Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat

Sanjay Pyare and William S. Longland

Abstract: During 1997–1998, we investigated the influence of both the relative abundance of truffles, preferred food items, and microhabitat structure on the occurrence of northern flying squirrels (*Glaucomys sabrinus* Shaw) in old-growth forest habitat of the Sierra Nevada Range, U.S.A. Following live-trapping sessions, we searched the forest floor for truffle diggings and sampled the soil for truffles. Diggings were more abundant where flying squirrels were captured, suggesting squirrels were active near areas of the forest floor where truffles had recently been excavated. The frequency of sampling plots with truffles was higher where squirrels were captured, further suggesting preferences for microhabitats where truffles were more abundant. We also measured 15 microhabitat variables at trap stations to evaluate the influence of aboveground microhabitat characteristics on squirrel occurrence. Results indicated that flying squirrels preferred microhabitats with understory cover, which may minimize predation from aerial predators like spotted owls (*Strix occidentalis* Merriam). Neither abundance of coarse woody debris, a feature conducive to fungal growth, nor the abundance of potential nesting sites (i.e., snags) measurably influenced squirrel occurrence. While various aboveground forest-microhabitat characteristics affect the use of old-growth forests by flying squirrels, these animals refine their use of these forests based on fine-scale changes in the availability of a highly preferred and ephemeral food item.

Résumé : Durant les années 1997 et 1998, nous avons investigué l'influence de l'abondance relative des truffes, la nourriture préférée, et la structure du microhabitat sur l'occurrence de l'écureuil volant (*Glaucomys sabrinus* Shaw) dans l'habitat des vieilles forêts du plateau de la Sierra Nevada, aux États-Unis. Suite à des sessions de piégeage d'animaux vivants, nous avons examiné le parterre forestier pour y déceler des indices de fouilles à la recherche de truffes et échantillonné le sol pour la présence de truffes. Il y avait plus de fouilles où des écureuils volants avaient été capturés, indiquant que les écureuils étaient actifs près des endroits où des truffes avaient récemment été excavées dans le parterre forestier. La fréquence des parcelles échantillons avec des truffes était plus élevée où des écureuils avaient été capturés indiquant également les préférences pour les microhabitats où les truffes sont les plus abondantes. Nous avons aussi mesuré 15 variables relatives au microhabitat où étaient placées les trappes pour évaluer l'influence des caractéristiques épigées du microhabitat sur l'occurrence des écureuils. Les résultats indiquent que les écureuils volants préfèrent les microhabitats avec un couvert en sous-étage qui réduit au minimum la prédation par les prédateurs aériens comme la chouette tachetée (*Strix occidentalis* Merriam). Ni l'abondance des débris ligneux grossiers, un élément qui favorise la croissance des champignons, ni l'abondance de sites potentiels de nidification (i.e., les chicots) influencent de façon mesurable l'occurrence des écureuils. Tandis que diverses caractéristiques aériennes des microhabitats forestiers affectent l'utilisation des vieilles forêts par les écureuils, ces animaux raffinent leur utilisation de ces forêts sur la base de changements à petite échelle dans la disponibilité de nourriture hautement prisée et éphémère.

[Traduit par la Rédaction]

Introduction

Detailed studies of habitat use by forest-dwelling animals provide a basic understanding of the ecological features that are particularly important for the conservation of forest biodiversity. For instance, specific habitat features associated with the occurrence of spotted owls (*Strix occidentalis* Merriam) were among the most important types of biological information incorporated into the forest conservation plan of the Pacific Northwest region, U.S.A. (Thomas et al. 1990; Carey et al. 1992; FEMAT 1993). Studies that document habitat use by other species, such as small mammals, will continue to provide valuable data that can be incorporated into comprehensive forest conservation plans addressing not just a single species but the needs of an entire suite of species (Carey and Johnson 1995; Bull et al. 1997).

Northern flying squirrels (*Glaucomys sabrinus* Shaw), the primary prey of spotted owls in coniferous habitats of the western United States (Carey et. al. 1992; Williams et al. 1992; Zabel et al. 1995; White 1996), are particularly important for forest conservation. Flying squirrels play an impor-

S. Pyare.[1,2] Ecology, Evolution, and Conservation Biology Program, University of Nevada, Reno, NV 89557, U.S.A.
W.S. Longland. Ecology, Evolution, and Conservation Biology Program, University of Nevada, Reno, NV 89557, and USDA Agricultural Research Service, 920 Valley Road, Reno, NV 89512, U.S.A.

[1]Corresponding author (e-mail: pyare@blissnet.com).
[2]Present address: Denver Zoological Foundation, P.O. Box 20377, Juneau, AK 99802, U.S.A.

DOI: 10.1139/X02-002

tant ecological role by dispersing the spores of ectomycorrhizal fungi in their feces to the forest soil, where fungal spores form symbiotic relationships with the roots of conifers (Kotter and Farentinos 1984; Maser et al. 1985; Maser and Maser 1988; Pirozynski and Malloch 1988; Johnson 1996; Claridge et al. 1997). Despite their importance, few studies have yet revealed the habitat associations of this species.

Flying squirrels predominantly consume the fruiting bodies of hypogeous fungi, or truffles, which occur 5–15 below the surface of the forest floor (Brink and Dean 1966; Maser et al. 1985; Hall 1991; Waters and Zabel 1995; Zabel and Waters 1997; Rosentreter et al. 1997; Cazares et al. 1999; Pyare and Longland 2001*a*). Truffles are ecto-mycorrhizal symbionts with the roots of trees and hence typically occur within 2 m of the bases of trees (Fogel 1976). As in other regions, hypogeous fungi appear to be among the most frequent food items in flying squirrel diets in the Sierra Nevada Range during snow-free periods (Hall 1991; Pyare and Longland 2001*a*). This empirical evidence, coupled with observations that truffles are relatively scarce, concealed below ground, and heterogeneously distributed, suggest a high degree of dietary specialization. Among the many factors that might influence habitat use by flying squirrels, the spatial pattern of truffle distribution may therefore be especially relevant. Waters and Zabel (1995) and Cazares et al. (1999) found a broad correlation between flying squirrel abundance and abundance of truffles among stands with different timber-harvest regimes. Within stands, however, there exists little information about the fine-scale relationship between flying-squirrel occurrence and the local abundance of truffles.

