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DEMOGRAPHY OF NORTHERN FLYING SQUIRRELS INFORMS ECOSYSTEM MANAGEMENT OF WESTERN INTERIOR FORESTS

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Abstract. We studied northern flying squirrel (*Glaucomys sabrinus*) demography in the eastern Washington Cascade Range to test hypotheses about regional and local abundance patterns and to inform managers of the possible effects of fire and fuels management on flying squirrels. We quantified habitat characteristics and squirrel density, population trends, and demography in three typical forest cover types over a four-year period. We had 2034 captures of flying squirrels over 41 000 trap nights from 1997 through 2000 and marked 879 squirrels for mark–recapture population analysis.

Ponderosa pine (*Pinus ponderosa*) forest appeared to be poorer habitat for flying squirrels than young or mature mixed-conifer forest. About 35% fewer individuals were captured in open pine forest than in dry mixed-conifer Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) forests. Home ranges were 85% larger in pine forest (4.6 ha) than in mixed-conifer forests (2.5 ha). Similarly, population density (Huggins estimator) in ponderosa pine forest was half (1.1 squirrels/ha) that of mixed-conifer forest (2.2 squirrels/ha). Tree canopy cover was the single best correlate of squirrel density ($r = 0.77$), with an apparent threshold of 55% canopy cover separating stands with low- from high-density populations.

Pradel estimates of annual recruitment were lower in open pine (0.28) than in young (0.35) and mature (0.37) forest. High recruitment was most strongly associated with high understory plant species richness and truffle biomass. Annual survival rates ranged from 45% to 59% and did not vary among cover types. Survival was most strongly associated with understory species richness and forage lichen biomass. Maximum snow depth had a strong negative effect on survival. Rate of per capita increase showed a density-dependent response.

Thinning and prescribed burning in ponderosa pine and dry mixed conifer forests to restore stable fire regimes and forest structure might reduce flying squirrel densities at stand levels by reducing forest canopy, woody debris, and the diversity or biomass of understory plants, truffles, and lichens. Those impacts might be ameliorated by patchy harvesting and the retention of large trees, woody debris, and mistletoe brooms. Negative stand-level impacts would be traded for increased resistance and resilience of dry-forest landscapes to now-common, large-scale stand replacement fires.

Key words: Cascade Range; demography; density; Douglas-fir; fuel management; Glaucomys sabrinus; *home range; mycophagy; northern flying squirrel; ponderosa pine.*

INTRODUCTION

Arboreal rodents are key species in an ecological web with important influences on forest productivity and biodiversity in the Pacific Northwest (PNW) (Carey 1991). They influence forest productivity by consuming the sporocarps of ectomycorrhizal fungi (EMF) and dispersing fungal spores and nitrogen-fixing bacteria via feces (Fogel and Trappe 1978, Li et al. 1986, Maser et al. 1986). They also are important prey for avian and mammalian forest carnivores (Barrows 1980, Forsman et al. 1984, Verner et al. 1992, Ward et al. 1998). The northern flying squirrel (*Glaucomys sabrinus*), in particular, is the primary prey of the threatened Northern Spotted Owl (*Strix occidentalis caurina*) in much of the PNW (Forsman et al. 1984, Thomas et al. 1990) where it comprises ~50% of the diet in both frequency and biomass (Forsman et al. 2001, 2004). As such, knowledge of prey dynamics is critical for understanding the ecology, demography, and viability of the Northern Spotted Owl and its habitats (Barrows 1985, Thrailkill and Bias 1989, Thomas et al. 1990, Ward et al. 1998). Although much is known about northern flying squirrel ecology in wet forests of the PNW west of the Cascade Range (Rosenberg and Anthony 1992, Zabel et al. 1993, Carey 1995, 2000*a*), little is known about flying squirrel ecology in interior dry forests.

Dry-forest managers critically need information to help resolve conflicts between the restoration of dry-forest pattern and process, especially the stabilization of fire regimes, and the maintenance of critical habitat for

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the Northern Spotted Owl and other late-successional forest associates. Spotted Owl habitats in the eastern Cascades of Oregon and Washington and the Klamath region of southern Oregon and northern California are at high risk of destruction by historically uncharacteristic stand replacement fires compared to wetter Spotted Owl habitats in western Washington and Oregon (Agee and Edmonds 1992). The last 100 years of human use and fire management in dry forests have wrought significant changes in stand and landscape composition and structure with a consequent shift from predominantly stable high-frequency, low- to moderate-intensity fire regimes to low-frequency high-intensity fire regimes that result in uncharacteristically large stand replacement fires (Agee 1993, 2003) and a repatterning of the landscape (Lehmkuhl et al. 1994, Hessburg et al. 1999*a*, Everett et al. 2000). As a consequence, dry forests are being targeted on public and private lands for large-scale density reduction or prescribed fire treatments to reduce fire hazards and restore natural ecosystem functions (Okanogan and Wenatchee National Forests 2000, Graham et al. 2004). Thorough and timely environmental impact assessment of these practices will depend on reliable information about wildlife habitat relationships in dry forests. Furthermore, arboreal rodent–forest relationships are of profound importance in understanding and managing temperate forest in general (Carey 2000*a, b*); eastern Washington offers a unique opportunity for gaining an understanding of forest biocomplexity and dynamics in relation to forest management.

Our primary goals were to quantify temporal and spatial variation in density, survival, recruitment, and rate of increase of northern flying squirrels in interior PNW dry forests. We used our data from three forest cover types arrayed along a typical temperature–moisture and stand development gradient to test hypotheses about patterns of abundance in landscapes at both local and regional scales. The cover types were selected based on a study by Forsman et al. (1990) wherein Northern Spotted Owls (1) avoided (use < availability) warm-dry ponderosa pine (*Pinus ponderosa*) forests, (2) used mesic young mixed-conifer forests in proportion to availability, and (3) selected (use > availability) yet more mesic mature mixed-conifer forests. Assuming that prey density/availability is the primary driver of Spotted Owl resource selection (Forsman et al. 1984, Carey 1985), we hypothesized that the pattern of flying squirrel density should reflect the pattern of habitat use by owls.

A pattern of increasing flying squirrel density from warm-dry pine forests to old mixed-conifer forests, as well as increasing survival and recruitment rates, also could be predicted from flying squirrel ecology elsewhere in the PNW. Mature stands in our study area have the highest number of large snags and non-cavity nest sites (e.g., dwarf mistletoe brooms) for potentially limiting den sites (Wells-Gosling and Heaney 1984, Carey et al. 1997, Bakker and Hastings 2002) and relatively high food production (fungi, lichen, fruit, seeds) associated with abundant down logs, shrub understory development, and large old trees (Lehmkuhl 2004, Lehmkuhl et al. 2004). Current young stands often have fewer large snags for den sites, although abundant mistletoe brooms might mitigate for the absence of snags, and have relatively less food production as a result of fewer large logs and associated truffles, more xeric understories less conducive to shrub (i.e., mast) development, and more open and younger canopies with lower forage lichen production than mature stands. Open pine stands have the fewest denning sites (snags and brooms) and the least food production associated with open canopies, low amounts of woody debris, and the greatest development of a xeric grass understory.

At a regional scale, Carey (1995) suggested that flying squirrel abundance increased from western Washington to southwestern Oregon along a north–south, temperature–moisture gradient of increasing EMF fungal richness, evenness, and seasonal availability. Extending Carey's hypothesis in an easterly direction from western Washington across the Cascade Range, we hypothesized that the relatively warm-dry forests of the eastern Cascades would support more flying squirrels than wet forests of western Washington because of the greater richness, evenness, and biomass of EMF truffles in eastern vs. western Washington forests (Lehmkuhl et al. 2004). Additionally, the open canopies and a patchy distribution of forest canopy in the eastern Cascades, a result of topo-edaphic conditions and patchy disturbance regimes (Franklin and Dyrness 1973, Agee 2003), create a diverse understory of potential food plants to supplement nutrient-poor fungal diets of squirrels (Cork and Kenagy 1989, Thysell et al. 1997, Claridge et al. 1999). Furthermore, abundant tree defect and pathology from nearly a century of fire exclusion in eastern forests (Agee and Edmonds 1992, Lehmkuhl et al. 1994, Hessburg et al. 1999*a*) provide many potential denning and nesting sites (e.g., cavities, mistletoe brooms). Fire exclusion also has resulted in high contagion and connectivity of late-successional forest habitat across the eastside landscape (Lehmkuhl et al. 1994, Hessburg et al. 1999*a*, Wright and Agee 2004), hence greater potential stability of arboreal rodent populations within those landscapes (Reunanen et al. 2000, D'Eon et al. 2002).

