

ABUNDANCES OF SMALL MAMMALS IN FIR FORESTS IN NORTHEASTERN CALIFORNIA

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We compared abundances of seven species of forest rodents among three types of fir (*Abies concolor* and *A. magnifica*) forest: unlogged old-growth, unlogged mature, and shelterwood-logged old-growth. Small mammals were livetrapped during summers 1991 and 1992 in four grids within each type of forest; grids were located in the Lassen National Forest in northeastern California. Shelterwood-logged forests had been logged 6-7 years previously. Differences in capture rates between unlogged, old-growth and shelterwood-logged, old-growth forests suggest that logging led to significant increases in populations of golden-mantled ground squirrels (*Spermophilus lateralis*), yellow pine chipmunks (*Tamias amoenus*), and lodgepole chipmunks (*Tamias speciosus*) but may have led to reduced populations of western red-backed voles (*Clethrionomys californicus*). Capture rates of Douglas' squirrels (*Tamiasciurus douglasii*), Allen's chipmunks (*Tamias senex*), and deer mice (*Peromyscus maniculatus*) did not differ significantly between unlogged and shelterwood-logged forests. Capture rate of *T. douglasii* was significantly greater in mature forests than in old-growth forests in 1992, but we did not detect significant differences between old-growth and mature forests for the other six species. These results illustrate how opening of the canopy and disturbance of the forest floor can lead to significant changes in patterns of abundance of forest rodents.

Key words: *Clethrionomys californicus*, *Peromyscus maniculatus*, *Spermophilus lateralis*, *Tamias amoenus*, *Tamias senex*, *Tamias speciosus*, *Tamiasciurus douglasii*, logging, small mammals

Four silvicultural systems traditionally have been recognized for harvesting and regenerating forests (Smith, 1986): clearcut, seed-tree, shelterwood, and selection. Numerous studies have evaluated effects of clearcutting on populations of small mammals (Corn and Bury, 1991; Gashwiler, 1959, 1970; Gunther et al., 1983; Hooven and Black, 1976; Kirkland, 1977; Raphael, 1988; Sims and Buckner, 1973; Tevis, 1956a; Van Home, 1981), but published studies on effects of seed-tree, shelterwood, and selection harvests are lacking. Losses of food and cover associated with harvested trees and disturbance of the forest floor, as well as increases in food and cover associated with increased production of herbaceous vegetation and shrubs following disturbance, typically lead to significant

changes in abundances of small mammals following clearcutting. Traditional clearcutting, in which all or nearly all live trees are cut, is being used less frequently on public forests in the western United States. Silvicultural practices in which live trees and other forest components such as large snags and logs are retained at the time of harvest are being used more frequently (Franklin et al., 1997).

In a previous paper, we compared densities of northern flying squirrels (*Glaucomys sabrinus*) among three types of fir (*Abies*) forest in northeastern California (Waters and Zabel, 1995): unlogged old-growth, unlogged mature, and shelterwood-logged old-growth. In the shelterwood silvicultural system, the mature stand is removed in at least two cuts, so that regen-

eration of the new stand occurs under a partial forest canopy (Smith, 1986). In this paper, we compare abundances among the three types of forest of seven additional species of small mammals captured during the study of flying squirrels: golden-mantled ground squirrel (*Spermophilus lateralis*), lodgepole chipmunk (*Tamias speciosus*), yellow pine chipmunk (*T. amoenus*), Allen's chipmunk (*T. senex*), Douglas' squirrel (*Tamiasciurus douglasii*), deer mouse (*Peromyscus maniculatus*), and western red-backed vole (*Clethrionomys californicus*). Our objectives were to evaluate effects of these shelterwood harvests on abundances of forest rodents and determine differences in abundances of forest rodents between old-growth and mature fir forests.

MATERIALS AND METHODS

Study area.—The three types of forest in which we sampled (unlogged old-growth, unlogged mature, and shelterwood-logged old-growth) were located within and around Swain Mountain Experimental Forest, Plumas Co., in the Lassen National Forest in northeastern California. This area lies at the southern extent of the Cascade Range, and soils are of volcanic origin. The unlogged, old-growth forest type (hereafter, old-growth forests) was characterized by forests with multi-layered canopies and numerous large, decayed logs, stumps, and snags. Dense patches of small firs occurred in the understory, but herbaceous plants (e.g., *Pyrola picta*, *Viola purpurea*, and *Corallorhiza maculata*) and shrubs (primarily *Chrysolepis sempervirens*) were uncommon. The organic soil included layers of litter and humus and large pieces of buried, decayed wood. Based on counts of growth rings on cut stumps in shelterwood-logged areas within Swain Mountain Experimental Forest, we estimated that the majority of codominant and dominant trees in the old-growth and shelterwood-logged forest types were 200–400 years old.