Aside from fungal distribution, a variety of forest microhabitat characteristics may influence the spatial pattern of habitat use by this species. Flying squirrels may be influenced by the presence of specific features that provide refuge from predators, serve as indicators of the relative availability of food, and enhance or limit movement. When foraging for truffles on the forest floor, flying squirrels may be particularly vulnerable to predation and, hence, prefer areas that are located near protective cover, such as understory vegetation (Lima et al. 1985; Lima and Valone 1986; Newman and Caraco 1987; Newman et al. 1988). Coarse woody debris, in addition to potentially providing protective cover, may serve as a moisture-rich reservoir for fungi (Maser and Trappe 1984; Amaranthus et al. 1994; Clarkson and Mills 1994), particularly in more xeric forest habitats such as those found in the Sierra Nevada mountains, U.S.A. Thus, decaying organic debris, such as a log, could be a specific aboveground microhabitat feature that flying squirrels associate with truffles. In captivity, for instance, flying squirrels tend to forage near logs for buried truffles (Pyare and Longland 2001*b*). In addition, given that flying squirrels move primarily by gliding between trees and infrequently move along the forest floor (Mowrey and Zasada 1984), structural aspects of forest microhabitats could constrain the utility of gliding behavior in the forest overstory (Thorington and Heaney 1981; Mowrey and Zasada 1984; Hokkanen 1992; Ims 1995). For instance, microhabitats with high densities of trees (e.g., restricted gliding space), large gaps in the forest canopy (e.g., excessive distance between trees), or

small diameter trees (e.g., poor "landing pads") may be avoided by these animals.

The purpose of this study was to investigate the use of old-growth forest habitat by flying squirrels. Specific objectives were to determine (*i*) whether the within-stand occurrences of flying squirrels were influenced by the fine-scale distribution of food (truffles) and (*ii*) which forest microhabitat characteristics also influence the occurrence of flying squirrels.

Materials and methods

The general protocol of this study was to livetrap flying squirrels using standardized methodology (Hayes et al. 1994) and sample and compare truffle abundance and microhabitat characteristics among trap stations where flying squirrels were and were not captured. Truffles fruit at heterogeneous temporal scales and persist only 2–3 weeks in the soil (Fogel 1976; Luoma et al. 1991). Thus, truffles were sampled immediately following each live-trapping session (described below). In contrast, microhabitat characteristics (e.g., tree size, abundance of coarse woody debris) were sampled once at the conclusion of all live-trapping effort, since these did not change appreciably over the duration of this 3-year study.

Study sites
We selected three, old-growth forest stands (Blackwood Canyon, Upper Ward Canyon, and Lower Ward Canyon) within the western region of the Lake Tahoe Basin Management Unit (Toiyabe National Forest, Placer County, California, U.S.A). Stands were 10–15 ha in size, separated by 2–7 km, and located on upper elevation (2200–2400 m), north-facing slopes. Red fir (*Abies magnifica* A. Murray) was the most common conifer in both the overstory and understory, and white fir (*Abies concolor* (Gord. & Glend.) Lindl.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and western white pine (*Pinus monticola* Dougl.) were infrequent components of the overstory and virtually absent in the understory (Oostings and Billings 1943). These sites were virgin timber stands with old (>250 years), large-diameter (>2 m diameter at breast height (DBH)) live trees, snags, and downed logs; they were devoid of stumps or logging roads. The matrix that surrounded study sites, however, was a combination of second-growth habitat that exhibited copious evidence of past logging activity (>25 years from present), and small tracts (0.25–1 ha) of remnant old-growth habitat. The study area was located in a subalpine zone in which snow remained on the ground 8 months of the year and, thus, was characterized by a short growing season. Snow persisted on the ground at study sites 3 weeks longer during spring of 1998 than spring of 1997.

Live trapping
We livetrapped flying squirrels in the Upper Ward and Lower Ward sites in 1997 and all three stands in 1998. In each stand, squirrels were trapped during two sessions: spring (May–June) and fall (August–September). The timing of these sessions corresponded to the phenology of fungal fruiting, which peaks in spring (beginning just after snowmelt) and then again in late summer – early autumn

(Hayes et al. 1986; Luoma et al. 1991; North et al. 1997). Based on an expected 3–5% live-trapping success of flying squirrels (Rosenberg et al. 1995), we estimated that a session consisting of four or five consecutive trap-nights would yield 12–25 captures per stand. This provided a sufficient sampling size of trap stations around which we would subsequently sample truffles and microhabitat characteristics (described below).

In each stand, we livetrapped flying squirrels on a 9 × 12 grid with 25 m intertrap spacing. We attached one Tomahawk live trap (18 × 18 × 40 cm) horizontally 2 m high on the trunk of the largest tree within 3 m of each grid point (Hayes et al. 1994). In each trap, we included a nest box (the bottom 40 cm of a 2-gallon milk carton; 1 gallon = 3.785 L) and cotton stuffing as nesting material. Each trap was baited approximately 1.5 h before dark with a small ball of peanut butter – rolled oats mixture and checked at 06:30–07:00 the following morning. Captured animals were removed from the trap, marked in one ear with a numbered, Monel-metal tag (National Band and Tag Co., U.S.A.), weighed, and released.

