

Microhabitat Associations of Northern Flying Squirrels in Burned and Thinned Forest Stands of the Sierra Nevada

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ABSTRACT.—Prescribed burning and mechanical thinning are used to manage fuels within many western North American forest ecosystems, but few studies have examined the relative impacts of these treatments on forest wildlife. We sampled northern flying squirrels (*Glaucomys sabrinus*) and microhabitat variables in burned, thinned and control stands of mixed-conifer forest of the southern Sierra Nevada at the Teakettle Experimental Forest. We used this information to determine the effects of burning and thinning on the microhabitat associations of flying squirrels. Across pretreatment stands, the probability of flying squirrel capture increased with decreasing distance to a perennial creek and increasing litter depth. The probability of flying squirrel capture also was greater with increased canopy cover in thinned stands and increased litter depth in burned stands. Greater canopy cover may provide protection from predators, thicker litter layers may harbor a greater abundance of truffles, a primary food of northern flying squirrels, and creeks may provide squirrels with food sources, drinking water and nest trees. Results from this study underscore the need for more information on the effects of forest management on northern flying squirrels near the southern extent of the species' geographic range.

INTRODUCTION

Decades of fire suppression in western North American forests have greatly increased understory fuels, amplified the frequency of high-intensity catastrophic fires and substantially changed forest stand composition and structure (Agee, 1993; Dickman and Rollinger, 1998). Forest managers use prescribed burning or mechanical thinning to reduce understory fuels and restore these ecosystems to a desired condition. Although prescribed fire and mechanical thinning may reduce the frequency of stand-replacing crown fires and restore stand structure (Biswell, 1989; Allen *et al.*, 2002; Schoennagel *et al.*, 2004), the relative effects of these treatments on wildlife habitat are not well understood for western North American forests.

The northern flying squirrel (*Glaucomys sabrinus*) is an important management species because it is the principal prey of the California spotted owl (*Strix occidentalis occidentalis*; Williams *et al.*, 1992), the northern spotted owl (*S. o. caurina*; Forsman *et al.*, 1991) and

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several mammalian carnivores in western and northern North America (Wells-Gosling and Heaney, 1984). As dispersers of ectomycorrhizal hypogeous fungal sporocarps (truffles), flying squirrels have a key role in the maintenance of mycorrhizal symbiosis and biodiversity (Maser and Maser, 1988). Flying squirrels also are important dispersers of epigeous sporocarps (mushrooms; Thysell *et al.*, 1997) and canopy forage lichens (*Bryoria* spp.; Rosentreter *et al.*, 1997). Recently, northern flying squirrels near the edge of their geographic range have become the focus of forest management plans in Virginia (Ford *et al.*, 2004) and southeastern Alaska (Smith *et al.*, 2004) and a species of management concern in the Sierra Nevada of California (Williams *et al.*, 1992), which is near the southern edge of the geographic range.

Northern flying squirrels have been associated with several microhabitat features in old-growth coniferous forests of western North America. Understory cover in the form of shrubs or logs could provide flying squirrels with protective cover from aerial predators (*e.g.*, owls; Pyare and Longland, 2002). The presence of decayed logs (Pyare and Longland, 2001b), coarse woody debris cover (Lehmkuhl *et al.*, 2004) or perennial creeks (Meyer and North, 2005) may serve as indicators of truffles, the primary food of flying squirrels during snow-free periods (Maser *et al.*, 1978; Pyare and Longland, 2001a). Structural characteristics of the forest understory (*e.g.*, herbaceous plant cover, coarse woody debris volume) or overstory (*e.g.*, canopy cover and complexity, tree density) could increase or decrease locomotion efficiency of flying squirrels between microhabitat patches (Mowrey and Zasada, 1984). However, most of our knowledge of the habitat requirements of the northern flying squirrel is based on studies conducted in undisturbed forest in the relatively mesic northern and central part of its geographic range (*e.g.*, Pacific Northwest). Notably, there is insufficient information for this species in managed stands particularly in the southwestern edge of its range, where habitat requirements may change or become more limiting (Brown, 1984).

