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Research Article

Differential response to fire by an introduced and an endemic species complicates endangered species conservation

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Abstract

Fire is a natural component of, and serves as a tool for, the restoration of forested ecosystems worldwide; however, disturbance due to fire also has been implicated in the proliferation of invasive species. How these fires affect occupancy and use of the forest by wildlife is of great concern, in particular, the differential response of non-native and native species. In the North American Southwest, prior to European settlement, frequent wildfires helped to maintain forest structure. We examined the effect of a large wildfire on an introduced population of the Abert's squirrel (*Sciurus aberti*) that has invaded the high elevation forests inhabited by the critically endangered Mt. Graham red squirrel (*Tamiasciurus fremonti grahamensis*). We found that introduced Abert's squirrels were more common than native red squirrels in burned areas. Abert's squirrels did not abandon burned areas but nested, foraged, and did not adjust their home range size in burned areas. This suggests that invasive Abert's squirrels are better able to exploit burned areas than native red squirrels and that fire can favor non-native species. This interaction between non-native species, native species, and fire adds new insight into the complexities of conservation and restoration of ecosystems and helps to inform conservation activities worldwide.

Introduction

Fire is an important component of forests worldwide. Periodic burning of forests influences forest structure and ecological processes in many forest types (Moser et al., 2010; Pratt et al., 2010; Smith et al., 2010). Fire suppression has altered many ecosystems around the world, influencing nutrient cycling, habitat suitability for wildlife, and the severity of wildfire (Parsons and DeBenedetti, 1979; McMurry et al., 1996; Zimmerman, 2003; Smith et al., 2010). Beginning in the latter half of the 20th Century, ecologists began to quantify these influences, and agencies began to reintroduce fire to landscapes. Prescribed fire is now a widely used technique for ecological restoration in many countries (Masters et al., 1998; Main and Richardson, 2002; Zimmerman, 2003; Moser et al., 2010; Smith et al., 2010).

In the North American Southwest, dendrochronological records indicate that many forests have experienced frequent, light ground fires (one fire every three to five years; Swetnam and Baisan, 1996a,b; Covington, 2003). Frequent fires maintained an open forest structure by reducing the number of small diameter trees and fuel loads in the form of coarse woody debris and cast needles, and created conditions for understory vegetation (Parsons and DeBenedetti, 1979; Swetnam et al., 1999; Covington and Moore, 1994; Allen et al., 2002; Zimmerman, 2003). Severe fires have recently been deemed more common than has been historically suspected due to the distribution, abundance, and ecology of some species of forest birds (Hutto et al., 2008). Fire suppression efforts begun in the early 1900s resulted in drastic changes to the fire regime of coniferous forests. Less frequent and more severe fires became more common than what would occur under natural conditions (Zimmerman, 2003). The change in fire regime resulted in increased density of small trees and unnatural accumulation of litter, both of which increase severity of subsequent wildfires (Parsons and DeBenedetti, 1979; Zimmerman, 2003).

The effects of fire are of increased concern to land and wildlife managers in recent decades (Fa and Sanchez-Cordero, 1993; Masters et al., 1998; Ballard et al., 2000; Main and Richardson, 2002; Conway and Kirkpatrick, 2007; Dickson et al., 2009). Research has proliferated with the increasing frequency of high-severity wildfires that has resulted in the use of prescribed fire as a fuels reduction and ecological restoration technique (Masters et al., 1998; Allen et al., 2002; Dickson et al., 2009; Garvey et al., 2010). What remains largely unclear is how the response of non-native wildlife to wildfire differs from that of native species.

The introduction of non-native species into ecosystems has been identified as one of the greatest threats to biodiversity, as well as one of the greatest conservation challenges worldwide (Elton, 1958; Cox, 1999; National Resource Council, 2002; Davis, 2006; Lockwood et al., 2007). Alien invasive species threaten native species either through direct (competition) or indirect effects (hyperpredation, adaptive mismatching in response, parasite spillover: Cox, 1999; Kondoh, 2006; Lockwood et al., 2007; Romeo et al., 2015). These interactions are often detrimental to native species, resulting in population declines or extinction (Humphrey and Barbour, 1981; van Riper et al., 1986; Marsh and Douglas, 1997; Courchamp and Caut, 2006). Conservation of native species in the presence of non-natives is often difficult. If detected immediately upon establishment, complete removal of non-native species from an area is feasible (Cox, 1999; Kessler, 2001; Courchamp and Caut, 2006). Eradication of non-native species is often not possible, and management of the non-native species and their effects on native species is the practical alternative (Karl and Best, 1982; Murphy and Bradfield, 1992; Cox, 1999; Courchamp and Caut, 2006). The management of non-native species presents a myriad of difficulties to biologists and researchers in that stochastic events and unforeseen ecological interactions often exacerbate problems caused by non-native spe-

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cies (Murphy and Bradfield, 1992; Cox, 1999; Courchamp and Caut, 2006).