The unlogged, mature forest type (hereafter, mature forests) was characterized by even-aged forests that grew back after stand-replacement wildfires. Few residual logs, snags, or trees from the previous forest were present (this forest type

was referred to as young by Waters and Zabel, 1995). These forests were dense and had closed canopies, and virtually no herbaceous plants or shrubs were present in the understory. Old, dead stems on the forest floor indicated that shrubs were abundant for some period of time after wildfires occurred. The organic soil included layers of litter and humus. Based on counts of growth rings from cored trees, we estimated that most codominant and dominant trees in this forest type were 80–100 years old.

The shelterwood-logged, old-growth forest type (hereafter, shelterwood-logged forests) was located in Swain Mountain Experimental Forest. The experimental forest was dominated by old-growth forests until 1984–1985 when large areas were logged to study natural regeneration rates using the shelterwood silvicultural system. These timber harvests left a park-like stand structure of widely spaced, large-diameter trees. The ground was intentionally disturbed to expose mineral soil for natural regeneration. Tractors with brush blades were used to remove logs and disturb soils, and slash was piled and burned or broadcast burned. At the time of our study, grasses, forbs, and low shrubs (primarily *Ceanothus cordulatus* and *Ribes roezlii*) had become established, and the little organic soil present on the forest floor primarily was characterized by undecomposed litter.

Sampling.—We selected four areas within each of the three types of forest that were similar in elevation and composition of trees, ≥ 150 m apart, relatively homogeneous, and sufficiently large. These restrictions precluded random selection from a larger number of potential areas, so we do not attempt to make inferences beyond the areas studied. Elevations of the 12 grids ranged from ca. 1,800 to 2,000 m. Each area was dominated by white fir (*Abies concolor*) or a mixture of white and red fir (*A. magnifica*). Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and lodgepole pine (*P. contorta*) occurred at low densities in some stands. The four areas in shelterwood-logged forests were located within Swain Mountain Experimental Forest. Three of the four areas in the old-growth forest type were located in residual stands of old-growth within the experimental forest, and the fourth area was located 6 km southwest of the experimental forest. One of the areas in the mature forest type was located in Swain Mountain Experimental

Forest, and three were located 8 km southwest of the experimental forest.

Within each of the 12 areas we established an 11.5-13.4-ha, rectangular-to-square grid (7 by 13, 8 by 13, 8 by 12, 9 by 11, or 10 by 10) with 40-m spacing between grid points (size and shape of grids varied depending on size and shape of stands). Each grid was surrounded by a strip of similar forest ≥ 40 m wide. During summer 1991, we sampled vegetation at every third point within each grid. Within circular plots, we measured diameter at breast height (dbh) of trees ≥ 5 -cm dbh and length and midpoint diameter of all logs with a diameter ≥ 12 cm at the midpoint. Trees < 5 -cm dbh were tallied, not measured. Size of vegetation plot differed among the three types of forest because of large differences in the densities of trees. In old-growth forests, small trees (< 18 -cm dbh) were measured within a 6-m radius and larger trees and logs within a 16-m radius. In mature forests, all trees and logs were measured within a 6-m radius. In shelterwood-logged forests, all trees and logs were measured within an 18-m radius. We used a spherical densiometer to obtain a relative measure of canopy cover at each vegetation plot (we used the average of three densiometer readings taken 8 m from the center of the plot). Ground cover was estimated using a point-intercept method; type of ground cover was recorded at 52 points/vegetation plot (13 points/transect along four transects following cardinal directions). We also dug a small soil pit at each point in the grid and measured the depth of organic soil (litter, humus, and buried decayed wood).