Animal digging and truffle surveys

After each trapping session, we randomly selected seven trap stations at which flying squirrels were captured (herein "capture-yes") and seven at which they were not captured ("capture-no"). For the selection procedure, we allowed trap stations where the same animal was captured to be potentially selected, because animals were rarely caught more than once per session. To survey truffles and microhabitat characteristics near these selected trap stations, we delineated a 7 m radius (154 m²) habitat-sampling plot around the tree to which each trap was attached. We selected plots of this size to maintain independence between any two adjacent trap stations (11-m separation distance between plots).

Firstly, we searched the forest floor within a 3-m distance from the bases of all trees (>20 cm DBH) that occurred within the 7 m radius habitat-sampling plot for evidence that mammals had excavated truffles. We counted the total number of these diggings in each of these habitat-sampling plots. These excavations resemble small pits in the upper forest soil layers (Waters et al. 1994), yet differ from other types of soil disturbances, like seed-cache retrieval sites, excavations for plant roots or bulbs, and burrow entrances of fossorial animals, because truffle diggings are typically deeper yet terminal. Fragments of partially consumed truffles occasionally remained near these diggings as further evidence that these diggings were associated with mycophagous activity.

Secondly, within the plots used for animal-digging surveys, we established three 1-m² circular truffle sampling plots at random distances (0–3 m) from the bases of randomly selected trees (>20 cm DBH). We dug up truffles within each truffle-sampling plot using a three-tine, metal rake to sift gently through the litter and organic soil layers (15–20 cm deep). Excavated truffles were placed into waxed paper bags and subsequently identified to the genus level. We superficially restored all soil layers, and marked the center of each truffle-sampling plot with a white, 10 cm long garden stake. We then recorded the frequency of truffle plots that contained truffles at each trap station (i.e., 0–3). We chose the frequency of truffle plots, rather than the actual number of truffles, as the best estimator of relative abundance given the inaccuracy in estimating the abundance of organisms that tend to clump inconsistently, like truffles (Bigwood and Inouye 1988).

Microhabitat sampling

At the conclusion of trapping, we described microhabitat characteristics around a subset of trap stations in each of three stands. We randomly selected 15 capture-yes trap stations and 15 capture-no stations. Within 7 m radius sampling plots centered on the trap station, we collected data on 15 forest-microhabitat variables (Table 1). We selected these microhabitat variables based on published studies of northern flying squirrels, southern flying squirrels (*Glaucomys volans* L.), and mycophagous small mammals (Mowrey and Zasada 1984; Wells-Gosling and Heaney 1984; Rosenberg and Anthony 1991; Clarkson and Mills 1994; Mills 1994; Waters and Zabel 1995; Bull et al. 1997).

We divided each habitat-sampling plot into quadrants, the axes of which were oriented along cardinal directions. To evaluate the influence of overstory characteristics on flying-squirrel occurrence, we recorded the following: (*i*) the total number of trees (>10 cm DBH) in the plot; (*ii*) distance (m) from the trap station to the nearest-neighboring tree in each quadrant; (*iii*) DBH (cm) of the tree to which the trap was attached and its nearest neighbor in each quadrant; (4) percentage of overstory cover in each quadrant 3 m from the trap station using a forest canopy densiometer (Forestry Suppliers, model C); and (*v*) whether an overstory gap was created in the forest canopy above the plot resulting from a fallen tree (Gilmore and Gates 1985). To evaluate the influence of potential nesting sites, we recorded the following: (*vi*) total number of snags (i.e., potential nesting sites) in the plot (Cowan 1936; Thomas et al. 1979); (*vii*) DBH of the largest snag (>10 cm DBH) in each quadrant; and (*viii*) total number of witches' brooms (dwarf mistletoe, *Arceuthobium* spp., or rust fungi, *Chrysomyxa* spp.; Bull et al. 1997), which are also used by northern flying squirrels as nesting sites (Mowrey and Zasada 1984; Waters and Zabel 1995). To evaluate the influence of coarse woody debris, we measured the following: (*ix*) total number of logs (>10 cm DBH) in the plot; (*x*) DBH of the largest log in each quadrant; and (*xi*) number of "class 3", or heavily decayed, logs in the plot (Bull et al. 1997). These types of logs are moist and nutrient-rich microhabitat features that are especially important for fruiting of hypogeous fungi (Maser and Trappe 1984; Amaranthus et al. 1994; Clarkson and Mills 1994). We also classified the substrate feature that physiognomically dominated each quadrant as rocky, bare soil, small litter, or coarse woody debris (*xii*). We also measured the distance from the trap station to understory cover <2 m height in each quadrant (*xiii*), and documented whether a stream, which typically was overgrown with *Alnus* spp., fell within the habitat-sampling plot (*xiv*). Finally, to account for the influence of microtopography on flying squirrel occurrence, we measured aspect using a compass (*xv*).

Statistical analysis

For analysis of truffle-foraging data, we used two-way ANOVA to analyze the relationship between two predictor variables, season (fall or spring) and capture status (capture-

Table 1. Fifteen microhabitat characteristics that were sampled within each 7-m radius (154 m^2) habitat-sampling plot in three stands in the Lake Tahoe Basin, 1997–1998.

Microhabitat variable	Description
(1) No. of trees	Total no. of trees (>10 cm DBH)
(2) Intertree distance	Mean distance (m) from center tree to nearest neighbor
(3) Total tree DBH	Sum (DBH) of nearest neighbors to centre tree
(4) Overstory cover	Mean percentage canopy cover
(5) Gap	Whether or not a fallen tree resulted in a gap in the canopy above the plot
(6) No. of snags	Total no. of snags (>10 cm DBH)
(7) Total snag DBH	Sum (DBH) for largest snag in each quadrant
(8) Brooms	No. of witches' brooms
(9) No. of logs	Total no. of down logs (>10 cm DBH)
(10) Total log DBH	Sum (DBH) of largest log in each quadrant
(11) Total class 3 DBH	Sum (DBH) of largest class 3 log in each quadrant
(12) Substrate	No. of quadrants dominated by coarse woody debris
(13) Distance to cover	Mean distance to understory cover
(14) Stream	Presence or absence of stream within 7 m
(15) Aspect	Direction of slope

Note: See text for more precise methods of data collection for each variable.

yes or capture-no), and both response variables: the number of truffle diggings observed per trap station and the frequency of truffle sampling plots containing truffles per trap station.