METHODS

Study area

The study area encompassed 160 km^2 of the upper Swauk Creek drainage of the Cle Elum Ranger District, Wenatchee National Forest, in the east-central Washington Cascade Range (47°15′00″ N, 120°37′30″ W). Forest structure in this area has been altered extensively since European settlement, primarily by fire suppression

TABLE 1. Environmental attributes of three common forest cover types of the eastern Washington Cascade Range for which the demography of northern flying squirrels was quantified during 1997–2000.

Attribute	Open pine	Young mixed conifer	Mature mixed conifer
Elevation (m)	1115	1092	1207
Aspect code†	3.8	2.5	1.5
Slope (%)	36	30	39
Canopy closure (%)	40	60	75
Basal area (m/ha)	20	24	32
Age largest trees‡	129	112	156
Pinus ponderosa density (trees/ha)	343	164	86
Pseudotsuga menziesii density (trees/ha)	453	319	170
Abies grandis density (trees/ha)	465	1765	1565
Large snags (trees/ha)‡	93	36	105
Coarse woody debris (% cover)	7.0	13.0	21.0
Soft large logs (% cover)§	1.2	0.9	3.0
Understory plant species richness	38	44	46
Understory plant cover (%)	55	60	61
Mistletoe severity index‖	10.8	11.4	6.3
Truffle richness (no. species)	7.3	9.3	10.8
Truffle biomass (kg/ha)¶	1.72	3.56	4.11
Bryoria forage lichen litter biomass (kg/ha)#	1.12	2.86	6.41

Note: Sample size was $n = 4$ stands in each cover type.

† Aspect code ranges from 1 (cool, moist) to 4 (hot, dry): 1 = north (315°–45°); 2 = east (45°–135°); 3 = west (225°–315°); 4 = south (135°–225°).

‡ Largest trees and snags were ≥40 cm dbh.

§ Downed wood >23 cm diameter in soft decay classes 3–5.

‖ Hawksworth (1977) mistletoe severity rating × frequency of infected trees.

¶ Spring truffle biomass in the soil (Lehmkuhl et al. 2004).

Bryoria litterfall biomass in the fall (Lehmkuhl 2004).

(Everett et al. 1997, Wright and Agee 2004) and several entries of selection cutting beginning around 1940 (S. Madden, *unpublished data*). As a result, most forest stands have an uneven age structure.

Study stands were on low-elevation (900–1400 m) forest sites characterized by varying dominance of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*). We randomly selected four replicate sample stands that met access and methodological (i.e., suitable size for trapping grids) constraints in each of three common forest cover types: open ponderosa pine, young mixed-conifer, and mature mixed-conifer. Stands ranged from 13 to 20 ha, typical in the dissected terrain of the area. Median nearest-neighbor distance between sample stands was 2.8 km, and the maximum distance between stands was 13 km.

Stand overstory and understory live and dead structure and composition in each stand were estimated from 16 0.02-ha plots using methods described by Everett et al. (1997) for the same area. Briefly, we recorded the species, diameter at breast height (dbh, measured at 1.4 m above the ground surface), height, and condition of all live and dead trees in each plot. The mean age of trees in six diameter classes was estimated by increment-coring two trees in that class. We rated each tree for the severity of dwarf mistletoe infection using Hawksworth's (1977) method. We estimated the percent cover and decay class for six diameter classes of downed logs and percent cover of all understory plant species. Tree basal area was estimated from variable-radius plots using a 20-basal-area factor prism. We estimated canopy cover by averaging four readings of a convex spherical densiometer. We used published biomass values for truffles of ectomycorrhizal fungi and *Bryoria* forage lichen litter (a proxy for arboreal biomass) for sample stands from Lehmkuhl et al. (2004) and Lehmkuhl (2004), respectively.

Open pine stands had canopy closure of 30–45% and were dominated by large (≥40 cm dbh) widely spaced ponderosa pine (Table 1). A patchy mid-story of smaller (<40 cm dbh) Douglas-fir and grand fir was often present in mesic microsites, such as draws. Tree density averaged 1200 trees/ha, of which 10% were large trees. Plant associations were mostly in the *Pseudotsuga menziesii* series, predominantly the dry *Pseudotsuga menziesii*/*Calamagrostis rubescens* plant association (Lilybridge et al. 1995).

Young, mixed-conifer stands had moderate canopy closure of 50–70%, with a relatively high density (2595 trees/ha) of trees, most (96%) of which were <40 cm dbh (Table 1). Dominant tree species were grand fir and Douglas-fir, with a few ponderosa pine. Plant associations were mostly in the mesic *Abies grandis* series, with *Abies grandis*/*Berberis nervosa*/*Calamagrostis rubescens* the dominant plant association (Lillybridge et al. 1995).

Mature, mixed-conifer stands had closed canopies (70–83%) dominated by a mixture of large grand fir and Douglas-fir (>40 cm dbh), with some scattered large ponderosa pine, and a well-developed mid-story and understory of grand fir and Douglas-fir (Table 1). Mean tree density (2206 trees/ha) was only slightly less than in young stands, but there were relatively more large trees in mature stands (12%) than in young (4%) or open pine (10%) stands. These sites had no record of being logged and were considered to be primary Spotted Owl habitat (E. Forsman, *personal communication*). The mesic *Abies grandis*/*Achlys triphylla* plant association dominated most sites (Lillybridge et al. 1995).

During the study period, mean yearly precipitation (98 cm) was 10% above and maximum snow depth was 20% above 55-year means at the Blewett Pass SNOTEL weather station (1300 m elevation) located at the north end of the study area (NRCS 2000). Snow depth peaked annually during March at a mean of 139 cm, ranging annually from 114 to 158 cm. Maximum snow depth during the winters of 1995–1996 and 1997–1998, prior to the first and third years of trapping, was 40% and 37% higher than the 55-year average and in the 90th and 85th percentiles of long-term annual values, respectively. Melt-out of the snow pack occurred during late April or early May. Summers were warm and dry, with a mean maximum daily temperature of 34°C.

Field methods

We live-trapped flying squirrels during the fall from 1997 through 2000. Trapping methods were based on design and sampling recommendations by Carey et al. (1991). We put two Tomahawk 201 live traps (Tomahawk, Wisconsin, USA) at each grid point on 8×8 or 7×9 sampling grids with 40-m spacing; the recommended 10×10 grids were too large for the cover type patches found in these landscapes. We placed one trap on the ground and another at 1.5 m aboveground on the trunk of the largest tree within 5 m of each grid point. We inserted traps into waxed milk cartons, topped the units with litter or woody debris, and provided a small milk-carton nest box with synthetic batting to shelter captured animals. A mixture of oats, peanut butter, and molasses was used as bait and to provide food to reduce the risk of hypothermia.

We trapped each stand for two consecutive weeks during late September or early October. We opened traps for four days each week and closed traps over the weekend to reduce trapping stress (Carey et al. 1991). The order of stand sampling was switched each of the four years to reduce bias in trapping success associated with annual variation in weather and food availability. Each trapped animal was identified to species, sex, and age (mass, pelage color, and morphology per Villa et al. [1999]), then weighed and ear-tagged on both ears. We collected dead animals for examination of reproductive tracts and for voucher specimens retained at the USDA Forest Service, Forestry Sciences Laboratory, Wenatchee, Washington, USA.

In addition to fall sampling, we used radiotelemetry during the summer of 1998 and 1999 to characterize den sites and to estimate home range sizes in cover types, which were used to estimate area trapped for density calculations and as an index of habitat quality (Carey 1995). We used fall live-trapping success to identify a sample stand in each cover type that had the most squirrels available for radiotelemetry studies the next summer, ultimately studying movements of 9 male and 19 female flying squirrels in six of the 12 stands (two stands per cover type) over the two-year period. We captured these squirrels during June of each year, anesthetized them with Metaphane (Pitman-Moore, Mundelein, Illinois, USA) under the supervision of a veterinarian, then fitted them with ear tags and radio collars (BR collar with SM1 radio; AVM Instrument, Livermore, California, USA). We located each radio-collared squirrel in day dens twice each week and tracked nightly movements on three occasions from July through September. On each night-tracking occasion, we located the animal in its den during the day, waited approximately 20 m from the den tree for the squirrel to leave the den, then tracked the squirrel for two hours. We followed the squirrel from a 20–40 m distance and recorded "activity" sites defined as locations where the squirrel stopped and stayed for ≥ 5 min. Locations were marked and recorded with GPS.