Each year (1991 and 1992), we live-trapped small mammals during two trapping sessions; six of the grids were trapped during the first session (two grids within each of the three types of forest were randomly selected) and the other six were trapped during the second session. Trapping sessions were in August and September in each year and 15-16 nights long (traps were closed for 2 days in the middle of each session); trapping sessions were long because our primary objective was to obtain estimates of population size of flying squirrels, whose capture probabilities were low (Waters and Zabel, 1995). At each grid point, we placed two Tomahawk live traps (13 by 13 by 41 cm): one on the ground and one attached to a tree ca. 1.5 m from the ground. We also placed a Sherman live trap (8 by 9 by 23

cm) on the ground at each grid point in 1991. Sherman live traps were not used in 1992 because of damage to traps in 1991 by bears. Bait was a mixture of rolled oats and peanut butter (a small amount of molasses was used in 1991 but not in 1992). After marking and weighing individuals, we determined sex and reproductive status. *S. lateralis* and *T. douglasii* were ear-tagged, and all other species were toeclipped.

Data analyses.—Numbers of captures and recaptures varied widely among species and grids. For several species, there were few or no recaptures in at least some of the grids, so we calculated capture rate as a measure of relative abundance for each species. Capture rate (CR) was expressed as number of individuals/1,000 trap nights and was determined using the formula of Nelson and Clark (1973):

$$CR = I \times 1,000 / (T - S/2),$$

where I = number of individuals captured, T = number of traps multiplied by number of nights traps were open, and S = number of traps sprung by all causes. To evaluate how well capture rates reflected abundance, we computed within-species correlations between capture rate and estimated population size for those species and grids in which one or more individuals was recaptured. Population size was estimated using the first-order jackknife estimate (Burnham and Overton, 1979), which has been shown to be a reliable estimator (low bias and precise), even when capture probabilities are low (Rosenberg et al., 1995). Capture rate was correlated highly with estimates of population size for the eight species-by-year combinations evaluated; the eight Pearson correlation coefficients ranged from 0.933 to 0.998, and the eight Spearman ranked correlation coefficients ranged from 0.952 to 1.000.

Sufficient data were available from both 1991 and 1992 for only *T. speciosus* and *T. senex*. For *S. lateralis*, *T. amoenus*, *P. maniculatus*, and *C. californicus*, capture data presented are from 1991. Few *T. amoenus*, *P. maniculatus*, and *C. californicus* were captured in 1992 because we did not use Sherman live traps that year. We did not ear-tag *S. lateralis* in 1992 because there were large differences in abundance among the three types of forest in 1991, and we needed to reduce total processing time of small mammals. Data for *T. douglasii* were from 1992 because only two individuals were caught in 1991.

TABLE 1.---Means and standard errors for measures of vegetation in three types of fir forest ($n = 4$ grids in each type of forest) in northeastern California in 1991. P -values are from ANOVA; means with the same letter did not differ at $\alpha > 0.05$.

Measure of vegetation	Old-growth		Mature		Shelterwood		P
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	
Basal area of trees ≥ 5 -cm dbh (m^2/ha)	72.6A	1.7	92.1B	1.5	22.6C	1.6	<0.001
Percent canopy cover	66.0A	0.4	78.3B	1.8	24.3C	1.7	<0.001
Number of snags/ha 13–52-cm dbh	69.3A	22.5	176.1B	42.6	5.0A	1.9	0.006
Number of snags/ha >52-cm dbh	9.7A	1.4	0.7B	0.7	5.8A	1.0	<0.001
Percent shrub cover	0.9A	0.4	0.5A	0.3	6.3A	3.6	0.149
Percent grass cover	1.4A	0.8	0.0A	0.0	3.6A	1.6	0.096
Percent forb cover	0.4A	0.3	0.0A	0.0	2.2B	0.6	0.005
Percent ground cover of logs ≤ 52 -cm diameter	2.1A	0.4	1.3A,B	0.1	0.6B	0.1	0.012
Percent ground cover of logs >52-cm diameter	3.3A	0.3	0.0B	0.0	0.5B	0.1	0.003
Depth of organic soil (cm)	6.8A	0.3	7.9A	0.4	1.7B	0.4	<0.001

We compared measures of vegetation and capture rates of small mammals among types of forest using analysis of variance (ANOVA). Equality of variances was first tested using the Brown-Forsythe homogeneity of variance test (SAS Institute, Inc., 1997). If variances did not differ significantly among the three types of forest, we used traditional ANOVA, but if variances differed significantly, we used Welch's variance-weighted ANOVA (SAS Institute, Inc., 1997). For *T. speciosus* and *T. senex*, we tested for a year effect using repeated-measures ANOVA; if the year effect was not significant, we performed ANOVA on the average capture rate between 1991 and 1992 to simplify presentation of results. We performed multiple-comparison tests using Tukey's studentized range test (SAS Institute, Inc., 1989) if variances did not differ significantly among types of forest or a variance-weighted, adjusted, Tukey's multiple-comparison test (SAS Institute, Inc., 1997) if variances differed significantly. For all tests, we used an alpha of 0.05.