Prior to evaluating the influence of forest microhabitat variables on flying-squirrel occurrence, we reduced the original set of 15 microhabitat variables in three ways to avoid model over-fitting and increase interpretability (Hosmer and Lemeshow 1989). First, using the binary response variable, capture status, we performed univariate analyses (t tests for continuous variables and chi-square contingency tests for categorical variables) of individual microhabitat variables and only included variables in the subsequent multivariate analysis that based on these univariate tests, yielded $p < 0.5$. Secondly, because microhabitat variables may have been nonindependent, we used a Pearson's correlation matrix to reveal correlation coefficients >0.50 between pairs of variables and eliminated the variable that yielded the higher probability in the univariate test procedure described above. Finally, we used a stepwise logistic regression procedure (SYSTAT version 7.0) with forward variable selection and a tolerance value of 0.15 to arrive at the best subset of microhabitat related predictor variables (Hosmer and Lemeshow 1989). For this subset of variables, we reran the multivariate logistic regression analysis, this time including any significant pairwise interaction terms, to interpret the relative influence of different microhabitat variables on the binary response variable, capture status.

Results

For analyses related to truffle foraging, differences between sessions, stands, and years were insignificant ($p > 0.10$), so we pooled these data. Thus, we ultimately performed comparisons between a total of 70 capture-yes and 70 capture-no trap stations (i.e., 7 stations of each type during 2 trap sessions in each of 2 stands in 1997 and in each of 3 stands in 1998). Fifty-eight different animals were captured at the 70 capture-yes trap stations selected for the truf-

fle surveys. Truffle diggings occurred more frequently near capture-yes trap stations than capture-no stations ($F = 6.84$, df = 1, 134, $p < 0.01$; Fig. 1). There was also a seasonal effect on the total number of truffle diggings observed (spring > fall; $F = 7.58$, df = 1, 134, $p < 0.01$). Interaction between flying squirrel occurrence and season, however, was negligible ($F = 1.14$, df = 1, 134, $p = 0.29$). In addition, frequency of plots containing truffles was significantly greater near capture-yes trap stations ($F = 11.97$, df = 1, 134, $p < 0.001$; Fig. 2). Although frequency of plots in which truffles were harvested were significantly greater in spring than fall collecting periods ($F = 12.93$, df = 1, 134, $p < 0.001$ for mean number of plots), interaction terms involving season and flying-squirrel occurrence were not significant ($F = 2.44$, df = 1, 134, $p = 0.12$).

For microhabitat analyses, we compared 15 capture-yes stations to 15 capture-no trap stations for individual stands (i.e., these data were not pooled). Sixty-three different animals were trapped at the 45 capture-yes trap stations selected for microhabitat analyses. Among the 15 microhabitat variables measured, logistic regression indicated that a model including two variables, proximity to understory cover (distance to cover) and the cumulative size of the largest trees in each of four quadrants (total tree DBH), best explained the occurrence of flying squirrels in the Upper Ward site (Table 2). Understory cover was significantly closer ($t = 2.506$, df = 28, $p = 0.018$) to capture-yes trap stations than capture-no trap stations. Total tree DBH was significantly less at capture-yes stations ($t = 2.109$, df = 27.2, $p = 0.044$). At the Blackwood site, distance to cover and proximity to nearest neighboring tree (Table 2, intertree distance) were significant variables in the model that best explained flying squirrel occurrence. Understory cover was significantly closer ($t = 4.350$, df = 28, $p < 0.001$) and the nearest tree was located significantly closer ($t = 3.045$, df = 23.7, $p = 0.006$) to capture-yes trap stations than capture-no stations. Finally, distance to cover, the percentage of canopy cover (Table 2, overstory cover), and presence of a canopy gap were all included in the best model for the Lower Ward hab-

Fig. 1. Comparison of the number of truffle diggings between capture-yes and capture-no trap stations. Truffle diggings were sampled around 140 total trap stations: 7 of each type of trap station in spring and autumn in 2 stands (1997) and in 3 stands (1998). Error bars are SEs.
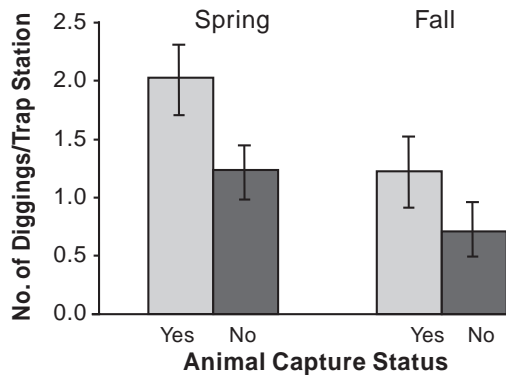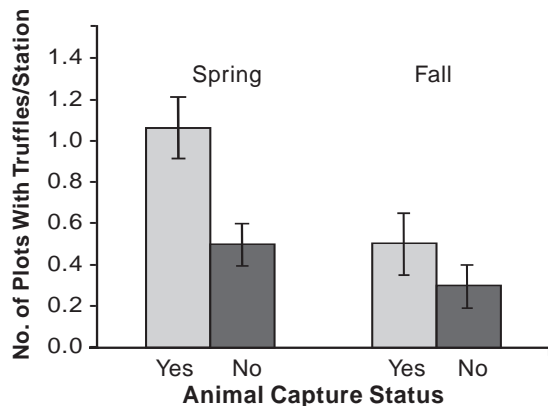

Fig. 2. Comparison of the number of truffle-sampling plots (from a total of three) that contained truffles between capture-yes and capture-no trap stations. Truffles were sampled around 140 total trap stations: 7 of each type of trap station in spring and autumn in 2 stands (1997) and in 3 stands (1998). Error bars are SEs.

itat data. In addition, there appeared to be a strong interaction between distance to cover and gap in determining flying squirrel occurrence in Lower Ward. Univariate analysis, however, indicated that distance to cover was not significantly different ($t = 1.662$, df = 1.082, $p = 0.110$) between the two types of trap stations, whereas overstory cover was significantly greater ($t = 2.587$, df = 22.2, $p = 0.017$), and gaps were less likely to occur ($\chi^2 = 4.658$, df = 1, $p = 0.031$) near capture-yes than capture-no trap stations.