The introduction of non-native species has changed ecosystem and management challenges for wildlife in southwestern United States pine forests (Covington, 2003). Over 50 non-native plant species have been identified in pine forests of the region (Sieg et al., 2003). Several species of non-native plants including Russian thistle (*Salsola tragus*), and cheatgrass (*Bromus tectorum*) readily invade disturbed sites in pine forests (Crawford et al., 2001; Sieg et al., 2003). Conversely, few non-native terrestrial vertebrates occur in southwestern pine forests, with the notable exception of domestic livestock (Brown and Davis, 1998; Chambers and Germaine, 2003); however, native mammals have been translocated outside their natural range (Brown, 1984; Hoffmeister, 1986; Davis and Brown, 1988; Brown and Davis, 1998; Chambers and Germaine, 2003). In the Southwest and other regions of North America, "homegrown" non-natives such as the brown-headed cowbird (*Molothrus ater*), bullfrog (*Rana catesbiana*), and eastern cottontail rabbits (*Sylvilagus floridanus*) have had negative effects on native species in the ecosystems into which these species were introduced (Verts and Carraway, 1980; Rosen and Schwalbe, 1995; Cox, 1999).

To investigate the effect of wildfire on non-native and introduced species, we examined the response of the introduced Abert's squirrel (*Sciurus aberti*) and the endemic and critically endangered Mount Graham red squirrel (*Tamiasciurus fremonti grahamensis*) in the Pinaleno Mountains of southeastern Arizona to fire. We assessed effects of wildfire on habitat use of Abert's squirrels and red squirrels by sampling species-specific feeding signs and employing radiotelemetry to reveal use of burned and unburned areas by both species.

Materials and methods

Study System

The Nuttall Complex fire burned ≈12029 ha in the Pinaleno Mountains of southeastern Arizona in summer 2004, including large areas of the upper elevation mixed conifer and spruce fir forests (Koprowski et al., 2006). Historically, mixed conifer forests in the Pinaleno Mountains experienced a low severity fire every 4 to 6 years, and spruce-fir forests experienced infrequent stand-replacement burns every 300 years (Grissino-Mayer et al., 1995). The Nuttall fire burned in a mosaic of severity, with some areas burned severely whereas other areas received less damage.

The Nuttall fire had a significant impact on the critically endangered/endemic Mount Graham red squirrel (*Tamiasciurus fremonti grahamensis*) through direct mortality and habitat destruction (Koprowski et al., 2006; Leonard and Koprowski, 2009). In forests burned by the Nuttall fire a 35% mortality rate of *T. f. grahamensis* was documented (Koprowski et al., 2006).

The non-native population of Abert's squirrels (*Sciurus aberti*) in the Pinalenos is of concern because of the presence of the Mount Graham red squirrel. The dispersal ability and ecological flexibility of Abert's squirrels could pose a threat to native squirrel species in forests with altered fire regimes (Minckley, 1968; Brown, 1984; Davis and Brown, 1988; Hutton et al., 2003; Edelman and Koprowski, 2009). Abert's squirrels were believed to be an obligate of ponderosa pine (*Pinus ponderosa*) for virtually every aspect of life history (Keith, 1965; Patton, 1977; Brown, 1984; Allred and Gaud, 1994; Dodd et al., 2003). However, Abert's squirrels occur in other forest types from pinyon pine (*Pinus edulis*) to mixed conifer stands, through alpine tundra (Reynolds, 1966; Ferner, 1974; Hall, 1981; Cooper, 1987; Edelman and Koprowski, 2005a). Moreover, Abert's squirrels on Mt. Graham live in mixed conifer forests where ponderosa pine is relatively uncommon (Edelman and Koprowski, 2005a,b; Edelman et al., 2005; Edelman and Koprowski, 2006, 2009; Edelman et al., 2009).