Data analysis

We estimated abundance of flying squirrels in each stand during each year in several ways to allow us to compare with other studies. We first calculated total individuals captured (Skalski and Robson 1992) and catch per 100 trap nights (Nelson and Clark 1973, Carey 1991) as simple indices of true abundance. Additionally, we estimated true abundance with the Chapman modification of the Lincoln-Peterson (LP) index (Seber 1982) to compare with other studies of northern flying squirrels in the PNW and Alaska (Carey 1995, Carey et al. 1999, Smith et al. 2003). To estimate LP abundance, we split the two-week trapping period into two equal periods: squirrels were marked during the first week and recaptures estimated during the second week (Menkins and Anderson 1983). Both of the abundance indices were highly correlated with LP estimates for individual stands and years ($r > 0.91$, $P < 0.001$). Finally, we estimated true abundance with a second, more rigorous mark–recapture "meta-analysis" approach (Boulanger et al. 2002) using Program MARK (White and Burnham 1999). This method allowed us to fit complex mark–recapture models with covariates that could potentially account for more variation in initial capture and recapture probabilities than the simpler LP estimator.

The meta-analysis approach to mark–recapture abundance estimation was designed to obtain the most parsimonious model(s) that explained the major forms of variation in capture probability. The meta-analysis process was simply the estimation of three separate cover-type models from data pooled by stands and years within cover types. The rationale for pooling by cover type was that stands within cover types remained relatively similar for each of the years sampled, and sample sizes (i.e., individual squirrels and recaptures) would be increased with corresponding increases in estimated precision.

We used Huggins (1991) closed mixture models (Pledger 2000) in MARK to estimate abundance because they allow use of habitat and individual animal covariates and they perform well with sparse data (G. White, *personal communication*). We tested the basic null (M_o), time (M_t), behavior (M_b), and heterogeneity (M_h) mark–recapture models and their combinations. For the M_h model we modeled heterogeneity in capture probability with a mixture model of two capture probabilities. We also used an individual animal covariate (mass), two stand-based covariates (canopy cover, understory cover), and two temporal covariates (maximum snowfall depth, precipitation) in various model formulations in an attempt to account for differences in capture probabilities between individual squirrels, stands, and years sampled within a cover type.

Huggins abundance modeling indicated time (annual) and heterogeneity (e.g., among animals) effects on capture probabilities in all cover types, but no support for behavioral (e.g., trap shyness) effects (Appendix C). No behavioral effect on capture probability indicated that initial and recapture probabilities were similar (Otis et al. 1978), hence not differentiated for subsequent mark–recapture modeling. There was an annual effect on capture probabilities in nearly all models, largely because of the extremely poor capture probabilities during the first year. Time effects within trapping sessions were not modeled in our approach, but summary catch statistics from Program CAPTURE (as implemented in MARK) indicated some time variation within trapping sessions. Heterogeneity in capture probabilities had both individual animal and stand-level components. Capture probabilities in open pine stands were best modeled as a two-mixture (low, high) model varying with understory cover among stands. In young and mature forests, capture heterogeneity generally was associated with squirrel mass (a proxy for age) and variation in understory cover or canopy cover (mature forest) among stands. Capture probability in mature forest was best modeled by a complex interaction between year and stand, but the mixture model also was well supported.

We calculated squirrel density (number per hectare) by adjusting LP and Huggins abundances for the area sampled using Bondrup-Nielson's (1983) method, which uses home range size to estimate area sampled for density calculations. Rosenberg and Anthony (1992) concluded that use of home range for density estimation probably is superior to adding one-half the mean maximum distance moved to trapping grid dimensions, a technique used by them and others (e.g., Carey 1995, Smith et al. 2003) with grid-based mark–recapture studies. We used activity sites and den locations from summer radiotelemetry to approximate minimum convex polygon (MCP) home ranges and maximum home range dimension for each animal with the Animal Movement Program (Hooge and Eichenlaub 2000). In our study, maximum distance moved by squirrels did not vary over time from early summer (July) through the fall trapping period (September) in each cover type ($r \leq 0.20$, $P \geq 0.258$), thus supporting use of June–September home range area to estimate fall density. Because stands were the sample unit in the study design, mean home range area and maximum dimension for each of the three cover types were estimated by first averaging values for all squirrels in a stand, i.e., squirrels were considered subsamples, then averaging stand means by cover type. Maximum home range dimension was used as a proxy for mean maximum distance moved in grid trapping methods (Carey et al. 1991, Smith et al. 2003).

We used the Pradel model (Pradel 1996), as implemented in program MARK, to estimate apparent year-to-year survival (ϕ, the probability of surviving and returning to the population) and recruitment (f, strictly, the rate of addition from births and immigration) and to explore the effect of individual squirrel covariates, temporal covariates, and stand- and treatment-based covariates on demography. We chose the Pradel model because it allowed inferences about both ϕ and f; the Cormack-Jolly-Seber (CJS) (Cormack 1964) and standard robust design (Kendall 1999) models only provide inference about ϕ. We judged the Pradel model to have the optimal amount of complexity given the large number of proposed model hypotheses and the relatively limited sample sizes in the data set. One stand whose trapping grid was unavoidably shifted about 120 m during the study was excluded from the Pradel analysis.

We used Akaike Information Criterion (AIC_c) model selection methods (Burnham and Anderson 2002) to assess relative fit of model hypotheses for both Huggins and Pradel analyses. Analysis of Pradel model goodness-of-fit using a reduced CJS model (ϕ [treatment $\times$ year] p[treatment $\times$ year]) and program RELEASE (Burnham et al. 1987) indicated moderate overdispersion (=1.38), so $QAIC_c$ was used for Pradel model selection. Delta AIC_c (or $QAIC_c$) from the "best" model was used to evaluate the relative fit of others models. Models with $\Delta AIC_c \leq 2$ had "substantial support" from the data, values from 3 to 7 had "considerably less support," and differences $\geq$10 had "essentially no support" (Burnham and Anderson 2002:70).

We used a three-step modeling process to find the most parsimonious Pradel model(s) among a set of plausible a priori model hypotheses based on flying squirrel ecology. First, we found the most parsimonious model hypothesis for capture probability (Appendix A), with survival and recruitment modeled in general form (i.e., ϕ + year, f + year). Then we used that best capture probability model to model ϕ and f as a function of temporal and biological covariates (Appendix A). Finally, we used the most parsimonious biological and environmental model developed in the second step to determine the influence of cover type and vegetation covariates on ϕ and f (Appendix B).

We did a separate Pradel analysis to estimate the annual rate of finite population change (λ) because λ cannot be derived when individual covariates are used to estimate ϕ and f in the current version of MARK (Franklin 2002). The Pradel λ model made some simplifying assumptions about influences of individual, temporal, and treatment covariates; so as a check, we compared Pradel estimates of λ with those estimated from successive changes in population size (Huggins estimator) as $\lambda_{t+1} = \hat{N}_{t+1}/\hat{N}_t$ (Franklin 2002, Hines and Nichols 2002) (hereafter the CPS estimator). Evidence of density-dependent response in per capita rate of increase $r_t = (\hat{N}_t/\hat{N}_{t-1})$ was examined by regressing r_t against $\ln(\hat{N}_{t-1})$ (Fryxell et al. 1998).

We tested hypotheses of cover type and time effects on all dependent variables for individual stands and years with analysis of variance (ANOVA) (Coffman et al. 2001) in a one-way, repeated-measures design. We screened data to ensure that they reasonably met assumptions of ANOVA; the data did not need transformation. An extreme outlier for Huggins-based density in one stand during 1997 was five times higher than subsequent estimates for that stand; that outlier value was trimmed to be one value higher than the next highest value in that cover type and year for ANOVA (Tabachnick and Fidell 1996). Differences in dependent variables over time were evaluated in ANOVA as difference contrasts between consecutive years. We used Tukey's honestly significant difference (hsd) test to evaluate multiple comparisons among cover type means if the main effect was significant. Correlations between density and stand covariates were described by Pearson correlation coefficients. We showed relationships between stand covariates and survival and recruitment with scatterplots and fitted lines; both survival and recruitment were estimated as linear functions of stand covariates in the mark–recapture analysis, hence Pearson correlation was inappropriate.

We accepted $P \leq 0.10$ as the observed probability level for Type I error in hypothesis tests. Although less conservative than $P \leq 0.05$, particularly with the relatively small sample size in this study ($n = 12$ sites), we considered $\alpha = 0.10$ to be an acceptable chance of Type I error for ecological field studies that was well within the bounds of statistical convention and that also allowed for reduced Type II error (Zar 1999). A significant difference is implied where a difference among means is reported, but we report exact P values in the text to allow readers to assess the probability of error relative to their own standard of significance (Zar 1999).

RESULTS

Capture rates

We had 2034 captures of flying squirrels and individually marked 879 squirrels during ~41 000 trap nights over the four-year period. The capture mortality rate was 2.8%. The sex ratio of captured squirrels was even and did not vary among cover types ($P = 0.898$) or over time ($P = 0.338$). Capture probabilities were low, averaging 0.14 overall, and ranged from 0.003 during 1997, when few individuals were captured (Fig. 1), to a stable 0.18 during the remaining three years. Capture probabilities differed slightly among cover types ($P = 0.043$): capture probability in young stands (0.16) was higher than in mature stands (0.12; $P = 0.036$), but similar to open pine stands (0.14; $P = 0.281$). The maximum capture probability in a single stand and session was 0.23.