RESULTS

Measures of vegetative structure differed greatly among the three types of forest. Compared to grids in old-growth forests, grids in shelterwood-logged forests had significantly less basal area and canopy cover,

significantly greater ground cover of forbs, significantly less ground cover of small-diameter and large-diameter logs, and a significantly thinner layer of organic soil (Table 1). Compared to grids in old-growth forests, grids in mature forests had significantly greater basal area and canopy cover, significantly more small-diameter snags and significantly fewer large-diameter snags, and significantly less ground cover of large-diameter logs (Table 1). Each of the three types of forest had its own characteristic distribution of diameter size classes (Fig. 1).

Mean capture rates were greatest in old-growth forests for two of the seven species: *T. senex* and *C. californicus*. For *T. senex*, repeated-measures ANOVA indicated that the effect of type of forest was not significant, but capture rate was significantly greater in 1992 than 1991, and differences in capture rate among types of forest also were significantly greater in 1992 (the interaction term between type of forest and year was significant; Fig. 2). Capture rates for *C. californicus* were low and variable, but the difference among types of forest was nearly significant (Fig. 3a). Mean capture rate of *C. californicus* was 5.7 times

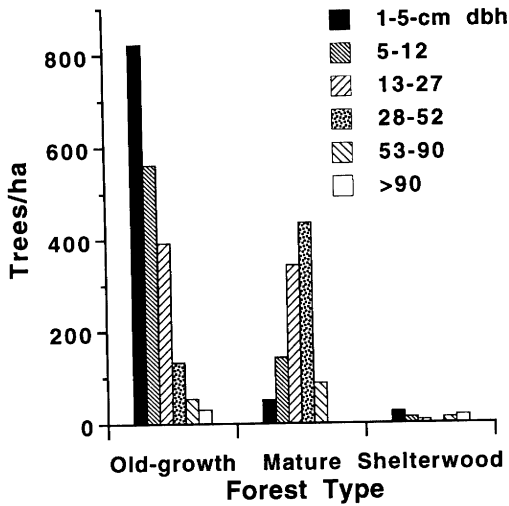


FIG. 1.—Mean densities of trees sampled in 1991 in four grids in old-growth, mature, and shelterwood-logged fir forests in northeastern California.

greater in old-growth forests than in mature forests, and none was caught in shelterwood-logged forests.

Tamiasciurus douglasii was the only species most abundant in mature forests. The two individuals captured in 1991 were both caught in grids in mature forests. In 1992, capture rate was significantly greater in mature forests than in old-growth and shelterwood-logged forests (Fig. 3b).

Mean capture rates were greatest in shelterwood-logged forests for four of the seven species: *S. lateralis*, *T. amoenus*, *T. speciosus*, and *P. maniculatus*. Capture rates of *S. lateralis* (Fig. 3c), *T. amoenus* (Fig. 3d), and *T. speciosus* (Fig. 3e) were significantly greater in shelterwood-logged forests than in old-growth and mature forests. Mean capture rate in shelterwood-logged forests was 39 times greater than in old-growth forests for *S. lateralis*, 13 times greater for *T. amoenus*, and 59 times greater for *T. speciosus*. Mean capture rate for *P. maniculatus* was two times greater in shelterwood-logged forests than in old-growth forests but did not differ significantly among the three types of forest (Fig. 3f).