The population of red squirrels has decreased in recent years with an estimated population of 550 animals in spring 1998 to 214 in fall 2010 (AZGFD, 2011). Many variables have caused decline of red squirrels including habitat destruction by severe wildfire as well as large scale insect outbreaks and the presence of Abert's squirrels (Minckley, 1968; USDA, 2000; Koprowski et al., 2005, 2006; Sanderson and Koprowski, 2009).

Two study sites (one in low to moderate burned and one unburned) about 1 km apart were in mixed-conifer forests at elevations between 2600 and 2900 m. Common tree species included ponderosa pine, southwestern white pine (*Pinus strobiformis*), corkbark fir (*Abies lasiocarpa* var. *arizonica*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*).

Squirrel Trapping & Telemetry

We used Tomahawk box traps (model 104; Tomahawk Live Trap, Tomahawk WI) baited with unsalted peanuts and peanut butter to trap Abert's squirrels. Once squirrels were captured, we restrained squirrels in a cloth handling cone to reduce stress and mortality (Koprowski, 2002). We had no mortalities during our study and all captured squirrels were successfully weighed, sexed, and marked with ear tags (#1 monel; National Band and Tag Company, Newport KY), stamped with unique numbers, as well as colored plastic ear tags (3/8 in colored plastic washers; National Band and Tag Company, Newport KY) so that individual squirrels could be identified at a distance.

We fitted squirrels with radio collars (SOM-2320; Wildlife Materials International Inc., Murphysboro IL) and homed in to track individuals until we could see the squirrel at a distance. We estimated the size of each collared squirrel's summer/fall home range by obtaining ⩾25 locations per between May and early October in 2006 and 2007. These points were analyzed using the Animal Movements software package in ARC GIS (ESRI 2009). We captured, collared and tracked 20 Abert's squirrels, but only 12 (6 in burned, and 6 in unburned forest) squirrels had ⩾25 locations gathered during daylight hours across the field season. Eight squirrels disappeared during the study before we could obtain at least 25 locations. We used the Animal Movement Analyst Extension (Hooge and Eichenlaub, 2000) for ArcView 3.3 (ESRI 2002) to calculate 50% and 95% fixed-kernel density home range areas and least squares cross validation to estimate the smoothing factor (Worton, 1989; Seaman and Powell, 1996; Wauters et al., 2007). We used the 50% core because 8 of 12 home ranges demonstrated an apparent core at this level; however, the remaining individuals did not show a clear core (Di Pierro et al., 2008). We tracked squirrels to nocturnal nests twice every month. Nests were classified as either a drey or a cavity (Rasmussen et al., 1975; Brown, 1984; Dodd et al., 1998) and vegetation data were gathered with the nest tree as a focal point.

We obtained research permits from Arizona Game and Fish Department, the U.S.D.A. Forest Service, and the U.S. Fish and Wildlife Service. We followed a protocol approved by the University of Arizona Institutional Animal Care and Use Committee and the American Society of Mammalogists Animal Care and Use Guidelines (Sikes et al., 2011).

Vegetation Sampling

To evaluate characteristics of sites used by Abert's squirrels in burned and unburned areas, we established 10-m radius circular vegetation plots centered on Abert's squirrel nests and at 25 random locations centered on a random focal tree. Random locations were generated with ArcView GIS and were located in the field using a hand-held GPS unit; squirrel nests were found by homing on radio-collared squirrels at night after these diurnal animals were sleeping.

Within each plot, we measured a central focal tree, which was selected at random, and recorded species, status (alive or dead), and diameter at breast height We recorded all logs >2 m in length and ⩾20 cm diameter at the large end occurring within the plot; logs highly decayed but >2 m long and ⩾20 cm diameter at the large end were tallied but not measured (Smith and Mannan, 1994). To estimate canopy closure at each circular plot, we used a spherical densiometer mounted on a tripod and quantified cover with the Strickler method of estimating the percent canopy cover (Strickler, 1959). We recorded these measurements at 5 m and 10 m from the center of each plot at each of the four

Table 1 – Percentage of feeding signs (cones and clippings) of endangered Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) and invasive Abert's squirrels (*Sciurus aberti*) by tree species collected from August to November along burned (n=20) and unburned transects (n=20) in the Pinaleno Mountains, Arizona, 2006–2007. Engelmann spruce, corkbark, and white fir were not counted in the cone tally due to a poor cone crop in spruce and ephemeral nature of fir cones.