Forest management can influence several structural characteristics of the forest overstory and understory related to flying squirrel microhabitat use. Mechanical thinning removes overstory features, such as canopy cover and large trees (Waters and Zabel, 1995; Waltz *et al.*, 2003), but can have less impact on understory features associated with truffles (*e.g.*, litter and decayed logs; Meyer *et al.*, 2005b). Low-intensity prescribed burning removes understory features such as surface litter (Waltz *et al.*, 2003), log cover (Knapp *et al.*, 2005) and herbaceous plant or shrub cover (Meyer *et al.*, 2005b) but typically has less impact on overstory features including canopy cover (Fule *et al.*, 2002; Meyer *et al.*, 2005b). Other structural features, such as snag density, can be reduced by both thinning and burning (Fule *et al.*, 2002). Since thinning and burning have fundamentally different impacts on forest overstory and understory structure, these two management methods should have different effects on microhabitat use by northern flying squirrels.

The purpose of our study was to examine the microhabitat associations of the northern flying squirrel in burned, thinned and undisturbed mixed-conifer stands of the southern Sierra Nevada. We examined microhabitat patterns of flying squirrels both before and following burn and thin treatments in order to understand the factors that influenced microhabitat use in both managed and undisturbed forest stands. In pretreatment stands, we predicted flying squirrels would be associated with microhabitat features that enhanced movement and provided nest sites (*e.g.*, large-diameter trees), potential indicators of truffle availability (*e.g.*, decayed logs, litter) or protection from predators (*e.g.*, distance to shrub cover). In posttreatment stands, we predicted that associations with overstory features (*e.g.*, density of large trees, canopy cover) would be more pronounced in thinned than control

stands and associations with understory features (*e.g.*, shrub cover, litter depth, log volume) would be more pronounced in burned than control stands.

STUDY AREA AND METHODS

We conducted our study at the Teakettle Experimental Forest, located in the southern Sierra Nevada of California. Teakettle Experimental Forest (1800–2400 m elev., 36°58'N latitude and 119°2'W longitude) experiences hot, dry summers and precipitation that falls almost exclusively in the form of snow during the winter (Major, 1990). Mean annual precipitation is 125 cm at 2100 m, and mean summer rainfall (Jun. through Aug.) during 2002–2003 was 0.7 ± 0.7 cm. Dominant trees include white fir (*Abies concolor*), red fir (*A. magnifica*), sugar pine (*Pinus lambertiana*), Jeffrey pine (*P. jeffreyi*) and incense cedar (*Calocedrus decurrens*). Teakettle Experimental Forest is an old-growth forest characterized by a multi-layered canopy and numerous large (>100 cm dbh) trees (many >200 y), snags and decayed logs.

Within Teakettle, 18 replicate 4-ha plots were established, and in 2000–2001 these plots were subjected to burning or mechanical thinning treatments using a full factorial design producing six treatments: (1) light thin only; (2) heavy thin only; (3) light thin followed by burn; (4) heavy thin followed by burn; (5) burn only; and (6) no burn or thin (control). Since we had very few (≤ 1 animal/plot) pretreatment and posttreatment captures of flying squirrels in treatments 2, 3 and 4, we limited our analysis to three treatments (light thin only, burn only and control) where we captured flying squirrels in all pretreatment plots (Fig. 1). All plots were randomly assigned a treatment with one exception; this exception was assigned a control treatment because it contained a significant riparian area around which Forest Service regulations precluded tree harvest. All plots were separated by untreated buffer zones of 50–150 m. The size and spatial placement of plots were determined following variogram and cluster analysis of mapped sample quadrats (North *et al.*, 2002). The distance to the nearest perennial creek was a blocked treatment factor for all selected plots. In Jul. through Sep. of 2000 and Jul.–Aug. of 2001, three plots were experimentally thinned following light-intensity CASPO (California Spotted Owl) guidelines. Under CASPO thinning, no trees >76 cm diameter were harvested and at least 40% of the canopy cover was left in place after harvest. In early Nov. 2001, after the first significant fall rain, three plots were prescribed burned. At this time, average daytime temperature was 13 C and relative humidity ranged 25–70%. The percentage of ground cover burned was approximately 20–40% in burned plots.