The strength of each of these models can be evaluated by testing their accuracy in successfully predicting whether or not a flying squirrel was likely to be captured at a trap station based on microhabitat data (Gilmore and Gates 1985; Hosmer and Lemeshow 1989). Using the reduced models derived by stepwise regression (Table 2), jackknife-classification procedures successfully predicted 63, 76, and 78% of the trap stations at which animals were captured in Upper Ward, Blackwood, and Lower Ward sites, respectively.

Discussion

This study reveals important predictors of flying squirrel occurrence using two different sampling protocols, suggest-

ing that habitat use of flying squirrels may be hierarchical. At a relatively static level, structural microhabitat variables like understory cover, tree density, and canopy cover explained 63–78% of the variation in flying squirrel occurrence. At a more dynamic level, the concordance between flying squirrel occurrence and truffle fruiting sites further suggests that flying squirrels may have been "tracking" short-term changes in the spatial pattern of fungal fruiting.

Understory cover, which was significantly closer to trap stations where flying squirrels were captured (distance 4.36 ± 1.26 m (mean $\pm$ SE); $n = 45$) than where not captured (6.20 ± 0.93 m; $n = 45$), was the only influential predictor variable common to all three stands. Both Doyle (1990) and Rosenberg and Anthony (1991) found similar evidence that shrub cover was an important factor in explaining either density or trapping success of flying squirrels, although Rosenberg and Anthony speculated that their finding may have been a statistical artifact of model over-fitting. This was not the case in this study, because we reduced the original set of 15 variables by eliminating both highly correlated and highly insignificant variables prior to application of multivariate models. Furthermore, given that correlation analysis failed to reveal any significant relationship between understory cover and any of the 14 other microhabitat variables, it appears that flying squirrels were responding to the proximity of cover rather than some other microhabitat variable we measured.

Understory cover could not have provided permanent shelter, because flying squirrels are known to nest well above the forest floor in cavities or witches' brooms (Harestad 1990; Mowrey and Zasada 1984). It is also unlikely that the dominant types of understory vegetation at these study sites (deciduous shrubs like *Alnus* and *Ribes* spp.) provided significant sources of truffles. Although *Alnus* are known to be associated with alder false truffles (*Alpova* spp.), we rarely found the spores of this truffle genus in fecal samples from flying squirrels captured at these study sites (Pyare and Longland 2001*a*), nor did we find *Alpova* in truffle-sampling plots during this study (unpublished data). Instead, flying squirrels may have utilized microhabitats characterized by abundant understory vegetation to obtain other food items such as insects, seeds, berries, seedlings, and mushrooms, although these items were relatively uncommon in their diets (Pyare and Longland 2001*a*).

Preferences for microhabitats in which both truffles and vegetation cover occur, however, are not necessarily incompatible. Animals may not be able to simultaneously forage in more open understories (i.e., where truffles occur) and decrease risk of predation (Gilliam and Fraser 1987; Newman and Caraco 1987; Lima et al. 1985). Thus, preference for nearby vegetation cover could simply reflect a strategy in which animals attempt to minimize vulnerability by foraging near refugia. Although we lacked observations of flying squirrels when exposed to a predator, this strategy implies that flying squirrels use a "rush for cover" tactic to avoid a predator (Endler 1989). Alternatively, because flying squirrels have been observed to consume food in locations other than where collected (Mowrey and Zasada 1984; Thysell et al. 1997), cover may simply provide a safe microhabitat nearby in which to manipulate and consume food items.

Table 2. Results of logistic regression analyses performed on reduced model in each stand.

Parameter	Estimate	SE	t	Odds ratio	95% CI Upper	Lower	p
Upper Ward							
Constant	4.050	1.693	2.390	—	—	—	0.017
Total tree DBH	–0.011	0.007	–1.550	0.989	1.003	0.976	0.120*
Distance to cover	–0.523	0.274	–1.912	0.592	1.013	0.346	0.056*
Blackwood							
Constant	7.319	2.928	2.500	—	—	—	0.012
Intertree distance	–0.846	0.454	1.865	0.429	1.044	0.176	0.062*
Distance to cover	–0.922	0.375	2.458	0.398	0.830	0.191	0.014*
Lower Ward							
Constant	32.161	13.837	2.324	—	—	—	0.020
Distance to cover	–3.019	1.697	1.779	20.467	569.840	0.735	0.075
Overstory cover	0.224	0.092	2.436	1.251	1.497	1.045	0.015*
Gap	21.946	9.840	2.230	3.3×10^9	8.1×10^{17}	14.290	0.026*
Distance to cover × gap	–4.023	1.979	2.033	0.018	0.866	0.000	0.042

Note: Unless included in analyses below, all possible pairwise interaction terms were nonsignificant ($p > 0.05$). Regression probability values that are marked with an asterisk indicate that univariate comparison resulted in statistically significant ($p < 0.05$) differences between capture-yes and capture-no trap stations. CI, confidence interval.

This may be particularly relevant for evading an aerial predator like the spotted owl, which ambushes prey in open areas and appears to be a specialist on flying squirrels (Carey et al. 1992; Williams et al. 1992; Zabel et al. 1995).