	Percentage of Feeding Signs			
Treatment	**Burned**		**Unburned**	
Feeding Signs	Abert's	Red	Abert's	Red
Cone Species	(%)	(%)	(%)	(%)
Douglas Fir	86.2	13.8	48.4	51.6
Ponderosa Pine	97.6	2.4	86.1	13.9
SW White Pine	89.5	10.5	82.1	17.9
Clip Species	(%)	(%)	(%)	(%)
Douglas Fir	70	30	100	0
Ponderosa Pine	100	0	100	0
SW White Pine	78.5	21.5	33.3	66.7
Engelmann spruce	100	0	41.4	58.6
Corkbark Fir	0	100	1.6	98.4
White Fir	0	100	100	0

cardinal directions (Smith and Mannan, 1994). The four readings were averaged and used to determine the percentage of canopy cover.

Squirrel Sign Transects

We established ten 250 m long transects and subdivided each transect into five 50 m segments in low to medium burned areas in mixed conifer forest. Also, we established ten transects originating from random locations in unburned mixed-conifer forest as a reference. To determine the location and severity of burned areas, we used USDA Forest Service Burned Areas Emergency Response (BAER) team maps. Direction of each transect was chosen at random. We counted and removed feeding signs within 2.5 m of each transect between August and November in 2006 and 2007 when cones mature and feeding signs accumulate. To increase the chances that we removed all cones from each transect; we traversed each line twice during each visit.

Clipped pine branch tips have been used to estimate populations of Abert's squirrels (Rasmussen et al., 1975; Brown, 1982; Dodd et al., 1998). We conducted sign surveys along burned and unburned transects. We recorded squirrel feeding signs (cones and branch tips) for red and Abert's squirrels to reveal presence and usage patterns of both squirrel species in both forest types. Abert's squirrel signs were easily discernable from red squirrel signs in that branch tips and twigs clipped by Abert's squirrels ($\geqslant$5 cm) are larger than those cut by red squirrels (<5 cm: Rasmussen et al., 1975; Elbroch, 2003). Also, cones eaten by Abert's squirrels have many fibers and scales attached after feeding relative to those eaten by red squirrels (Rasmussen et al., 1975; Elbroch, 2003). Conifer species that are commonly eaten by both species but were not encountered included Engelmann spruce, which did not produce a good cone crop during our study, and corkbark fir and white fir, which could not be sampled due to the deciduous nature of cones that results in early loss of cone scales from cores (Kearney and Peebles, 1960).

Data Analysis

We used a natural log transformation ($\log(x+1)$) to transform transect data to meet assumptions of normality. We used two-sided t-tests to ascertain a difference between the number of red and Abert's squirrel signs found in burn and unburned transects and used a Bonferroni correction for multiple comparisons to adjust the p-value required to achieve significance to p=0.0082. For each species of cone that we detected as feeding signs, we performed a two-way ANOVA by means of a general linear model comparing the number of cones eaten for all transects; we used squirrel species, fire impact, and the interaction as main effects. For clippings, we performed a two-way ANOVA comparing total number of clippings detected to which species of squirrel the feeding sign was attributed to for burned and unburned transects.

Table 2 – Results from the general linear models that compare cone species feeding signs the squirrel species that created the signs, and the number of signs found on burned (n=20) and unburned transects (n=20) in the Pinaleno Mountains, Arizona, 2006–2007. Note the strong interactions between effects for Douglas fir and Ponderosa pine cones.

Cone Species	Main Effect	F	df	P
Total cones	Burned/Unburned	5.51	1.35	0.03
	Squirrel Species	6.69	1.35	0.01
	Interaction	9.8	1.35	0.004
Douglas Fir	Burned/Unburned	0.0056	1.35	0.94
	Squirrel Species	6.02	1.35	0.02
	Interaction	88.06	1.35	<0.0001
Ponderosa Pine	Burned/Unburned	5.93	1.35	0.02
	Squirrel Species	6.29	1.35	0.02
	Interaction	7.84	1.35	0.008
SW White Pine	Burned/Unburned	0.53	1.35	0.47
	Squirrel Species	2.99	1.35	0.09
	Interaction	5.6	1.35	0.02
Clippings	Burned/Unburned	2.62	6.36	0.03
	Squirrel Species	2.28	6.36	0.05
	Interaction	4.56	6.36	0.002

We examined the influence of number of telemetry fixes, sex, and burn status on the size of 50% and 95% fixed kernels within a multi-model selection framework. We developed 8 general linear models (glms) which included a null (intercept only) and global model (k=5) in addition to models that examined the influence of each variable individually and additively. We used R (R Core Team, 2015) to run each model and calculate Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson, 2002) scores. We considered models with the lowest AICc score the top model and models with delta AICc scores$\leqslant$2 as competing.