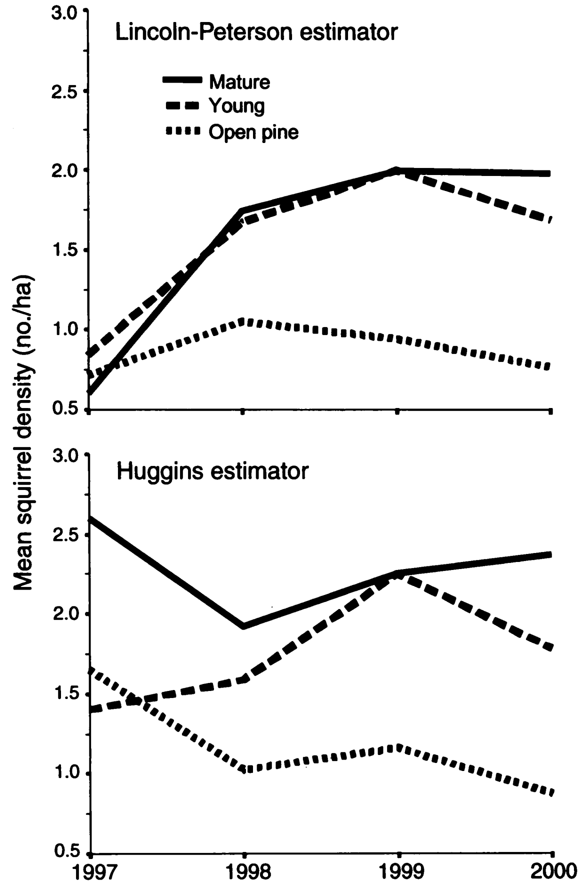

FIG. 1. Density estimates for northern flying squirrels in open ponderosa pine forest and in young and mature mixed-conifer dry forests of eastern Washington, USA, from 1997 to 2000.

Abundance and density

Open ponderosa pine forest appeared to be poorer habitat for flying squirrels than young or mature mixed-conifer forest, which were relatively similar in habitat value based on several estimators. Catch per unit effort (CPUE) differed among cover types ($P = 0.073$), with about 35% fewer individuals captured in open pine (1.9 squirrels/100 trap nights) than in young (2.9 squirrels/100 trap nights; $P = 0.125$) or mature forests (3.0 squirrels/100 trap nights; $P = 0.09$). Home range area and maximum home range dimension similarly differed

TABLE 2. Mean area and maximum dimension of home ranges and 90% CI (in parentheses) for northern flying squirrels in three low-elevation forest cover types in the eastern Washington Cascades, 1997–2000.

Cover type	Home range (ha)	Maximum dimension (m)
Open ponderosa pine	4.6^{A} (1.2)	351^{A} (62)
Young mixed conifer	2.7^{B} (1.0)	260^{B} (56)
Mature mixed conifer	2.3^{B} (1.3)	242^{B} (70)
Mean	3.2 (0.7)	286 (38)

Notes: Cover type means followed by the same letter are not significantly different ($P \leq 0.10$) by Tukey's HSD multiple-comparison test. Mixed-conifer forest includes grand fir, Douglas-fir, and ponderosa pine.

among cover types ($P = 0.05$), with squirrels in open pine forest having 85% larger home ranges ($P \leq 0.10$) and 42% larger maximum home range dimension ($P \leq 0.065$) than in either young or mature forests, which were similar in both respects ($P > 0.43$; Table 2).

Lincoln-Peterson (LP) density estimates likewise indicated low habitat quality of open pine forest relative to both mixed-conifer types (Table 3). With fewer captures and larger home ranges in open pine vs. mixed-conifer forest, flying squirrel density was about 50% lower in open pine forest (0.87 squirrels/ha) compared to young (1.55 squirrels/ha, $P = 0.058$) or mature (1.58 squirrels/ha, $P = 0.048$) forests, in which squirrel density was similar ($P = 0.992$). Moreover, open pine forest consistently supported low-density populations over time, whereas squirrel density in young and mature forests increased markedly during the second year and remained relatively stable in subsequent years (interaction $P = 0.06$; Fig. 1). The near doubling of overall density among all cover types from 1997 to 1998 ($P = 0.002$; Table 3) and the subsequent plateau during the following three years ($P > 0.196$; Fig. 1) was largely due to increased populations in young and mature forest.

Huggins density estimates averaged 10% higher than LP estimates (Table 3), and the pattern of density among cover types was similar except during 1997 (Fig. 1). As with LP estimates, Huggins density differed among cover types ($P = 0.025$), with open pine stands supporting fewer squirrels per hectare (1.18 squirrels/ha) than mature forest (2.29 squirrels/ha, $P = 0.020$). In contrast to LP estimates, however, Huggins density estimates indicated that the ability of young forest to support high flying squirrel densities was equivocal. Huggins density in young forest (1.76 squirrels/ha) appeared intermediate between open pine and mature forest vs. similar to mature forest as with LP estimates; but those differences were not statistically significant ($P > 0.237$) for the four-year period. If the first year's (1997) Huggins estimates were excluded as unreliable because of a sparse data set, or at least as greatly deviant compared to the catch index or LP estimates (Fig. 1), then density during the latter three years in open pine (1.0 squirrel/ha) was less than both young (1.9 squirrels/ha, $P = 0.032$) and mature (2.2 squirrels/ha, $P = 0.006$) forest, which were similar ($P = 0.530$).

Although Huggins and LP estimates were closely correlated during 1998–2000 ($r = 0.932$), the two density estimators deviated markedly for the sparse-data year of 1997 when Huggins estimates were about four times higher than LP estimates, most notably in mature stands (7.25 times higher) and with coefficients of variation up to four times greater (Fig. 1). As a result of such high variation, Huggins estimates of density did not vary over time ($P = 0.304$), whereas LP estimates of density were found to be lower during 1997 than for subsequent years (Table 3).

Other indicators of relatively low habitat quality, such as few juveniles or lighter individuals, were similar among cover types. Juveniles made up about 10% of the captures over all cover types and years, and that percentage was similar among cover types ($P = 0.415$) and did not differ over time among cover types (interaction $P = 0.301$). Subadults made up 42% and adults 48% of the captured individuals. Mean mass of adult squirrels was similar in all cover types (152 ± 1.2 g

TABLE 3. Two mark–recapture estimates of northern flying squirrel mean density (no./ha) and 90% CI of means (in parentheses) in three low-elevation forest cover types in the eastern Washington Cascades, 1997–2000.

Cover type	1997	1998	1999	2000	Mean
Lincoln-Peterson estimator					
Open ponderosa pine	0.72	1.05	0.94	0.76	0.87^{A} (0.33)
Young mixed conifer	0.84	1.67	2.00	1.69	1.55^{B} (0.33)
Mature mixed conifer	0.61	1.74	1.99	1.98	1.58^{B} (0.33)
Mean	0.72^{A}† (0.34)	1.49^{B} (0.24)	1.64^{B} (0.25)	1.48^{B} (0.21)	1.33 (0.17)
Huggins estimator					
Open ponderosa pine	1.65	1.03	1.16	0.87	1.18^{A} (0.43)
Young mixed conifer	1.40	1.59	2.25	1.78	1.76^{AB} (0.43)
Mature mixed conifer	2.60	1.92	2.25	2.37	2.29^{B} (0.43)
Mean	1.89^{A}‡ (0.52)	1.51^{A} (0.22)	1.89^{A} (0.30)	1.68^{A} (0.33)	1.74 (0.19)

Notes: Cover type means followed by the same letter are not significantly different ($P \leq 0.10$) by Tukey's HSD multiple-comparison test. Mixed-conifer forest includes grand fir, Douglas-fir, and ponderosa pine. Consecutive yearly means followed by the same letter are not significantly different ($P \leq 0.10$) in repeated-measures ANOVA.

† Lincoln-Peterson estimator cover type × year interaction significant ($P = 0.060$).

‡ Huggins estimator cover type × year interaction not significant ($P = 0.258$).