Before treatments, nine sample points were established within each plot in a 3×3 grid with 50 m spacing between points and a 50 m buffer from the plot boundary. We sampled northern flying squirrels at each site by attaching a single Tomahawk live trap (model 201; $13 \times 13 \times 40$ cm) to the trunk of a large (>50 cm dbh) tree at each sample point (traps were fixed 1.5 m high). Traps were opened for three consecutive nights in Jun. and 4 nights in Jul. and Aug., for a total of 1134 trap-nights both pretreatment (1999–2000) and posttreatment (2002–03). Traps were baited with a mixture of peanut butter and rolled oats. Traps were checked at dawn, closed in the day and opened at dusk. Animals were marked with individually numbered metal ear tags and body mass, sex, reproductive condition and age class were recorded for all captured squirrels. Research on live animals followed guidelines of the University of California Davis Animal Use and Care Advisory Committee and American Society of Mammalogists (Animal Care and Use Committee, 1998).

We selected all stations where flying squirrels were captured pretreatment ($N = 30$; 1999–2000) and posttreatment ($N = 22$; 2002–03) and a random subset of 30 and 22 stations

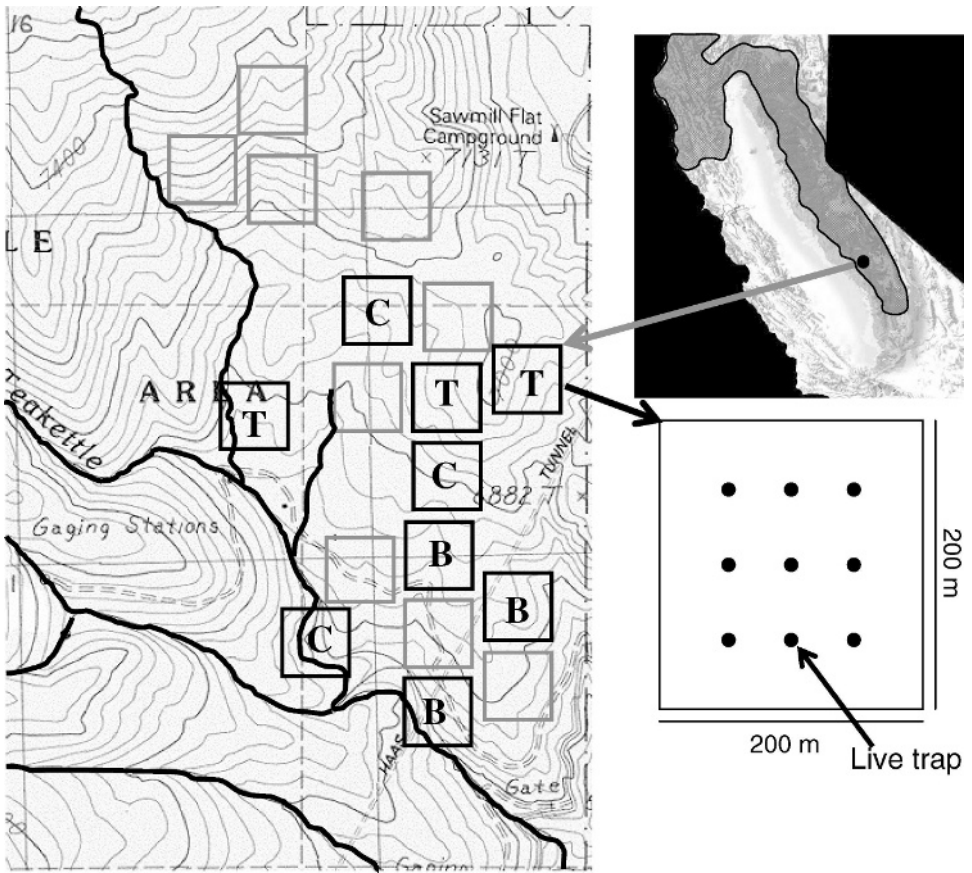


FIG. 1.—Location of northern flying squirrel sampling grids within nine separate 4-ha plots at the Teakettle Experimental Forest (Fresno Co., California). Treatment plots used in this study include control (C), light thin only (T) and burn only (B). Perennial creeks on topographic map are represented by bold sinuous lines. Shaded area on map on upper right indicates the geographic range of the northern flying squirrel in California excepting one isolated subspecies (*Glaucomys sabrinus californicus*) located in the Transverse Ranges of southern California