Results

Feeding signs

We collected 5462 cones from 3 conifer species of which 4028 (74%) were attributed to Abert's squirrels, and 1434 (26%) to red squirrels (Tab. 1). We collected 3448 clipped branch tips of all conifers from all 20 transects. Of these clippings, 2229 (64%) were clipped by Abert's squirrels and 1219 (36%) were attributed to red squirrels (Tab. 1). Burned and unburned transects did not differ in amount of feeding signs as determined by a complete count of all signs (two-sided t-test; t=-0.72; df=20; p=0.47).

When we accounted for species of squirrel (Abert's or red), we found an association between feeding signs, squirrel species, and whether an area was burned or unburned (two-way ANOVA: Tab. 2; Fig. 1). Abert's squirrel signs were 11 times higher on all sign transects than were red squirrel signs (95%CI=3.2 to 38.6: Fig. 1).

Variation in feeding signs by tree species

Southwestern white pine (t=-0.80; df=20; p=0.43) and Douglas-fir cone (t=-0.05; df=20; p=0.95) detections did not differ between burned or unburned sites. However, ponderosa pine cone detections were more common on burned versus unburned sites (t=-2.39; df=20; p=0.03).

Feeding signs for Abert's and red squirrels

The two species of squirrels differed in the species of cone eaten for two of the three conifer species (Fig. 2). Squirrel species and fire impact interacted to explain patterns of feeding signs for each of the three species of tree: Douglas-fir, ponderosa pine, and southwestern white pine (Tab. 2). Douglas-fir cone feeding attributed to Abert's squirrels was two times more abundant and ponderosa pine 17 times more abundant than red squirrels (Fig. 2). Southwestern white pine cones attributed to Abert's squirrels and red squirrels differed slightly (Fig. 2).

We found that the number of clippings attributed to both squirrel species differed in burned and unburned areas (Tab. 2). Abert's squirrel

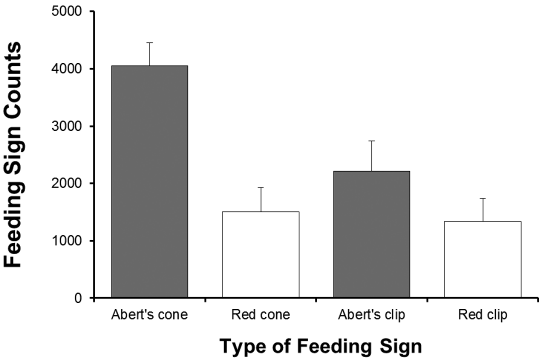

Figure 1 – Total number (n) of feeding signs for invasive Abert's squirrels (grey: *Sciurus aberti*) and endangered Mount Graham red squirrels (white: *Tamiasciurus fremonti grahamensis*) collected; broken down by cones and clippings, Pinaleno Mountains, Arizona. Abert's squirrel signs were 11.08 times higher on all sign transects than red squirrel signs (95%CI=3.18 to 38).

clippings were 3.4 times more abundant in burned areas than in unburned areas. The opposite pattern was true of red squirrels with clippings being 39.4 times lower on burned areas than on unburned areas.

Abert's squirrel feeding signs (cones and clippings) were in greater abundance on burned transects than on unburned transects (t=-2.77; df=20; p=0.012). Burned transects had 0.2 times more Abert's squirrel feeding signs than did unburned transects (95%CI=0.04 to 0.65: Fig. 2). Conversely, red squirrel feeding signs were found in greater abundance on unburned transects than on burned transects (t=4.39; df=20; p<0.0001). Unburned transects had 13.9 times more red squirrel signs than unburned transects (95%CI=4.15 to 46.85: Fig. 2).

Nest Characteristics

We gathered vegetation and site characteristic data on seven Abert's squirrel nests that were found in burned forest and compared these to the 31 random vegetation plots. Species composition of trees was similar between nest and random plots. We found no difference in the diameter at breast height of trees on nest (mean±SE=19.3±0.98 cm) and random plots (mean±SE=17.0±0.47 cm; t=-0.53; df=36; p=0.60) or the number of snags on nest (mean±SE=12.4±4.3 snags) and random plots (mean±SE=17.5±2.1 snags; t=1.06; df=36; p=0.32). We found more logs on random (mean±SE=7.0±0.7 logs/plot) than on nest plots (mean±SE=3.0±1.6 logs/plot: t=3.65; df=36; p=0.0008). Abert's squirrel nest sites in burned areas were similar in canopy cover (mean±SE=79±5.7%) to random (mean±SE=69±2.7%) sites (t=-2.28; df=36; p = 0.033).