In general, the availability of cover has significant implications for predation rates and microhabitat preferences of many small mammals when exposed to aerial predators (Leger et al. 1983; Kotler et al. 1988; Longland and Price 1991). In addition, distance to cover influences many parameters related to sciurid foraging behavior, including food-handling times, vigilance rates, and food intake rates (Lima et al. 1985; Lima and Valone 1986; Newman et al. 1988). Therefore, it seems conceivable that spatial use of habitat by flying squirrels could be influenced by the relative availability of protective cover as well.

Two additional variables that influenced habitat use in the Blackwood and Lower Ward sites were "mean distance to the nearest-neighbor tree" and "mean percentage of canopy cover", respectively. Trees where animals were captured more frequently had nearest-neighbor trees located closer (3.76 ± 1.64 m; $n = 45$) than trees at which animals were not captured (5.28 ± 1.03 m; $n = 45$). Although flying squirrels at these sites are capable of gliding linear horizontal distances >50 m (personal observation), shorter glides may be advantageous, perhaps because vulnerability to aerial predators like spotted owls may be reduced (Carey et al. 1992; Williams et al. 1992; Zabel et al. 1995) and energetic costs associated with longer climbs (i.e., higher launching sites) may be minimized (Thorington and Heaney 1981; Scheibe et al. 1996). Regression analyses also indicated that greater overstory cover was associated with flying squirrel occurrence, although we could not detect significant differences between trapping locations using simpler univariate tests (74.24 ± 7.20% where captured versus 64.51 ± 12.68% where not captured; $n = 45$ for each category). Greater overstory cover may provide greater protection for animals moving on upper tree limbs in the canopy and, hence, may also reflect a strategy to limit exposure to predators.

All microhabitat characteristics relating to the amount of coarse woody debris were unimportant in explaining habitat use by flying squirrels. We found this surprising for two reasons. Firstly, similar to other investigators that have found a general association between coarse woody debris and truffles (Amaranthus et al. 1994; Clarkson and Mills 1994; Waters et al. 1997; Carey et al. 1999), in a related study at these same sites we, too, found that coarse woody debris was more prevalent where we found truffles: truffle sampling plots in which we found truffles were both closer to logs and more frequently composed of cubical rotting woody debris than plots in which we found no truffles (Pyare and Longland 2001b). Despite that, truffles are ectomycorrhizal and, thus, more likely to be associated with live hosts and not decaying substrates, like saprophytic fungi are, coarse woody debris may provide moist microsites for truffle fruiting, especially in the xeric conditions characteristic of these Sierra Nevada forests. Secondly, in seminatural cage experiments, captive flying squirrels exhibited a propensity to forage near logs for buried truffles (Pyare and Longland 2001b). Thus, we expected the relative availability of decaying matter on the forest floor to influence animal occurrence, but we found no evidence for such a relationship. One possible explanation for the absence of this relationship is that coarse woody debris was so abundant in these old-growth stands that it was simply not a limiting resource. Alternatively, perhaps simple counts of surface logs do not accurately measure the abundance of the appropriate types of coarse woody debris that are conducive for fungal growth. We crudely classified logs into three general stages of decay, and perhaps, this does not reflect the complex relationship that may exist between coarse woody debris and hypogeous fungi (Amaranthus et al. 1994; Bull et al. 1997). Yet another explanation for the lack of this relationship is that truffles are ephemeral, and hence, few logs may have been associated with truffles at the time of sampling.

The capture probability of flying squirrels within a stand (ca. 5–20 ha) is notoriously heterogeneous and varies sub-

stantially within the time frame of a few months (Rosenberg et al. 1995; this study; and personal observations in southeastern Alaska). Perhaps not coincidentally, it is also well known that different species of truffles fruit at distinct periods of the year, and they persist only ephemerally (<3 weeks). During this rapid period of maturation and subsequent decay, truffles usually emit pungent and fruity odors that attract small mammals (Talou et al. 1990; Donaldson and Stoddart 1994; Pyare and Longland 2001*b*). Thus, the pattern of habitat use by flying squirrels may reflect their ability to use olfaction to "track" the spatial and temporal dynamics of fungal fruiting. Here, we present two types of indirect evidence suggesting that short-term and fine-scale changes in truffle distribution may contribute to this heterogeneity in flying squirrel occurrence.

Firstly, the correlation between flying squirrel occurrence and animal diggings indicates that flying squirrels were active where truffles had recently fruited and been consumed. Although many small mammals may consume truffles (Fogel and Trappe 1978; Malajzuk et al. 1987), northern flying squirrels most commonly consumed truffles at these sites (Pyare and Longland 2001*a*). Thus, the same individuals that we captured in nearby traps may have made a large portion of these animal diggings. Secondly, using a truffle sampling protocol that measured the relative abundance of truffles at the time of animal live trapping, we found strong evidence that flying squirrels were exploiting microhabitats in which truffle fruiting sites were abundant and avoiding areas that were relatively depauperate of truffles.

Both our truffle sampling and microhabitat sampling procedures independently revealed factors that may explain habitat use by flying squirrels, suggesting these animals may use a complementary set of factors in old-growth habitat. Zollner et al. (2000) revealed different sets of microhabitat associations for different behaviors (e.g., browsing, resting, and defecating) of swamp rabbits (*Sylvilagus aquaticus* Buchman), and recommend stratifying microhabitat analyses according to specific behaviors prior to analyses. Hence, although in our case we had no information regarding squirrel behavior at the time of capture, the intensive truffle sampling procedure may have revealed associations while animals were actively foraging, whereas the broader microhabitat sampling revealed associations more relevant to movements via gliding or while on the ground. A slightly different interpretation is that the habitat use of flying squirrels may be organized hierarchically (Johnson 1980). The fact that both types of sampling regimes independently revealed the influence of variables in determining flying squirrel occurrence, despite differences in temporal scale, reinforces this interpretation. Hence, we conclude that although the variation in local occurrence of flying squirrels is most probably related to fine-scale changes in fungal distribution, certain aboveground microhabitat characteristics, such as the availability of understory cover, may limit where these animals choose fungi as a food resource.