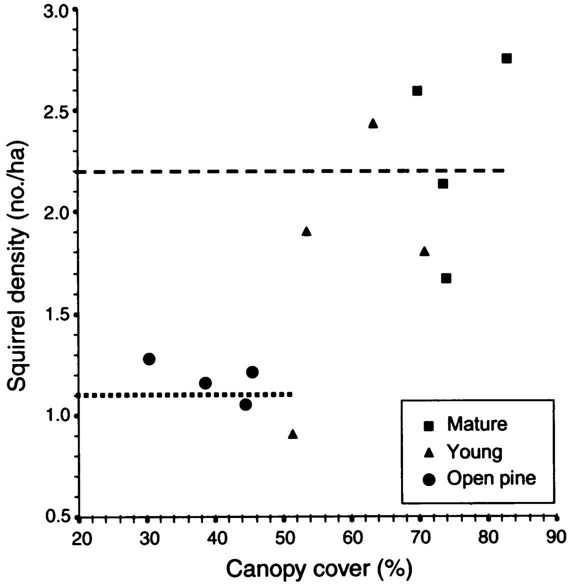

FIG. 2. The relationship between northern flying squirrel density (Huggins estimator) and tree canopy cover in 12 stands of ponderosa pine and mixed-conifer dry forest in eastern Washington. Horizontal lines indicate mean density for the low- and high-density stand groups.

[mean ± 90% CI], $P = 0.246$), and there was no difference in mean mass of adults over time among cover types (interaction $P = 0.586$). Mean mass of subadults and juveniles was 124 ± 1.3 g and 98 ± 3.0 g, respectively.

Among sample stands, tree canopy cover was the single best habitat correlate ($r = 0.77$) of squirrel density (Huggins) (Fig. 2). Density also was correlated positively with estimates of truffle biomass ($r = 0.68$) and richness ($r = 0.58$), basal area ($r = 0.60$), large tree density ($r = 0.57$), and severe mistletoe infection ($r = 0.55$); but those factors each were highly correlated with tree canopy cover ($0.61 < r < 0.75$). Instead of a continuous linear relationship between density and canopy cover in sample stands, there appeared to be a threshold of approximately 55% canopy cover that separated low-density, mostly open pine stands from high-density mixed-conifer stands (Fig. 2). Squirrel density in low-density stands averaged 1.1 squirrels/ha, whereas high-density stands supported twice as many squirrels (2.2 squirrels/ha).

Recruitment and survival

Patterns of recruitment and survival among cover types were relatively consistent with patterns observed for density (Table 4). Recruitment varied by cover type ($P = 0.092$), with clearly lower recruitment in open pine (0.28) than in mature forest (0.37; $P = 0.10$) and probably in young forest (0.35; $P = 0.175$). Recruitment in young and mature forests was similar ($P = 0.877$). Among all cover types, recruitment changed at most 9% over the study period ($P \leq 0.001$). Among model hypotheses, there was strong support ($\mathrm{QAIC_c} \leq 2$; Appendix D) for recruitment increasing with understory species richness and truffle biomass (Fig. 3).

Apparent annual survival of all age classes varied from 47% to 51% over time ($P < 0.001$; Table 4). In contrast to density and recruitment, survival rate did not vary among cover types ($P = 0.125$) from an average of 50%, although survival appeared to be approximately 5% lower in open pine than in young and mature stands. In support of apparent differences in survival among stands, there was strong support ($\mathrm{QAIC_c} \leq 2$) among model hypotheses (Appendix D) for survival increasing with understory species richness (Fig. 3) and lichen biomass (Fig. 4). Maximum winter snow depth had a strong additive negative effect with understory species richness on survival among years; i.e., the negative effect of winter snow depth on survival was similar across all levels of understory species richness (Fig. 4, Appendix D).

TABLE 4. Annual apparent mean survival and recruitment rates and 90% CI (in parentheses) for northern flying squirrels from Pradel mark–recapture modeling in three low-elevation forest cover types in the eastern Washington Cascades, 1997–2000.

Cover type	1997–1998	1998–1999	1999–2000	Mean
Survival rates				
Open ponderosa pine	0.48	0.44	0.49	0.47^{A}† (0.03)
Young mixed conifer	0.53	0.49	0.53	0.52^{A} (0.03)
Mature mixed conifer	0.52	0.48	0.52	0.51^{A} (0.03)
Mean	0.51^{A}‡ (0.02)	0.47^{B} (0.02)	0.51^{C} (0.02)	0.50 (0.02)
Recruitment				
Open ponderosa pine	0.33	0.26	0.25	0.28^{A}§ (0.05)
Young mixed conifer	0.41	0.33	0.32	0.35^{AB} (0.05)
Mature mixed conifer	0.43	0.35	0.34	0.37^{B} (0.06)
Mean	0.39^{A}‖ (0.04)	0.31^{B} (0.03)	0.30^{C} (0.03)	0.33 (0.04)

Notes: Recruitment is the sum of immigration and births. Individual means followed by the same letter are not significantly different ($P \leq 0.10$) by Tukey's HSD multiple-comparison test. Mixed-conifer forest includes grand fir, Douglas-fir, and ponderosa pine.

† Mean survival rates similar among cover types ($P = 0.125$).

‡ Mean annual survival rate differs ($P < 0.001$); no cover type × year interaction ($P = 0.238$).

§ Mean recruitment rate differs among cover types ($P = 0.092$).

‖ Annual mean recruitment rates differ ($P < 0.001$); no cover type × year interaction ($P = 0.172$).

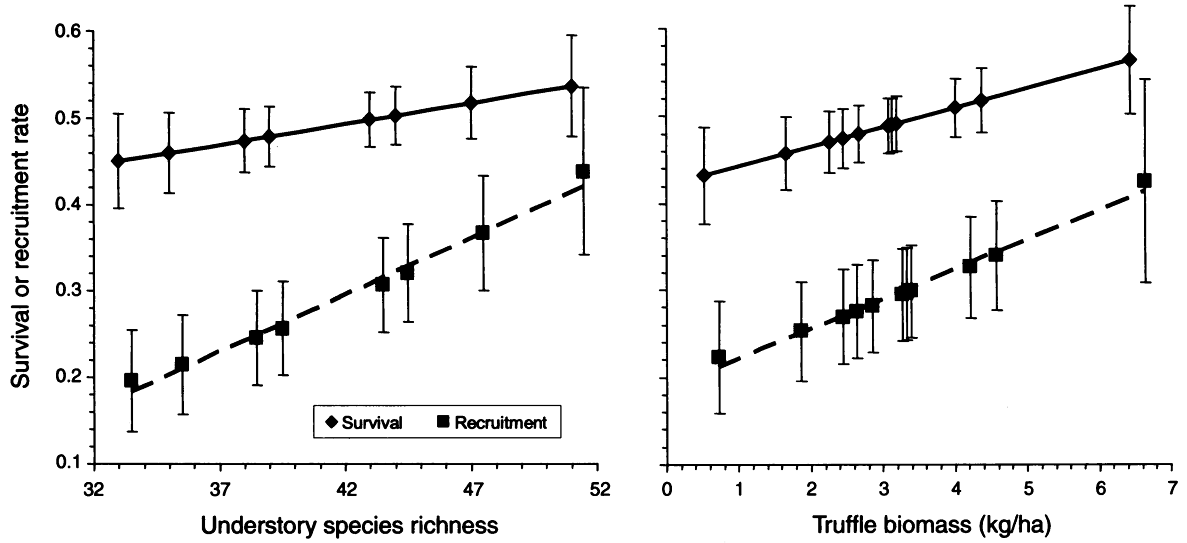

FIG. 3. Relationships between annual apparent survival and recruitment rates of northern flying squirrels and understory plant species richness and truffle biomass as determined by Pradel mark–recapture modeling for ponderosa pine and mixed-conifer dry forests of eastern Washington. Error bars are ±SE of mean estimates.

Consistent with other demographic variables, the realized rate of population change (λ) was approximately 13–15% lower in open pine than in young or mature forest types, but differences were not significant for either the Pradel ($P = 0.197$) or the change in population size (CPS; $P = 0.647$) estimators (Table 5). Based on the most optimistic CPS estimator, flying squirrel populations overall were stable to slightly increasing ($\lambda = 1.03$), with no differences among years ($P = 0.205$). Pradel estimates of λ, in contrast, indicated an overall lower and declining $\lambda = 0.91$, with annual changes varying from a 19% increase during the first period to −21% and −23% declines during the subsequent periods ($P < 0.001$), a pattern fairly consistent with changes in LP abundance estimates. Per capita rate of increase responded in a density-dependent manner to population size ($r = 0.87$, $P < 0.001$; Fig. 5). The mark–recapture model selection procedure indicated that a cover type effect on λ was not supported by the data ($QAIC_c \geq 10$); rather, rate of change was most strongly and positively affected by understory species richness among stands and among years ($QAIC_c \leq 1$).