Home Range

Mean home range of Abert's squirrels in unburned forest was 1.44 ha±0.54 SE (50% core) and 8.40 ha±2.67 SE (95% kernel home range: Fig. 3). Mean home range in the burned area was 1.02 ha±0.50 SE (50% core) and 5.07 ha±1.82 SE (95% home range: Fig. 3). Home range and core size were not influenced by number of locations with only weak influence of burn status on 95% home ranges; null models received the greatest support with no competing models (Tab. 3).

Discussion

We document a positive response of a non-native species and negative response of a native species to habitat changes resulting from wildfire and suggest that fire must be used judiciously as a restoration tool. Abert's squirrels thrive in mixed conifer forest that is home to the endangered Mt. Graham red squirrel (Hutton et al., 2003; Edelman and Koprowski, 2005a,b, 2006). Non-native Abert's squirrels fed, moved and nested within mixed conifer forest affected by wildfire. Home ranges of Abert's squirrels did not differ between burned and unburned forest. This suggests that conditions created by wildfire did not decrease quality for Abert's squirrels from unburned areas even in heavily burned sites (Blount and Koprowski, 2012). Abert's squirrels selected sites that had more live trees, fewer logs, and more canopy closure than random sites within the burned area, similar to characteristics of mature ponderosa pine forests that Abert's squirrels prefer; characteristics include high basal area, mature trees with interlocking crowns, and an understory with little down and woody debris (Patton and Green, 1970; Patton, 1977; Prather et al., 2006). Transect data on feeding signs also indicated that Abert's squirrels remained in burned areas. In effect, wildfire may be improving habitat for Abert's squirrels in mixed conifer forests by creating preferred structure.

Our findings are troubling for conservation of the critically endangered Mount Graham red squirrel. Red squirrels differ in fire response in different areas of the species' extensive range. In the Pacific Northwest, the density of red squirrels did not differ after application of a low-intensity prescribed burn in mixed conifer forests (Russell et al., 2010). These prescribed burns did not cause significant tree mortality, and left much of the understory intact including down and woody debris (Russell et al., 2010). In burned areas on Mt. Graham where middens were lost, the red squirrel population declined 35% (Koprowski et al., 2006). Areas with low burn severity remain inhabited by Mt. Graham red squirrels (Leonard and Koprowski, 2009; Blount and Koprowski, 2012). Given the different responses of Abert's and red squirrels to a single fire event, it is reasonable to assume Abert's squirrels have an adaptive advantage in their ability exploit burned areas and either remain or move back into them very quickly following fire (Patton, 1984; Dodd et al., 2003; Hutton et al., 2003). The common occurrence of black or dark pelage morphs across the range of Abert's squirrels may be another adaptive advantage of Abert's squirrels occurring in areas blackened by wildfire (Ramey and Nash, 1976; Hall, 1981).