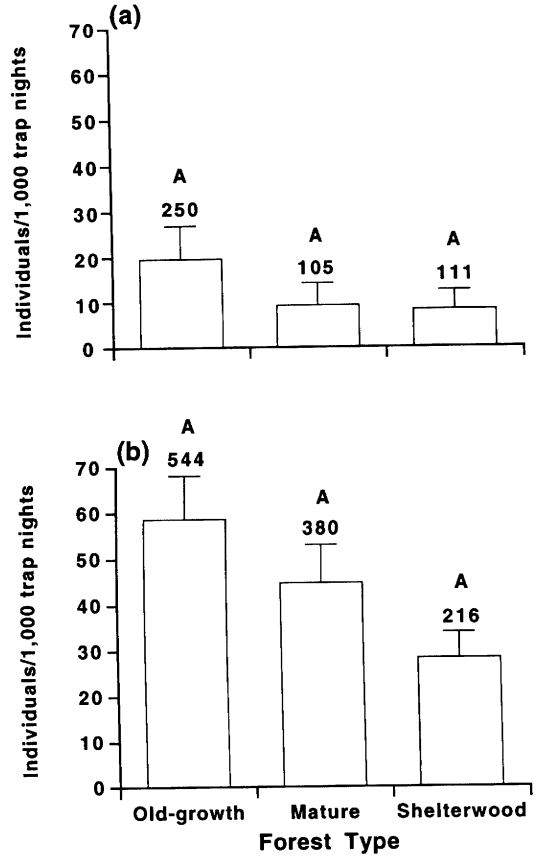


FIG. 2.—Mean capture rates and standard errors of *Tamias senex* captured in four grids in old-growth, mature, and shelterwood-logged fir forests during (a) 1991 and (b) 1992 in northeastern California. Number of individuals caught in each type of forest is listed above the column. Effect of type of forest from repeated-measures ANOVA was $F = 2.49$, $d.f. = 2,9$, and $P = 0.137$, effect of year was $F = 180.03$, $d.f. = 1,9$, and $P < 0.001$, and the interaction effect between type of forest and year was $F = 6.16$, $d.f. = 2,9$, and $P = 0.021$. Columns with the same letter did not differ within years at $\alpha \geq 0.05$.

DISCUSSION

We conclude that the shelterwood harvests and subsequent site preparation that occurred in Swain Mountain Experimental Forest had significant effects on patterns of abundance of forest rodents. Differences in capture rates between unlogged, old-growth forests and shelterwood-logged, old-growth

