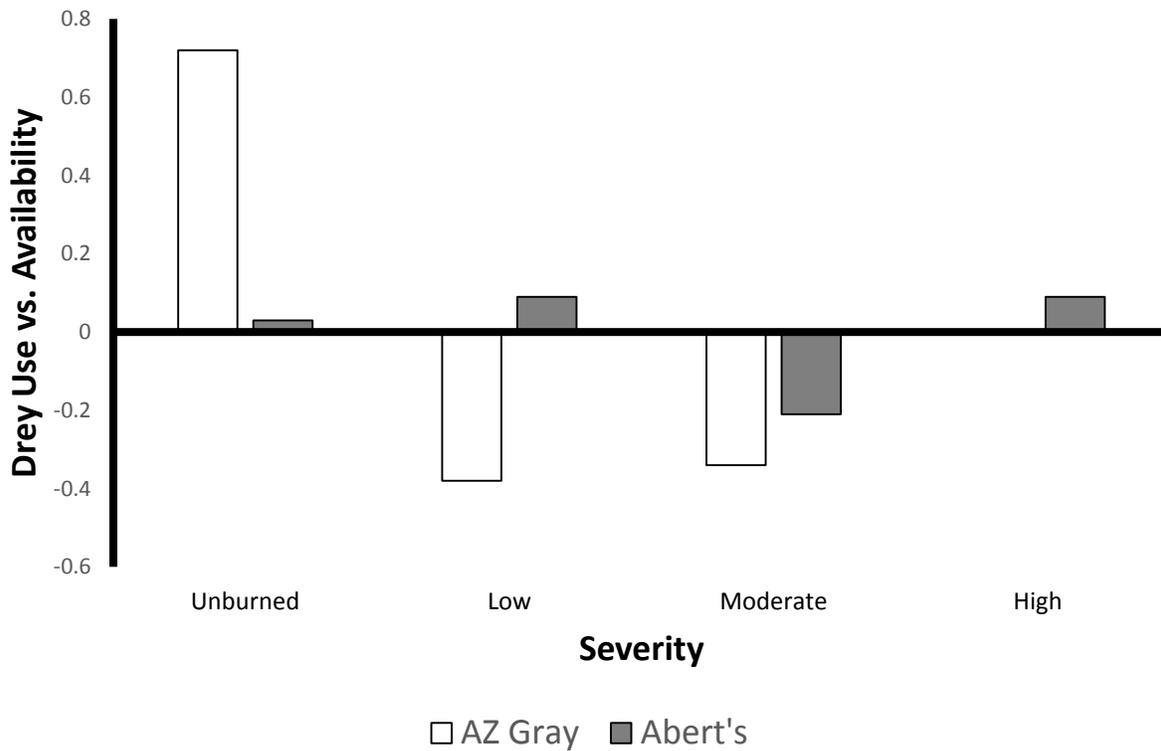
Figure 5. Abert's squirrel and Arizona gray squirrel drey habitat type and drey tree species type use versus availability. Abert's squirrels used ponderosa more than other vegetation communities and Arizona grays squirrels used riparian more than other vegetation communities. Abert's squirrels used mixed conifer trees for dreys more than other tree species, and Arizona gray squirrels used oak trees for dreys more than other tree species. Bars above zero indicate habitat types occupied more than their availability; bars below zero indicate habitat types used less than proportionately available.
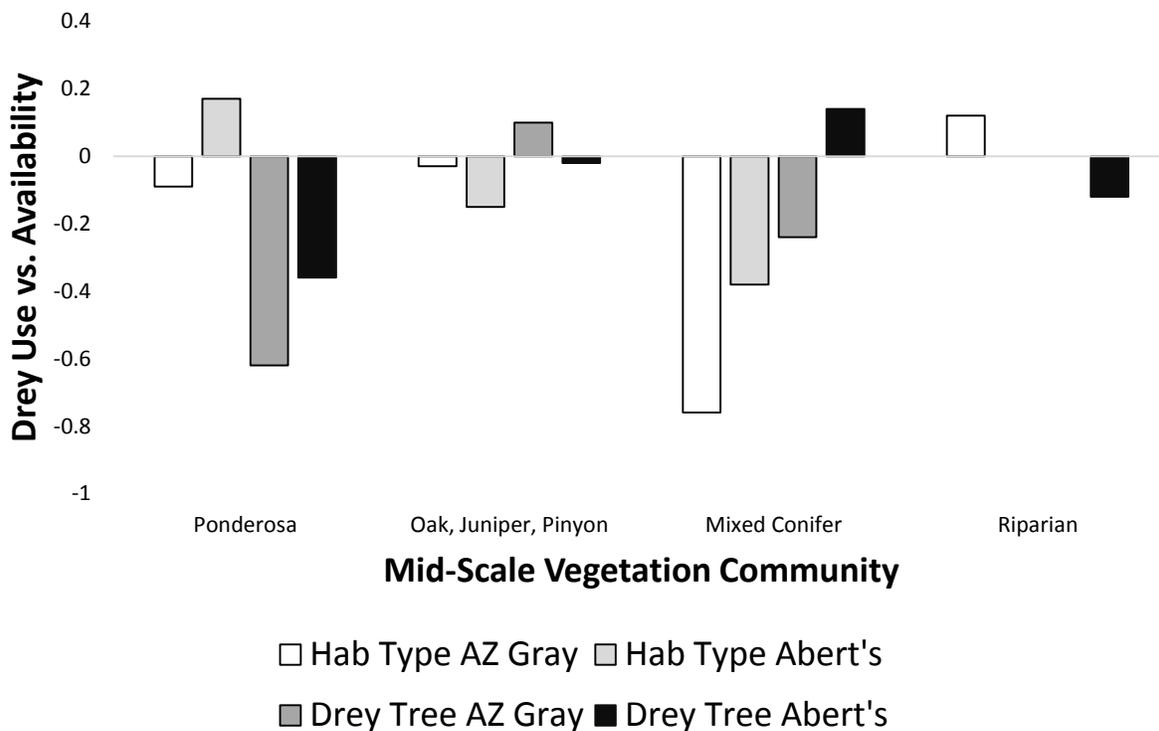
Figure 6. Combined and individual feeding sign use versus availability within burn severities. Combined feeding sign and cones were found in unburned areas more than other severities. Clippings were found in low and moderate burned areas more than other severities. Bars above zero indicate those areas are occupied more than their availability; bars below zero indicate areas are used less than proportionately available.
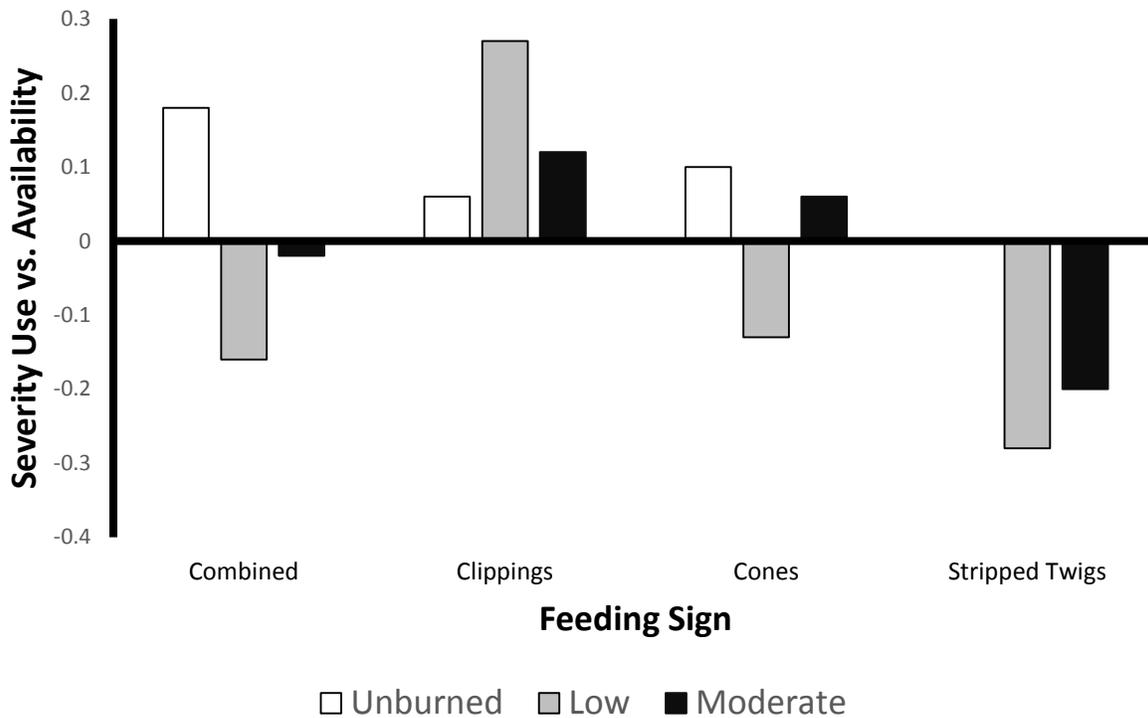
APPENDIX B TABLES