Acknowledgments

References

Amaranthus, M., Trappe, J.M., Bednar, L., and Arthur, D. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Can. J. For. Res. **24**: 2157–2165.

Bigwood, D.W., and Inouye, D.W. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology, **69**: 497–507.

Brink, C.H., and Dean, F.D. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. J. Wildl. Manage. **30**: 503–511.

Bull, E.L., Parks, C.G., and Torgerson, T.R. 1997. Trees and logs important to wildlife in the interior Columbia River basin. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-391.

Carey, A.B., and Johnson, M.L. 1995. Small mammals in managed, young, and old-growth forests. Ecol. Appl. **5**: 336–352.

Carey, A.B., Horton, S.H., and Boswell, B.L. 1992. Northern spotted owls: influence of prey base and landscape character. Ecol. Monogr. **62**: 223–250.

Carey, A.B., Kershner, J., Biswell, B., and Dominguez de Toledo, L. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildl. Monogr. **142**: 1–71.

Cazares, E., Luoma, D.L., Amaranthus, M.P., Chambers, C.L., and Lehmkuhl, J.F. 1999. Interaction of fungal sporocarp production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade Range. Northwest Sci. **73**: 64–76.

Claridge, A.W., Tanton, M.T., Seebeck, J.H., Cork, S.J., and Cunningham, R.B. 1997. Establishment of ectomycorrhizae on the roots of two species of *Eucalyptus* from fungal spores contained in the faeces of the long nosed potoroos (*Potorous tridactylus*). Aust. J. Ecol. **17**: 207–217.

Clarkson, D.A., and Mills, L.S. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Sci. **68**: 259–265.

Cowan, I.M. 1936. Nesting habitat of the flying squirrel *Glaucomys sabrinus*. J. Mammal. **17**: 58–60.

Donaldson, R., and Stoddart, M. 1994. Detection of hypogeous fungi by Tasmanian bettong. J. Chem. Ecol. **20**: 1201–1207.

Doyle, A.T. 1990. Use of riparian and upland habitats by small mammals. J. Mammal. **71**: 14–23.

Endler, J.A. 1989. Interactions between predators and prey. *In* Behavioral ecology. *Edited by* J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford, U.K. pp. 169–196.

Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocap phenology in a western Oregon Douglas-fir stand. Can. J. Bot. **54**: 1152–1162.

Fogel, R., and Trappe, J.M. 1978. Fungus consumption (mycophagy) by small mammals. Northwest Sci. **52**: 1–31.

Forest Ecosystem Management Assessment Team (FEMAT). 1993. Forest ecosystem management: an ecological, economic, and social assessment. FEMAT, Washington, D.C. Rep. 1993-793-071.

Gilliam, J.F., and Fraser, D.F. 1987. Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows. Ecology, **68**: 1227–1253.

Gilmore, R.M., and Gates J.E. 1985. Habitat use by the southern flying squirrel at a hemlock – northern hardwood ecotone. J. Wildl. Manage. **49**: 703–710.

Hall, D.S. 1991. Diet of the northern flying squirrel at Sagenhen Creek, California. J. Mammal. **72**: 615–617.

Harestad, A.S. 1990. Nest site selection by northern flying squirrels and Douglas squirrels. Northwest. Nat. **71**: 43–45.

Hayes, J.P., Cross, S., and McIntire, P.W. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. Northwest Sci. **60**: 250–257.

Hayes, J.P., Horvath, E.G., and Hounihan, P. 1994. Securing live-traps to small-diameter trees for studies of arboreal mammals. Northwest. Nat. **75**: 31–33.

Hokkanen, H., Tormala, T., and Vuorinen, H. 1992. Decline of the flying squirrel *Pteromys volans* populations in Finland. Biol. Conserv. **23**: 273–284.

Hosmer, D.W., and Lemeshow, S. 1989. Applied logistic regression. John Wiley & Sons, Inc., New York.

Ims, R.A. 1995. Movement patterns related to spatial structures. *In* Mosaic landscapes and ecological processes. *Edited by* L. Hansson, L. Fahrig, and G. Merriam. Chapman & Hall, London. pp. 85–109.

Johnson, C.N. 1996. Interactions between mammals and ectomycorrhizal fungi. Trends Ecol. Evol. **11**: 503–507.

Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, **61**: 65–71.

Kotler, B.P., Brown, J.S., Smith, R.J., and Wortz, W.O., II. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. Oikos, **53**: 145–152.

Kotter, M.M., and Farentinos, R.C. 1984. Formulation of ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. Mycologia, **76**: 758–760.

Leger, P.W., Owing, D.H., and Cross, R.C. 1983. Behavioral ecology of time allocation in ground squirrels (*Spermophilus beecheyi*). J. Comp. Psychol. **97**: 283–291.

Lima, S.L., and Valone, T.J. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. Anim. Behav. **34**: 536–544.

Lima, S.L., Valone, T.J., and Caraco, T. 1985. Foraging efficiency – predation risk tradeoff in the grey squirrel. Anim. Behav. **33**: 155–165.

Longland, W.S., and Price, M.V. 1991. Direct observations of owls and heteromyid rodents: can predation explain microhabitat use. Ecology, **72**: 2261–2273.

Luoma, D.L., Frenkel, R.E., and Trappe. J.M. 1991. Fruiting of hypogeous fungi in Oregon Douglas fir forests: seasonal and habitat variation. Mycologia, **83**: 335–353.

Malajczuk, N., Trappe, J.M., and Molina, R. 1987. Interrelationships among some ectomycorrhizal trees, hypogeous fungi, and small mammals: western Australian and northwestern American parallels. Aust. J. Ecol. **12**: 53–55.

Maser, C., and Maser, Z. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Nat. **48**: 358–369.