where northern flying squirrels were not captured pretreatment and posttreatment, respectively. In Jul. 2000 (pretreatment) and 2003 (posttreatment), we collected data on nine microhabitat variables within a 12.6 m radius of each station (0.05 ha plot): (1) total basal area of large (>50 cm dbh) trees, (2) canopy cover (%), (3) total number of large (>50 cm dbh) snags, (4) total volume (m³/ha) of heavily decayed logs (decay classes 3–5; Cline *et al.*, 1980), (5) litter depth (cm), (6) distance to shrub cover (m), (7) herbaceous plant cover (%), (8) aspect and (9) distance to perennial creek (m). We chose these variables based on published studies of northern flying squirrels (Carey, 1995; Waters and Zabel, 1995; Carey *et al.*, 1999; Cotton and Parker, 2000; Pyare and Longland, 2001a, 2002; Bakker and Hastings, 2002; Ford *et al.*, 2004; Smith *et al.*, 2004; Meyer *et al.*, 2005a) and truffles (Amaranthus *et al.*, 1994; Lehmkuhl *et al.*, 2004). In each 12.6 m plot, the dbh of all trees and snags >50 cm dbh were measured. Canopy cover was estimated using

hemispherical photographs that were analyzed using Gap Light Analyzer 2.0 (Simon Fraser University, Burnaby, British Columbia, Canada) software. Aspect was determined using a compass, and litter depth was estimated at three points set 1 m from the trap station at 0, 120 and 240° directions.

We used Akaike's Information Criterion (AIC) to reduce our original set of nine pretreatment and seven posttreatment (excluding aspect, distance to creek) microhabitat variables to avoid model over-fitting (Burnham and Anderson, 1998). We removed aspect and creek distance from our posttreatment analysis because these variables were not expected to change following treatments. We used a corrected AIC (AIC_c) for model selection, since sample sizes were small relative to the number of model parameters (Burnham and Anderson, 1998). Once a suitable model was selected, we used logistic regression to relate all selected microhabitat variables to the presence or absence of flying squirrels. We did not conduct separate analyses for each season due to the small number of Jun. 2003 captures. For each significant parameter in the logistic regression model, we calculated odds ratios and their confidence intervals based on a Quasi-Newton estimation that approximates the second-order derivatives of the retrospective loss function (Statistica, 2003). The odds-ratio estimates were interpreted as the odds of capturing a flying squirrel given a one unit change in a microhabitat parameter (*e.g.*, litter depth) after being adjusted for the effects of other microhabitat parameters in the model (Smith *et al.*, 2004). Odds ratios provide information regarding the relative importance of microhabitat parameters on squirrel occurrence and do not imply cause and effect relationships between these variables. We used a sensitivity analysis of each treatment type to evaluate the performance of the reduced logistic regression model and assess model accuracy in successfully predicting captures of flying squirrels among trap stations (Hosmer and Lemeshow, 2000). We tested the assumption of multicollinearity by examining correlations between independent factors and calculating the Variance Inflation Factor for each significant microhabitat factor. All statistics were conducted with Statistica 6.1 (Statsoft Inc., Tulsa, Oklahoma) and an α level of 0.05.

RESULTS

Before treatments, we captured 45 animals at 30 stations in 1999–2000 (21 Male, 24 Female). Of the 30 flying squirrel capture stations, 9 were in prethinned, 11 were in preburned and 10 were in control plots. Across all pretreatment plots, creek distance and litter depth were the microhabitat variables that best explained the occurrence of flying squirrels ($AIC_c = 49.059$, $\chi^2 = 21.150$, $df = 2$, $P < 0.001$; Table 1). A one unit increase in distance from a creek on a \log_2 scale decreased the odds of squirrel capture by a factor of 2. A single cm increase in litter depth increased the odds of capture of a squirrel by a factor of 3.5. The proportion of capture and noncapture trap stations that were correctly classified by the AIC_c selected logistic regression model was 78% and 87%, respectively.