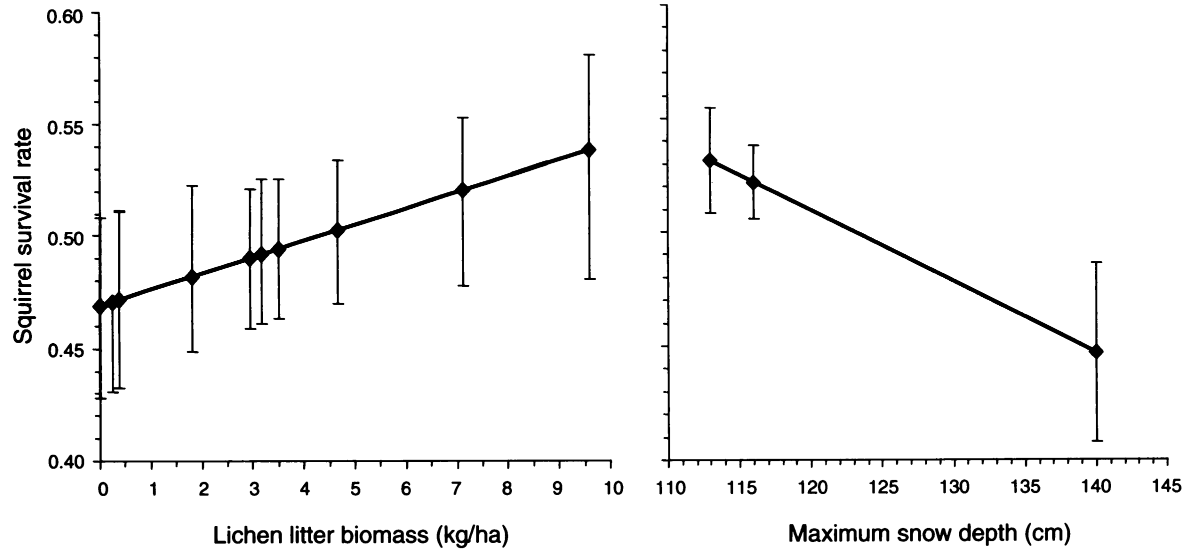

FIG. 4. Relationships between apparent annual survival rate of northern flying squirrels and forage lichen biomass and maximum snow depth as determined by Pradel mark–recapture modeling for ponderosa pine and mixed-conifer dry forests of eastern Washington. Error bars are ±SE of mean estimates.

TABLE 5. Finite rates of mean population rate of change (λ) and 90% CI (in parentheses) for northern flying squirrels based on Pradel mark–recapture modeling in three common low-elevation forest cover types in the eastern Washington Cascades, 1997–2000.

Cover type	1997–1998	1998–1999	1999–2000	Mean
N_{t+1}/N_t estimator				
Open ponderosa pine	0.81	1.16	0.82	0.93^{A}† (0.23)
Young mixed conifer	1.20	1.36	0.74	1.10^{A} (0.26)
Mature mixed conifer	0.70	1.06	1.15	0.97^{A} (0.26)
Mean	0.90^{A}‡ (0.30)	1.19^{A} (0.22)	0.90^{A} (0.19)	1.03 (0.13)
Pradel estimator				
Open ponderosa pine	1.02	0.74	0.72	0.83^{A}§ (0.10)
Young mixed conifer	1.18	0.86	0.84	0.96^{A} (0.10)
Mature mixed conifer	1.19	0.87	0.85	0.97^{A} (0.12)
Mean	1.12^{A}‖ (0.08)	0.82^{B} (0.06)	0.80^{C} (0.05)	0.91 (0.07)

Notes: Individual means followed by the same letter are not significantly different ($P \leq 0.10$). Mixed-conifer forest includes grand fir, Douglas-fir, and ponderosa pine.

† Mean N_{t+1}/N_t λ similar among cover types ($P = 0.647$).

‡ Annual N_{t+1}/N_t λ did not differ ($P = 0.205$); no cover type × year interaction ($P = 0.384$).

§ Mean Pradel λ did not differ among cover types ($P = 0.197$).

‖ Annual Pradel λ differed ($P < 0.001$); no cover type × year interaction ($P = 0.115$).

DISCUSSION

Habitat relationships

Our hypothesis of increasing habitat quality among open pine and young and mature mixed-conifer forests, as reflected in density and demographic rates, was partially supported by the data. Open pine forest clearly was poorer habitat for northern flying squirrels compared to young or mature mixed-conifer forests. Density and recruitment were lower and home ranges larger in open pine forest than in mixed conifer types. Moreover, open pine forest consistently supported low-density populations over time, based on LP and catch indices, whereas density in young and mature forests increased markedly during the second year and remained relatively stable in subsequent years with close to normal snowfall. Rates of survival (Pradel) and increase (Pradel λ) also were lower in open pine forest than young or mature stands, if a somewhat more liberal probability of error ($P \leq 0.20$) is accepted.

Open pine forest, thus, might be "sink" habitat (sensu Pulliam 1988) for northern flying squirrels relative to mixed-conifer forests in eastern Cascades forests. Availability of dens, truffle and vascular plant foods, and predation could limit density of flying squirrel populations (Wells-Gosling and Heaney 1984, Carey 1991, 2002, Ransome and Sullivan 1997) in open pine forest. Predation by the Northern Spotted Owl, an important predator of flying squirrels in this area, is probably low because open pine stands are generally avoided by Spotted Owls (Forsman et al. 1990). The Great Horned Owl (*Bubo virginianus*) may be an important predator on flying squirrels in open pine forest, but we have no information about their impact. Weasels (*Mustela* spp.), an important predator in western Oregon and Washington (Carey 2000*a*), were uncommon in the study area, or at least not easily trapped or detected: we trapped weasels only eight times over the four-year period and saw little sign of weasel predation on squirrels or chipmunks caught in traps. Several experimental studies in temperate coastal forests found that the availability of food, not dens, controls densities of flying squirrels (Ransome and Sullivan 1997, 2004, Carey 2002). Den sites in open pine forest, moreover, appeared abundant with relatively high numbers of large snags and much mistletoe (Table 1). Even though snags were relatively abundant in open pine stands, they were mostly unused for cavity dens: only 3% of 36 dens used by radio-collared squirrels in open pine forest were in snags, whereas 67% of the dens were in dwarf mistletoe brooms in Douglas-fir (25 dens) and ponderosa pine (8 dens) trees (J. F. Lehmkuhl, *unpublished data*). Yellow-pine chipmunks (*Tamias amoenus*) were nearly three times more abundant than flying squirrels in open pine stands

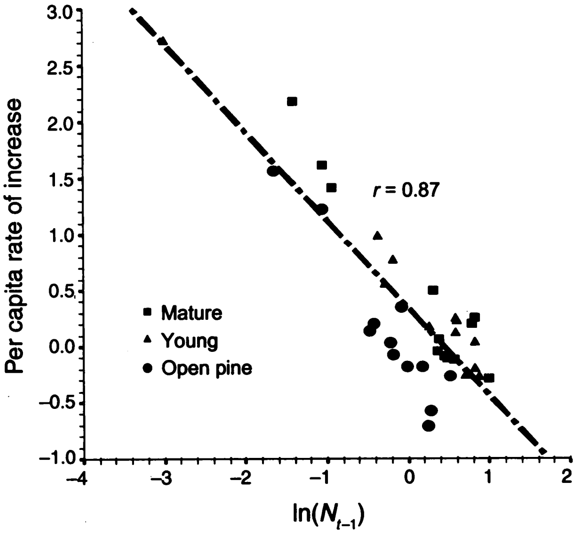

FIG. 5. Per capita rate of increase, $r_t = \ln(\hat{N}_t/\hat{N}_{t-1})$, in relation to $\ln(\hat{N}_{t-1})$ for northern flying squirrels in ponderosa pine and mixed-conifer dry forests of eastern Washington, 1997–2000.

(~3.0 individuals/ha; J. F. Lehmkuhl, *unpublished data*); hence, competition for relatively scarce truffle, seed, and fruit resources may also limit flying squirrels (Carey 1995) in open pine forest.

Compared to mixed-conifer forests, low food availability (truffle and lichen biomass, understory plant richness, Table 1) appeared to limit squirrel density, survival, and recruitment in open pine forests. To compensate for low food productivity in pine forest, squirrels apparently forage over larger home ranges (Carey 1995), which in our case included adjacent patches of more productive mixed-conifer forest. Evidence of that cross-boundary subsidy in the study area has been found in squirrel diets in open pine forest that are similar to diets in mixed-conifer forests, despite differences in truffle assemblages (Lehmkuhl et al. 2004). Despite relatively lower habitat quality of open pine forest compared to mixed-conifer forests, density in open pine forest (0.8–1.2 squirrels/ha depending on estimator) was greater than or equal to densities reported for young Douglas-fir and western hemlock forest regenerated on clearcuts in western Washington, western Oregon, and northern California (reviewed by Smith et al. 2003) or in western hemlock (*Tsuga heterophylla*) forests of coastal British Columbia (Ransome and Sullivan 2003). Estimates of squirrel density in large (>20 ha), homogenous blocks of open pine forest likely would be lower than observed in our typically small stands (13–20 ha), where cross-boundary food subsidies from nearby mixed-conifer forest were available.