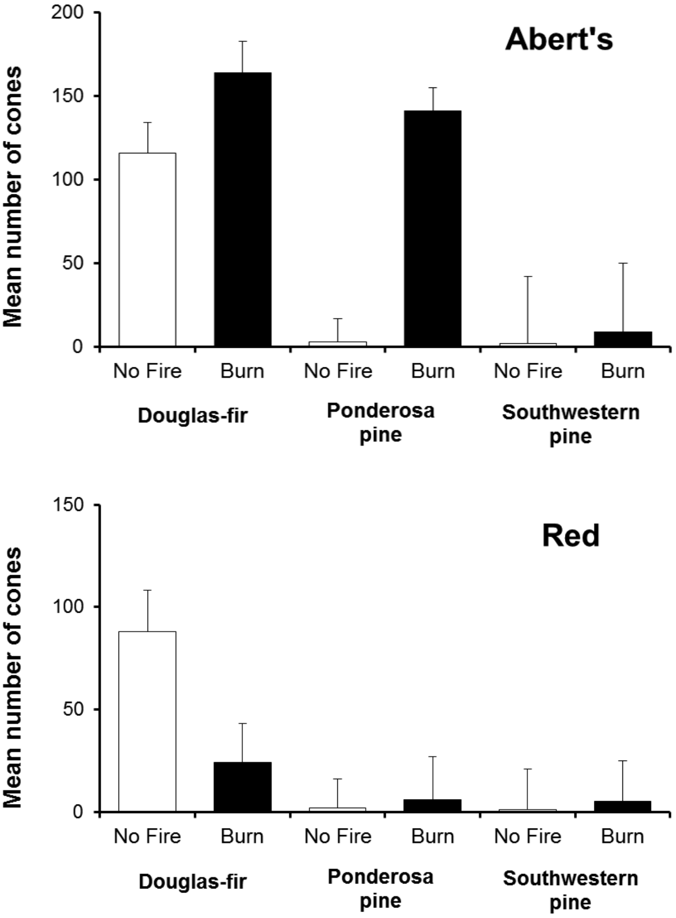

Figure 2 – Mean feeding signs (cones) collected on transects for invasive Abert's squirrels (*Sciurus aberti*) and endangered Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) on burned (dashed) and unburned transects Pinaleno Mountains, Arizona. When cone species were combined, burned transects had 17 times more Abert's squirrel signs than did unburned transects (t20=-2.77; p=0.0119; 95%CI=0.04 to 0.65). Unburned transects had 13.94 times more red squirrel signs than unburned transects (t20=4.39; p<0.0001; 95%CI=4.15 to 46.85).

Table 3 – Model selection results for general linear models to assess influence of number of telemetry points, sex and burn status on 50% and 95% fixed kernel home ranges of 12 Abert's squirrels (*Sciurus aberti*) in burned and unburned forest in the Pinaleno Mountains, Arizona, 2006–2007.

50% Core Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
null (intercept only)	2	43.51	0	0.61	0.61	-19.09
points	3	46.74	3.24	0.12	0.73	-18.87
burn status	3	46.78	3.28	0.12	0.85	-18.89
sex	3	46.98	3.47	0.11	0.96	-18.99
points + burn status	4	50.86	7.35	0.02	0.98	-18.57
sex + points	4	51.32	7.81	0.01	0.99	-18.8
sex + burn status	4	51.43	7.93	0.01	1	-18.86
full (sex + points + burn status)	5	57.14	13.63	0	1	-18.57

Evidence ratio between models "null" and "points": 5.05

95% Home Range Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
null (intercept only)	2	79.76	0	0.53	0.53	-37.21
burn status	3	82.21	2.45	0.16	0.68	-36.61
points	3	82.52	2.75	0.13	0.82	-36.76
sex	3	82.8	3.04	0.12	0.93	-36.9
points + burn status	4	85.36	5.59	0.03	0.97	-35.82
sex + burnstatus	4	86.7	6.94	0.02	0.98	-36.49
sex + points	4	86.73	6.97	0.02	1	-36.51
full (sex + points + burn status)	5	91.58	11.81	0	1	-35.79

Evidence ratio between models "null" and "burn status": 3.41

Mount Graham red squirrels have large home ranges (up to 26.9 ha), and travel farther to nesting sites than other *T. fremonti* subspecies (Leonard and Koprowski, 2009), perhaps increasing the likelihood of negative interactions with Abert's squirrels. Abert's squirrels kleptoparasitize red squirrel middens for cached food stuffs, possibly exacerbating competition for food (Edelman et al., 2005), and may also compete for nests (Merrick et al., 2007; Edelman et al., 2009; Leonard and Koprowski, 2009). Northern goshawks (*Accipiter gentilis*) feed on heavily on Abert's squirrels much more commonly than on red squirrels (Boal and Mannan, 1994; Rogers et al., 2006), perhaps resulting in hyperpredation on the rare endemic (Holt, 1977; Courchamp and Caut, 2006).

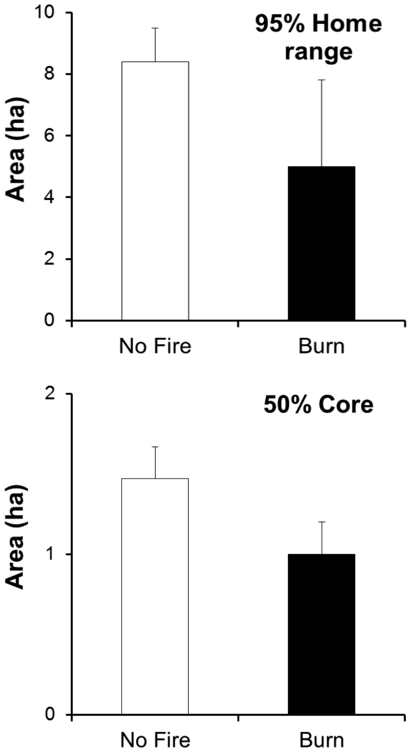

Figure 3 – Home ranges of invasive Abert's squirrels (*Sciurus aberti*), in burned and unburned areas of mixed conifer forest in the Pinaleno Mountains, Arizona. Home ranges as well as cores appear to be smaller in the burn versus unburned areas; however, the relationship is not statistically significant.