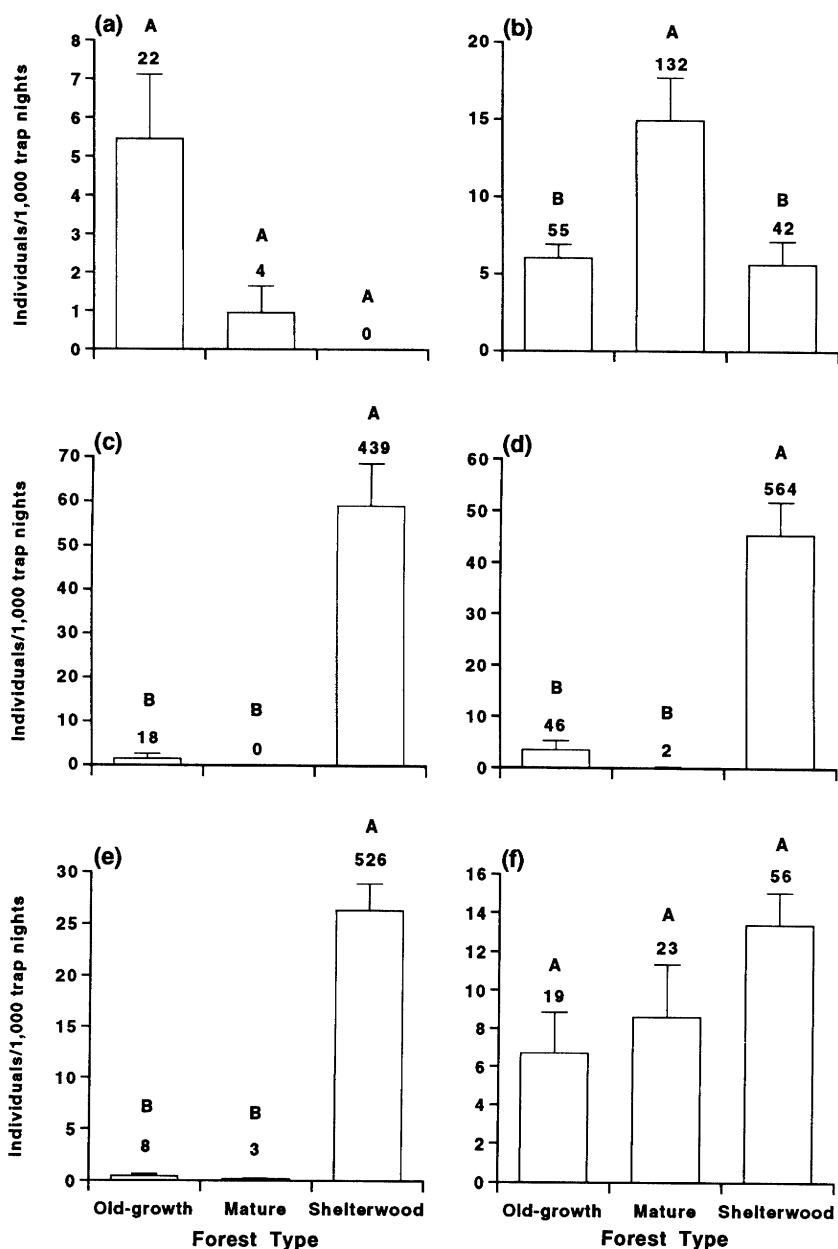


FIG. 3.—Mean capture rates and standard errors of small mammals captured in four grids in old-growth, mature, and shelterwood-logged fir forests in northeastern California. Number of individuals captured in each type of forest is listed above the column. Columns with the same letter did not differ at $\alpha \geq 0.05$: a) *Clethrionomys californicus* captured in 1991 ($F = 6.23$; $d.f. = 1,4.03$; $P = 0.067$); b) *Tamiasciurus douglasii* captured in 1992 ($F = 7.61$; $d.f. = 2,9$; $P = 0.012$); c) *Spermophilus lateralis* captured in 1991 ($F = 36.35$; $d.f. = 2,9$; $P < 0.001$); d) *Tamias amoenus* captured in 1991 ($F = 27.05$; $d.f. = 2,3.13$; $P = 0.011$); e) *Tamias speciosus* captured in 1991 and 1992 (capture rate was averaged between years because there was no significant difference between years; $F = 102.79$; $d.f. = 2,9$; $P < 0.001$); f) *Peromyscus maniculatus* captured in 1991 ($F = 2.33$; $d.f. = 2,9$; $P = 0.153$).

forests suggest that populations of *S. lateralis*, *T. amoenus*, and *T. speciosus* increased significantly following logging and site preparation, and populations of *C. californicus* probably decreased. In a previous paper, we concluded that populations of *G. sabrinus* decreased significantly following silvicultural treatments within the experimental forest (Waters and Zabel, 1995).

Consistent with our results, McKeever (1961) captured few *S. lateralis*, *T. amoenus*, and *T. speciosus* in a stand of old-growth fir within Swain Mountain Experimental Forest in 1958 before any of the shelterwood harvests; these three species, however, were captured frequently in open stands of ponderosa pine outside of the experimental forest. Sharples (1983) trapped small mammals at similar elevations to our stands in the northern Sierra Nevada and found that *T. amoenus* and *T. speciosus* were rare in closed-canopy stands but common in more open and disturbed stands. Grasses, forbs, and shrubs were more abundant in shelterwood-logged forests than in old-growth and mature forests, and these plants provide a variety of foods such as leaves, flowers, seeds, and fruit that are eaten commonly by *S. lateralis* and *Tamias* (Bartels and Thompson, 1993; McKeever, 1964a; Nowak, 1991; Sutton, 1992; Tevis, 1952, 1953). Tevis (1953) found that seeds of *Ceanothus cordulatus* and *Ribes roezlii* were abundant in the stomachs of *T. amoenus*, *T. speciosus*, and *T. senex*. These shrubs were present in shelterwood-logged forests in our study area but not in old-growth and mature forests. The disturbed soil profile and exposed mineral soil also may have provided favorable burrowing substrate for these ground-dwelling sciurids.

Seeds and arthropods are primary foods of *P. maniculatus* (Gunther et al., 1983; Tevis, 1956a; Williams, 1959), whose mean capture rate was greatest in shelterwood forests. Most studies that have compared populations of *P. maniculatus* between logged and unlogged forests have found

greater abundances in logged forests (Ahlgren, 1966; Gashwiler, 1959, 1970; Hooven and Black, 1976; Martell and Radvanyi, 1977; Raphael, 1988; Sims and Buckner, 1973; Tevis, 1956a, 1956b; Van Horne, 1981).