Contrary to our predictions, squirrel density and demography in young and mature mixed-conifer forests were similar in nearly all respects. In both wet coastal and dry interior forests of the Pacific Northwest, young and old forest appear to be similar source habitats for northern flying squirrels (Rosenberg and Anthony 1992, Carey 1995, Waters and Zabel 1995, Ransome and Sullivan 2003, Smith and Nichols 2003). However, density of flying squirrels in young forest is expected to be lower than mature forest where young forest regenerates from clearcut logging and lacks substantial large tree and log legacies (Carey 1995). Our mean 2.2 squirrels/ha for high-density young (three of four stands) and mature stands (four of four stands) is nearly equal to (~2.3) or greater than that found at 8 of 10 sites in Douglas-fir, western hemlock, or white fir/red fir (*Abies concolor*/*Abies magnifica*) forest in the Pacific Northwest (reviewed by Smith et al. 2003), in old western hemlock forest of coastal British Columbia (Ransome and Sullivan 2003), and in peatland–mixed conifer forest in southeastern Alaska (Smith and Nichols 2003). Squirrel densities exceeding ~2.2 squirrels/ha have been reported for mature white fir/red fir forest in northern California (3.3 squirrels/ha; Waters and Zabel 1995) and for old-growth western hemlock/Sitka spruce (*Picea sitchensis*) forest in southeastern Alaska (3.2 squirrels/ha; Smith and Nichols 2003). In support of our west–east regional gradient hypothesis, flying squirrel densities in mixed-conifer forests of the eastern Cascades exceeded those in mature or old-growth western hemlock forest in western Washington (~0.5 squirrels/ha) and were comparable to densities in Douglas-fir forests of southwestern Oregon (~2.1 squirrels/ha; Carey 1995).

These density comparisons should be treated with caution because of different methods among studies for estimating abundance and density. For example, our density estimates based on LP abundance were 10% lower than those based on Huggins abundance: several studies have relied on LP estimates of abundance (Carey 1995, Smith and Nichols 2003). Also, nearly all previous investigators estimated density using mean maximum distance moved (MMDM) on trapping grids to estimate area trapped, whereas methods using home ranges, as in this study, that do not assume uniform home range dimensions, likely yield more accurate estimates of density (Rosenberg and Anthony 1992). In our study, density estimates using maximum home range dimension as a proxy for MMDM were from 29% to 38% (mean = 31%) lower among the three cover types than estimates based on the home range method. Adjusting our estimates downward by approximately 30% yields density estimates comparable (~1.5 squirrels/ha) to most Douglas-fir forests in western Oregon and Washington (reviewed by Smith et al. 2003).

High flying squirrel density in both young and mature stands was strongly associated with closed canopy cover (>55%), abundant den sites, inherently high productivity of truffles and forage lichens, and diverse understory plant foods. Spotted Owl predation in their preferred mature mixed-conifer habitat might have influenced observed squirrel densities (Carey et al. 1992, Carey 1995), but we attempted to minimize that effect by choosing study stands >800 m from active Spotted Owl nests located during a concurrent owl demography study (Forsman et al. 1996). Among our radio-tagged squirrels, 2 of 28 (7.1%) were confirmed killed by predators in mature stands only, most likely by Spotted Owls or Barred Owls (*Strix varia*). Canopy cover would have a direct effect via canopy connectivity and its effects on squirrel movement (Carey 1991). Canopy cover also has indirect effects on food resources: canopy cover and truffle food production in all study stands are strongly correlated ($r = 0.75$; Lehmkuhl et al. 2004). Truffle production in young and mature stands falls at the high end of the range for coastal and interior forests in the PNW (Lehmkuhl et al. 2004).

The 55% canopy threshold for stands with low vs. high densities of squirrels was confounded by plant association because all but one (young) stand with <55% canopy cover were in the most xeric, least-productive Douglas-fir plant associations. Stands with <55% canopy cover might be below a threshold for canopy connectivity or site productivity, but little support for such a threshold can be found in the literature as canopy cover values for study stands are rarely given for natural or thinned stands (Carey 2000*a*, *b*, Ransome and Sullivan 2002, Bull et al. 2004). Waters and Zabel (1995), however, found that old white fir/red fir forest logged by shelterwood harvesting to about 25% canopy cover 6–7 years prior to sampling supported approximately one-tenth the density of flying squirrels compared to unlogged forest in northern California.

The importance of understory species richness to flying squirrel survival and recruitment in our study area supports the importance of rich understory plant food resources in northern flying squirrel diets (Carey 1995, Thysell et al. 1997, Carey et al. 1999, Pyare and Longland 2002, Smith et al. 2004; but see Waters and Zabel 1995). The importance of plant material is supported by a concurrent diet study that found plant material was 22% of fall flying squirrel diets in our study area, which is at the high end of reported values for flying squirrels in the PNW (Lehmkuhl et al. 2004). Our vegetation data showed Douglas maple (*Acer glabrum douglasii*), serviceberry (*Amelanchier alnifolia*), Cascade Oregon grape (*Berberis nervosa*), baldhip rose (*Rosa gymnocarpa*), huckleberries (*Vaccinium* spp.), and snowberry (*Symphoricarpos* spp.) were more abundant in mixed-conifer stands than in open pine stands where understories were dominated by pine grass (*Calamagrostis rubescens*). Persistent seeds and fruit of those species likely provided important supplements to nutrient-poor truffle diets (Cork and Kenagy 1989, Thysell et al. 1997, Claridge et al. 1999), particularly during the winter when snow cover would affect truffle availability. We confirmed the importance of forage lichen biomass for winter survival (McKeever 1960, Maser et al. 1985, Hall 1991, Rosentreter et al. 1997; but see Currah et al. 2000).

Den sites in young and mature stands did not appear to be a limiting factor in our study area, with one exception. In young stands large snags were relatively rare, but dwarf mistletoe was frequent and severe; the reverse generally was true in mature stands (Table 1). Dwarf mistletoe brooms housed 40% and 33% of dens in young and mature stands, respectively; 6% and 19% of dens in young and mature stands were snag cavities, respectively (J. F. Lehmkuhl, *unpublished data*). Den site limitation may have occurred in the one young stand that was grouped with open pine stands in the low-density group. In that stand, there were very few large trees, snags, or mistletoe brooms compared to other young stands, whereas understory species richness, truffle biomass, and lichen biomass were similar to other young stands. The abundance of mistletoe, and the relatively weatherproof den sites it affords (Mowrey and Zasada 1984), is perhaps one reason that snags were not an important correlate of density (Rosenberg and Anthony 1992) or demographic parameters in our study area. Other investigators, however, found snags are either important den sites or correlates of density (Carey 1995, Smith et al. 2004, Meyer et al. 2005).

Finally, the best predictors of high survival or recruitment were habitat covariates (e.g., understory species diversity, truffle biomass) and maximum snow depth, not the general stand classification. Thus, specific attributes of stands rather than an overall stand classification per se were the dominant drivers of flying squirrel demography (Carey 1995, Carey et al. 1999).

Demography

Our estimates of survival rates in young and mature stands were intermediate among the few rates reported in the literature. Our Pradel modeling did not support different survival rates among age classes, but only about 10% of our captures were juveniles <1 year old. Hence, our estimated survival rate of 0.50 represents mostly subadults and adults. Villa et al. (1999) reported relatively lower rates of subadult and adult survival (estimated as the percentage of individuals surviving from one age class to the next) that averaged 0.37, 0.25, and 0.25 for old-growth, mixed age, and young forests in coastal Oregon forests and 0.20 for young forests in the Puget Trough, western Washington. They reported relatively higher juvenile survival rates in old-growth (0.54) and mixed-age (0.43) forests in coastal Oregon. Ransome and Sullivan (2003) reported high overall Jolly survival rates of about 0.80 for coastal forests of British Columbia. Our results suggest a density-dependent response in per capita rate of increase of northern flying squirrels. Fryxell et al. (1998) reported similar findings for northern flying squirrels and other small mammals in conifer and mixed forests of Ontario, Canada, and evidence of a four-year population cycle in northern flying squirrels. Our four-year study was too short to make conclusions about population cycling in our study area.

Management implications

Current forest management in the dry-forest zone represented by our study area is focused on conserving habitat for the Northern Spotted Owl, restoring characteristic fire regimes, and restoring dry-forest ecosystems that have developed anomalously after nearly a century of fire exclusion (Okanogan and Wenatchee National Forests 2000, Graham et al. 2004). Management in Spotted Owl habitat, represented by the mature mixed-conifer type in this study, is primarily conservatory with little active manipulation of forest structure at this time. However, active management of dry-forest types represented by the open pine and much of the young mixed-conifer types is being designed and implemented for restoring dry-forest composition, structure, and disturbance processes. Management objectives for dry forest are: (1) reduce stand density; (2) alter species composition for more fire-tolerant species; (3) reduce fuel loads to levels consistent with presettlement fire regimes; and, (4) reduce vegetation susceptibility to insects and disease to levels consistent with presettlement patterns (Okanogan and

Wenatchee National Forests 2000). The primary management options for achieving those objectives are: (1) pre-commercial or commercial thinning; (2) pruning; (3) favoring insect/disease-resistant tree species; or (4) prescribed burning. Such management likely will negatively impact flying squirrel populations at stand and landscape scales.