Following treatments, we captured 34 squirrels at 22 stations in 2002–03 (13 Male, 21 Female). Of the 22 flying squirrel capture stations, 7 were in thinned, 6 were in burned and 9 were in control plots. The number of pretreatment capture stations where squirrels were absent during posttreatment sampling was 5, 5 and 3 stations in thinned, burned and control plots, respectively. In thinned plots, canopy cover best explained the occurrence of flying squirrels ($AIC_c = 15.988$, $\chi^2 = 8.420$, $df = 1$, $P = 0.004$). One percent increase in canopy cover increased the odds of squirrel capture by a factor of 1.5 in thinned stands (Table 1). In thinned plots, the proportion of capture and noncapture stations that were correctly classified by the reduced logistic regression model was 100% and 86%, respectively.

TABLE 1.—Results of logistic regression model of microhabitat variables associated with northern flying squirrel occurrence in pretreatment ($N = 9$ plots) and posttreatment (thinned, burned; $N = 3$ plots) stands at Teakettle Experimental Forest (2002–03)

Parameter	Estimate (SE)	χ^2	Odds ratio ^a (95% CI)	P
Pretreatment – across plots				
Constant	2.518 (2.257)	2.249	—	0.265
Creek	-0.672 (0.229)	8.621	0.5 (0.3–0.8)	0.003
Litter depth	1.240 (0.624)	3.950	3.5 (1.0–12.2)	0.047
Posttreatment – thinned				
Constant	-44.571 (23.058)	4.037	—	0.046
Canopy cover	0.559 (0.276)	4.145	1.5 (0.9–2.5)	0.042
Posttreatment – burned				
Constant	-3.089 (1.662)	3.454	—	0.063
Litter depth	1.236 (0.612)	4.082	3.4 (0.9–13.1)	0.043

^a Effect of a one unit increase of creek distance (\log_2 scale), litter depth or canopy cover on the probability of capture

In burned plots, litter depth best explained flying squirrel presence ($AIC_c = 4.800$, $\chi^2 = 16.636$, $df = 1$, $P < 0.001$), and a 1 cm increase in litter depth increased the odds of squirrel capture by a factor of 3.4. The selected logistic regression model correctly classified 86% and 100%, of capture and noncapture stations in burned plots, respectively. In control plots, there was no model of microhabitat variables that was significantly associated with flying squirrel occurrence.

DISCUSSION

Since our study was limited in scope and sampling effort, our results do not represent robust quantitative estimates of capture probabilities of northern flying squirrels among microhabitats in managed forest stands of the Sierra Nevada. Our results should be viewed with caution and represent an exploratory experimental study documenting qualitative patterns of flying squirrel microhabitat use. Despite these limitations, northern flying squirrel microhabitat use was associated with canopy cover in thinned but not control plots, although there was no association with other overstory features (*e.g.*, large-diameter trees or snags) in pretreatment or posttreatment stands. In unharvested forest stands, canopy cover did not influence flying squirrel capture. In contrast, in thinned stands where canopy cover was significantly reduced, the probability of flying squirrel capture increased with greater canopy cover. Greater canopy cover in thinned plots may have provided greater protection from predators in the foliage of the upper canopy (Pyare and Longland, 2002). Greater vegetation cover also reduces understory nighttime lunar illumination that can limit predation risk from owls (Kotler *et al.*, 1991; Longland and Price, 1991). Greater canopy cover increased the probability of flying squirrel capture in one of three old-growth red-fir stands of the northern Sierra Nevada (Pyare and Longland, 2002).