Other studies have shown that populations of *C. californicus* were low in recently logged or young stands (Gashwiler, 1959, 1970; Hooven and Black, 1976; Raphael, 1988; Rosenberg et al., 1994). Truffles are a primary food of *C. californicus* (Maser and Maser, 1988; Maser et al., 1978; Ure and Maser, 1982), and we found that truffles were significantly less abundant in shelterwood-logged forests than in old-growth and mature forests in 1991 (Waters and Zabel, 1995). *C. californicus* has been shown to be associated closely with large logs (Hayes and Cross, 1987; Tallmon and Mills, 1994), and there were significantly more large logs in old-growth forests than in mature and shelterwood-logged forests. Organic soil also may be an important habitat component for *C. californicus* (Rosenberg et al., 1994), and lack of a well-developed layer of organic soil may have reduced quality of shelterwood-logged forests as habitat for *C. californicus*.

Unlike *T. amoenus* and *T. speciosus*, *T. senex* was abundant in old-growth forests. This result is consistent with Sharples (1983), who found that of these three species of chipmunks, only *T. senex* was common in closed-canopy forest. Raphael (1988) and Tevis (1956a), however, found that the abundance of *T. senex* was greater in recent clearcuts than in older stands in northwestern California. Anthony et al. (1987) found that the closely related Townsend's chipmunk (*T. townsendii*) was more abundant in younger forests than in older forests in the Oregon Cascade Range. Rosenberg and Anthony (1993), however, found that density of *T. townsendii* was significantly greater in old-growth stands than in young stands in western Oregon, and Hayes et al. (1995) found no significant association between density of *T. townsendii*

and age of stand in the Oregon Coast Range.

Unlike comparisons between old-growth and shelterwood-logged forests, we did not observe large differences in relative abundances of small mammals between old-growth and mature forests. *C. californicus* may have been less abundant in mature forests than in old-growth forests, but we were not able to detect a significant difference with our limited data for that species. *T. douglasii* was the only species whose capture rate differed significantly between these two types of forest. Although fungi can be an important part of its diet (McKeever, 1964b), seeds of conifers are the primary food of *T. douglasii* (Flyger and Gates, 1982; McKeever, 1964b; Smith, 1970). One hypothesis explaining why *T. douglasii* was most abundant in mature forests in 1992 is that production of cones was greatest in that forest type. We cannot test this hypothesis because we did not quantify production of cones, but basal area of conifers was significantly greater in mature forests than in old-growth and shelterwood-logged forests.

The dramatic increase in captures of *T. douglasii* between 1991 and 1992 may have been related to a prolific crop of fir cones in autumn 1991. The forest floor was blanketed with bracts of fir cones that autumn. Populations of *T. douglasii* and red squirrels (*Tamiasciurus hudsonicus*) are known to fluctuate greatly with variation in cone crop (Flyger and Gates, 1982; Kemp and Keith, 1970; Smith, 1970), and Sullivan and Sullivan (1982) reported a 5-10-fold increase in density of *T. douglasii* as a result of supplemental feeding. The significantly greater abundance of *T. senex* in 1992 than in 1991 also may have been related to the huge crop of fir cones in autumn 1991. We observed *T. senex* eating seeds from fir cones along the roads during spring 1992. Sullivan et al. (1983) found that abundance of *T. townsendii* in British Columbia increased significantly following supplementation of food with seeds. The

significant effects of year and the interaction between type of forest and year for *T. senex* and the large difference in captures of *T. douglasii* between 1991 and 1992 suggest that caution should be taken in generalizing about patterns of abundance from 1 or 2 years of data.

Rodents are prey to a variety of predators, and changes in populations of rodents may affect populations of predators. Waters and Zabel (1995) noted the possibility of a causal relationship between limited use of shelterwood-logged forests within Swain Mountain Experimental Forest by California spotted owls (*Strix occidentalis occidentalis*) and low densities of *G. sabrinus*, the owl's primary prey in the Lassen National Forest. American martens (*Martes americana*), however, used shelterwood-logged forests greater than expected based on availability during summer (L. M. Ellis and C. J. Zabel, in litt.). On several occasions, we observed martens killing or chasing *S. lateralis* and *Tamias* in shelterwood-logged forests, and Zielinski et al. (1983) found that primary prey of martens in summer at a site in the northern Sierra Nevada were ground-dwelling sciurids (*Spermophilus* and *Tamias*). Ground squirrels and chipmunks, however, are less available as prey in winter because they hibernate.

Our results illustrate how patterns of abundance of forest rodents can change significantly following opening of the canopy and disturbance of the forest floor. Our results also illustrate how varied effects of logging can be, even among closely related and relatively few species. Negative effects on some species most likely mean positive effects on others and vice versa, so caution should be taken to avoid simplified generalizations about potential effects of logging on communities of small mammals.

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