Non-native squirrels often negatively impact native squirrel species. In Europe, the spread of eastern gray squirrels (*Sciurus carolinensis*) has caused decline of native Eurasian red squirrels (*Sciurus vulgaris*). Replacement of *S. vulgaris* by *S. carolinensis* is attributed to direct competition between the species as well as disease (Gurnell, 1987; Okubo et al., 1989; Wauters et al., 2000; Bertolino and Genovesi, 2003; Long, 2003; Martinoli et al., 2010; Romeo et al., 2015). In California, spread of non-native *S. carolinensis* and *S. niger* has been simultaneous with range contraction of native western gray squirrels (*S. griseus*; Macdonald et al., 1988; Long, 2003). Our study differs from past research on non-native tree squirrels in that we consider the effects of a stochastic event on a non-native *Sciurus* species and a native species of *Tamiasciurus*. Our results help inform conservation efforts in other parts of North America that have a long history of fire suppression and management (California, the Pacific Northwest, Baja California), where non-native *Sciurus* species come in contact with native *Tamiasciurus*.

Given the tendency of introduced *Sciurus* species to replace native squirrels, managers should consider the potential impact of introduced populations of Abert's squirrels on the native Mt. Graham red squirrel (Minckley, 1968; Rushton et al., 2006; Edelman and Koprowski, 2009). Competition between Abert's squirrels and red squirrels may be in the form of dietary overlap between the two species (Ferner, 1974; Hutton et al., 2003), or in the reduction of cone production in trees due to Abert's squirrel feeding (Soderquist, 1987; Allred et al., 1994). Competitive interactions may be exacerbated by the higher breeding frequency of Abert's squirrels (having more than 1 litter a year) and the similar litter sizes of Abert's squirrels relative to red squirrels (Nash and Seaman, 1977; Pogany and Allred, 1995; Allred and Pogany, 1995; Steele, 1998).

Abert's squirrels use open as well as closed canopy forests (Dodd et al., 1998). We saw habitat flexibility with Abert's squirrels occurring in burned and unburned forests. Management activities such as thinning and prescribed burning must consider the ecological requirements of both squirrel species. Abert's squirrels used burned areas more than red squirrels and red squirrel signs were much more abundant on unburned transects. Silvicultural techniques designed to decrease forest fires often result in more open stands of trees like those encountered on our burn transects (Covington et al., 1997; Mast et al., 1999; Moore et al., 1999; Mast, 2003). As a result these silvicultural techniques might improve habitat for Abert's squirrels, while at the same time degrade red squirrel habitat. A differential response to fire is evidenced in other species of birds and mammals (Friend, 1993; Ballard et al., 2000; Covert-Bratland et al., 2006; Dickson et al., 2009). The potential for adaptive mismatching between other non-native and native species is high and forest managers should account for this ecological consequence in management plans.

Conclusions

The spread and establishment of non-native species is considered to be one of the greatest threats to native and imperiled species worldwide (Flather et al., 1994; Wilcove et al., 1998; Stein et al., 2000; Sieg et al., 2003). We found a difference in the response to fire that seems to favor the non-native over the native species. For the latter half of the 20th Century, humans have implemented treatments in forested ecosystems in order to reduce the likelihood of wildfire and create forest structures that are the legacies of natural disturbances (Swetnam et al., 1999; Cortner, 2003; Oelschlaeger, 2003). It is unclear how these treatments will affect non-native species, especially vertebrates, in these ecosystems (Sieg et al., 2003). Well intentioned management techniques designed to restore ecological balance and decrease the impact of non-native species can have negative effects on native and endangered species. If the complexity of interactions between non-native and native species is not taken into account, the result could be an exacerbation of the problems presented by non-natives (Murphy and Bradfield, 1992; Courchamp et al., 1999; Courchamp and Caut, 2006).

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