Also in accordance with our predictions, flying squirrels were positively associated with an understory feature, litter depth, in burned but not control plots. Flying squirrels prefer microhabitats where truffles are present (Pyare and Longland, 2002), and microhabitat features associated with truffle abundance (*e.g.*, litter depth, presence of decayed logs; Amaranthus *et al.*, 1994) also may be important for explaining microhabitat use by flying

squirrels (Pyare and Longland, 2001b). Although there was no association between flying squirrels and log volume in our study, there was a positive association between flying squirrel presence and litter depth both in pretreatment and postburn analyses, indicating that flying squirrels may have preferentially foraged near patches of deeper litter in order to obtain truffles. At Teakettle, truffle abundance was associated with treatment plots that had thicker litter layers (Meyer *et al.*, 2005b). There was no relationship between northern flying squirrels and coarse woody debris (including soil substrate) in red-fir stands of the northern Sierra Nevada (Pyare and Longland, 2002), possibly because litter was spatially homogenous relative to our heterogeneous mixed-conifer stands; litter at Teakettle varied from thick organic layers in closed canopy forest to extensive patches of bare ground in open canopy gaps (North *et al.*, 2005).

Several factors could account for the association of flying squirrels with creeks. Forest stands near creeks had a higher frequency, biomass and species richness of truffles (100% frequency of occurrence in flying squirrel diets in our study) than neighboring upland stands at our study site (Meyer and North, 2005). Flying squirrels at our study site used a higher proportion of nest trees located <150 m from a perennial creek (Meyer *et al.*, 2005a). Creeks are a primary source of drinking water for flying squirrels and other small mammals, particularly in the drier summer months. In addition, creeks at our site often supported a higher density of red fir (North *et al.*, 2002) that, in turn, harbors a greater abundance of *Bryoria fremontii* (T. Rambo, pers. comm.), an important winter forage and nesting material for northern flying squirrels (Hayward and Rosentreter, 1994; Rosentreter *et al.*, 1997). Availability of secondary food items, such as fruits and seeds, also may be more abundant in riparian habitats (Doyle, 1990).

Northern flying squirrels may be attracted to creeks in other arid (southern) parts of its geographic range (*e.g.*, southwestern Utah, Transverse Ranges of California). In northern and central California, northern flying squirrels appear to live in close proximity to rivers and streams (Zeiner *et al.*, 1990). In southwestern Utah, northern flying squirrels are common in stream-bottom stands of white fir (in addition to upland Engelmann spruce forest; Musser, 1961). Pyare and Longland (2002) found no association between flying squirrels and creeks in the northern Sierra Nevada of California, but their study did not sample for streams outside a relatively small 7 m radius of flying squirrel capture locations. Interestingly, flying squirrel densities in the central Cascade Range of Oregon were lower in riparian habitat whereas reproduction and body masses were higher (Doyle, 1990), suggesting that riparian habitat acted as higher-quality source habitat for flying squirrels than nearby upland habitat.

Current management policies in National Forests of the Sierra Nevada use prescribed burning and mechanical thinning to reduce fuels and wildfire risk (SNFPA, 2001). Prescribed burning may reduce fine fuels associated with litter but also reduce the number of truffle-rich microhabitat patches (Meyer *et al.*, 2005b) that directly influence flying squirrel microhabitat use (Pyare and Longland, 2002). These short-term post-fire changes are expected to change rapidly as litter accumulates beneath the forest canopy (Agee *et al.*, 1977), providing organic material for truffle-producing ectomycorrhizae (Meyer *et al.*, 2005b) and foraging flying squirrels. In contrast, mechanical thinning that removes a significant portion of the forest overstory may increase the amount of dry understorey fuels that leads to increased fire risk (van Wagtenonk, 1996) as well as reduce the number of microhabitat patches with sufficient canopy cover for flying squirrels. These post-thinning reductions in canopy cover and flying squirrel microhabitat are expected to recover more gradually in Sierra Nevada forests, as regeneration processes required to fill

in overstory gaps often require several decades (Helms and Tappeiner, 1996). Forest management treatments that retain patches of minimum canopy ($\geq 75\%$) and litter (≥ 2 cm depth) cover over time may be sufficient for maintaining key habitat for northern flying squirrels. Future long-term (> 2 y) studies are needed to examine whether our recommendations are adequate for the management of northern flying squirrels in forests of California's Sierra Nevada.

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