Maser, C., and Trappe, J.M. 1984. The unseen world of the fallen tree. U.S. For. Serv. Gen. Tech. Rep. PNW-164.

Maser, Z., Maser, C., and Trappe, J.M. 1985. Food habits of the northern flying squirrel in Oregon. Can. J. Zool. **63**: 1084–1088.

Maser, C., Maser, Z., Witt, J.W., and Hunt, G. 1986. The northern flying squirrel: a mycophagist in Oregon. Can. J. Zool. **64**: 2086–2089.

Mills, L.S. 1994. Edge effects and isolation: red-backed voles on forest remnants. Conserv. Biol. **9**: 395–403.

Mowrey, R.A., and Zasada, J.C. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. *In* Fish and Wildlife Relationships in Old-Growth Forests: Proceedings of a Symposium. *Edited by* W.R. Meehan, T.R. Merrell, and T.A. Hansley. Bookmasters, Ashland, Ohio. pp. 351–356.

Newman, J.A, and Caraco, T. 1987. Foraging, predation hazard, and patch use in grey squirrels. Anim. Behav. **35**: 1804–1813.

Newman, J.A., Recer, G.M., Zwicker, S.M., and Caraco, T. 1988. Effects of predation hazard on foraging constraints: patch use strategies in grey squirrels. Oikos, **53**: 93–97.

North, M., Trappe, J.M., and Franklin, J. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology, **78**: 1543–1554.

Oostings, H.J., and Billings, W.D. 1943. The red-fir forest of the Sierra Nevada: *Abietum magnificae*. Ecol. Monogr. **13**: 260–274.

Pirozynski, K.A., and Malloch, D.W. 1988. Seeds, spores, and stomachs: coevolution in seed dispersal mutualisms. *In* Coevolution of fungi with plants and animals. *Edited by* K.A. Pirozynski and D.L. Hawksworth. Academic Press, London. pp. 196–211.

Pyare, S., and Longland, W.S. 2001*a*. Patterns of ectomycorrhizal fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. J. Mammal. **82**: 681–689.

Pyare, S., and Longland, W.S. 2001*b*. Mechanisms of truffle detection by northern flying squirrels. Can. J. Zool. **79**: 1007–1015.

Rosenberg, D.K., and Anthony, R.G. 1991. Characteristics of northern flying squirrel populations in young second-growth and old-growth forests in western Oregon. Can. J. Zool. **70**: 161–166.

Rosenberg, D.K., Overton, W.S., and Anthony, R.G. 1995. Estimation of animal abundances when capture probabilities are low and heterogeneous. J. Wildl. Manage. **59**: 252–261.

Rosentreter, R., Hayward, G.D., and Wicklow-Howard, M. 1997. Northern flying squirrel seasonal food habits in the interior conifer forests of central Idaho, USA. Northwest Sci. **71**: 97–101.

Scheibe, J.S., Hendershott, A.J., Robins, J.H., and Essner, R. 1996. Abstract presented at the meeting of the Amercian Society of Mammalogists, N. Dak.

Talou, T., Gaset, A., Delmas, M., Kulifaj, M., and Montant, C. 1990. Dimethyl sulfide: the secret for black truffle hunting by animals? Mycol. Res. **94**: 277–278.

Thomas, J.W., Anderson, R.G., Maser, C., and Bull, E.L. 1979. Snags. *In* Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. *Edited by* J.W. Thomas. U.S. Department of Agriculture, Forest Service, Portland, Oreg. pp. 60–77.

Thomas, J.W., Forsman, E.D., Lint, J.B., Meslow, E.C., Noon, B.R., and Verner, J. 1990. A conservation plan for the northern spotted owl. U.S. Department of Agriculture, Forest Service, U.S. Fish and Wildlife Service, and National Parks Service, and Bureau of Land Management. Portland, Oreg.

Thorington, R.W., and Heaney, L.R. 1981. Body proportions and gliding adaptations of flying squirrels (Petauristinae). J. Mammal. **62**: 101–114.

Thysell, D.R., Villa, L.J., and Carey, A.B. 1997. Observations of northern flying squirrel feeding behavior: use of non-truffle food items. Northwest. Nat. **78**: 87–92.

Waters, J.W., and Zabel, C.J. 1995. Northern flying squirrel densities in fir forests of northeastern California. J. Wildl. Manage. **59**: 858–866.

Waters, J.W., McKelvey, K.S., Zabel, C.J., and Oliver, W.W. 1994. The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi. Can. J. For. Res. **24**: 1516–1522.

Waters, J.W., McKelvey, K.S., Luoma, D., and Zabel, C.J. 1997. Truffle production in old-growth and mature fir stands in northeastern California. For. Ecol. Manage. **96**: 155–166.

Wells-Gosling, N., and Heaney, L.R. 1984. *Glaucomys sabrinus*. Mamm. Species 229. pp. 1–8.

White, K. 1996. Comparison of fledgling success and sizes of prey consumed by spotted owls in northwestern California. J. Raptor Res. **30**: 234–236.

Williams, D.F., Verner, J., Sakai, H.F., and Waters, J.R. 1992. General biology of major prey species of the California spotted owl.

In The California spotted owl: a technical assessment of its current status. U.S. For. Serv. Gen. Tech. Rep. PSW-GTR-133. pp. 83–111.

Zabel, C.J., and Waters, J.R. 1997. Food preferences of captive northern flying squirrels from the Lassen National Forest in northeastern California. Northwest Sci. **71**: 103–107.

Zabel, C.J., McKelvey, K.S., and Ward, J.P., Jr. 1995. Influence of primary prey on home range size and habitat use patterns in northern spotted owls *(Strix occidentalis caurina)*. Can. J. Zool. **73**: 433–439.

Zollner, P.A., Smith, W.P., and Brennan, L.A. 2000. Microhabitat characteristics of sites used by swamp rabbits (*Sylvilagus aquaticus*). Wildl. Soc. Bull. **28**: 1003–1011.