Table 1. Top occupancy models with covariates for Abert's squirrels and Arizona gray squirrels in the Santa Catalina Mountains. Psi (ψ) is the proportion of sites occupied and p is detection probability.

Santa Catalina Top Occupancy Models

Species	Model	Parameters	AIC	ΔAIC	AIC wt	Cumulative wt
Abert's	ψ(elevation)p(elevation)	4	688.67	0.00	0.39	0.39
	ψ(habitat)p(.)	3	689.02	0.35	0.33	0.71
Arizona gray	ψ(.)p(.)	2	765.98	0.00	0.36	0.36
	ψ(habitat)p(.)	3	767.53	1.56	0.16	0.52
	ψ(.)p(habitat)	3	767.97	2.00	0.13	0.65
	ψ(.)p(severitypatchsize)	3	767.97	2.00	0.13	0.78

Table 2. Top pooled distance sampling models of drey density and feed sign density of Abert's squirrels and Arizona gray squirrels in the Santa Catalina Mountains. Psi (ψ) is the proportion of sites occupied and p is detection probability.

		Pooled Data					
Data Analyzed	Key	Adjustment Terms	Parameters	AICc	ΔAICc	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
Feed 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

Table 3. Top stratified distance sampling models of drey density and feed sign density of Abert's squirrels and Arizona gray squirrels in the Santa Catalina Mountains. Psi (ψ) is the proportion of sites occupied and p is detection probability.

Stratified Data							
Data Analyzed	**Key**	**Adjustment Terms**	**Parameters**	**AICc**	**ΔAICc**	**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

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