Those prescriptions would result in treated stands with fewer trees, a less complex and more open canopy structure, a higher variability in stand microclimate, fewer mistletoe-infested trees and large brooms, and more dominance of ponderosa pine compared to Douglas-fir or grand fir. A basic prediction from our results is that simply reducing canopy cover below ~50% will result in a shift to low-density populations of flying squirrels in treated stands, but there is little firm guidance on such thresholds in the literature, other than that much-reduced squirrel densities occur when old-forest canopies are reduced to 25% cover (Waters and Zabel 1995). Thinning likely will have a drying effect on high-canopy, high-density young stands in dry grand fir plant associations, with a shift to less-rich understories and greater dominance by pine grass (Lillybridge et al. 1995). Based on our data, we predict that reductions in understory species richness will reduce both survival and recruitment of flying squirrels. Shifting stand microclimate to relatively more xeric conditions likely would also result in lower richness and biomass of truffles (Lehmkuhl et al. 2004), with consequent impacts on squirrel recruitment. Prescribed burning following thinning likely will increase the drying effect on understories by reducing woody debris and the mesic microsites that it creates and by top-killing shrubs and favoring fire-resistant species such as pine grass. Biomass of *Bryoria* and *Alectoria* forage lichens also would decline with reduction of stand density and basal area and the consequent reduction in canopy complexity and moisture (Lehmkuhl 2004).

Lehmkuhl (2004) and Lehmkuhl et al. (2004) reviewed ways to ameliorate the effects of dry-forest thinning and prescribed burning on lichen and truffle food resources in this area. Retention of the largest or oldest trees may retain some reduced level of lichen diversity and biomass of forage lichens in particular. Large trees are mostly unaffected by typical low-intensity prescribed fire, and important forage lichens would be most abundant at mid- to upper levels in the canopy of large trees beyond scorch heights created by typical flame lengths of ≤1 m (J. Agee, *personal communication*). Retaining some patches in higher stand density and variable species composition, as opposed to homogenous thinning, also may reduce the impact on truffle and lichen richness and abundance.

There is evidence that retention of large downed wood may ameliorate opening the canopy by creating or maintaining relatively mesic microsites important for truffle production through shading or moisture retention without increasing hazardous fuels (see review by Lehmkuhl et al. 2004). Such mesic microsites also would benefit understory plants not well adapted to xeric conditions. Carey (2002) recommends that ≥15% cover of coarse woody debris be retained in wet Douglas-fir forests to maintain critical truffle habitat. That recommendation seems well suited to our study area where woody debris averaged 13–21% cover in young and mature stands, which had very high truffle biomass (Lehmkuhl et al. 2004). Downed wood would be hard to retain in the long term, however, with regular prescribed burning at ~10-year intervals (Agee 2002) and without recruitment of new downed wood. Retention of some dwarf mistletoe brooms will be important for retaining den sites (Bull et al. 2004), especially in areas where few snags occur as a result of past management. Mistletoe brooms also are important nesting platforms for Northern Spotted Owls (Forsman et al. 1984, Buchanan et al. 1993), feeding and resting sites for other mammals and birds (Parks et al. 1999), and keystone species in a broad array of mistletoe–animal interactions (Watson 2001).

For wet Douglas-fir and western hemlock forests of western Washington, Carey et al. (1999) and Carey (2000*b*) suggested variable-density thinning, with retention of dead wood legacies (large snags and woody debris) on the scale of 0.2–0.5 ha patches, that opens stands enough to promote understory development but not enough to disrupt fungal communities and canopy connectivity. Carey's approach may be best suited to restoration management of young or mature mixed-conifer stands where variable density thinning may emulate mixed-severity fire regimes that could have been relatively more important in those types compared to drier pine sites (Wright and Agee 2004, Hessburg et al. 2005). An initial decline in squirrel abundance might be expected in stands with good habitat, but such stands might continue to support low populations (Carey 2000*b*). Given our results, however, variable-density thinning of mesic stands might be neutral or beneficial to flying squirrel habitat if canopy cover remained above 50%, den sites and truffle and lichen biomass were unaffected, and understory plant diversity increased. Each of these stand-level management practices for retaining important habitat elements or managing stand pattern should be considered hypotheses for testing through adaptive management studies that incorporate effectiveness and validation monitoring.

Structural variability of managed stands, however, will be difficult to sustain with a regular program of post-thinning prescribed fire at regular intervals (~10 years) that is patterned after low-intensity, high-frequency presettlement fire regimes (e.g., Everett et al. 2000, Wright and Agee 2004), unless fire management objectives specifically prescribe patchy coverage of fires and include localized fire refugia. Ultimately, restoration of natural processes would create patchiness of a different sort in treated portions of the landscape: open pine stands dominated by large fire-resistant ponderosa pine and some Douglas-fir with small (<0.4 ha) patches of pine regeneration (Agee 1993, Harrod et al. 1999, Youngblood et al. 2004) on dry sites. Untreated mesic, mixed-conifer, closed-canopy forest on northerly facing slopes in the complex landscape would remain as primary source habitat for flying squirrels.

The potential negative stand-scale impacts on flying squirrels, truffles, and lichens of dry-forest thinning for fire and fuel management are traded for potential long-term stability of dry-forest landscapes (Agee and Edmonds 1992, Agee 1998, 2003). The potential loss of truffle or lichen diversity at stand scales may be balanced by increased beta diversity across the landscape (Lehmkuhl 2004, Lehmkuhl et al. 2004). Potential losses from silviculture or prescribed fire are trivial compared to the large-scale losses of high-quality young and mature mixed-conifer habitat following 5000—60 000 ha stand-replacement fires that have occurred with historically uncharacteristic frequency in the eastern Cascades during the last decade (Gaines et al. 1997, Everett et al. 2000, Agee 2003). An added benefit of dry-forest silvicultural practices that restore or maintain stable fire regimes and fuel management is the consequent restoration of single-story large ponderosa pine forests that have declined during the last century (Lehmkuhl et al. 1994, Hann et al. 1997, Hessburg et al. 1999*a*) and their associated wildlife (Lehmkuhl et al. 1997, Wisdom et al. 2000). These landscape-level effects, too, should be considered hypotheses for testing.

Moreover, the amount of thinning for restoration of interior forest landscapes might not significantly impact the viability of flying squirrel populations because the area and location of treatments will be constrained by many factors that preclude habitat loss beyond a critical threshold. Accessibility, roadless area restrictions, soil erodibility, sensitive species, recreation, and other resource issues will limit treatment area (Okanogan and Wenatchee National Forests 2000). For example, thresholds for "take," which includes modification or degradation of habitat that impairs animal fitness, for Northern Spotted Owl habitat under the Endangered Species Act limits owl habitat reduction to <40% of the area within 2.9 km of an owl activity center (W. Gaines, *personal communication*). Maximizing scarce management resources by strategic placement of fuel treatments might require treatment of only 20–30% of the landscape to significantly reduce fire severity and spread across a landscape (Finney 2001, Loehle 2004). The historical range of natural variability used as a guide for ecosystem restoration (Hessburg et al. 1999*b*, Landres et al. 1999) indicates that 50% or more of eastern Cascades landscapes might be retained as flying squirrel habitat with medium to large tree (>40 cm dbh) structural classes of dry Douglas-fir and grand fir plant associations, with an additional 15–20% in the small-tree (20–40 cm dbh) classes (Agee 2003). Considering the demonstrated breadth of forest conditions in which flying squirrels can persist in dry forest and the ability of flying squirrels to move readily across matrix habitats in forest-dominated landscapes (Selonen and Hanski 2003), it seems unlikely that dry-forest restoration will significantly impact the viability of flying squirrel populations, or their ecological webs, in many dry-forest landscapes.

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APPENDIX A

A priori biological and environmental hypotheses on northern flying squirrel demography used to estimate environmental and biological effects on capture probabilities and demography in Pradel demography model building process (*Ecological Archives* A016-025-A1).

APPENDIX B

A priori hypotheses of the effects of cover type and vegetation attributes on northern flying squirrel demography used in the third step of the Pradel demography model building process (*Ecological Archives* A016-025-A2).

APPENDIX C

The Akaike Information Criterion (AIC) model selection results for Huggins mark–recapture estimation of northern flying squirrel abundance in dry forests of eastern Washington (*Ecological Archives* A016-025-A3).

APPENDIX D

The QAIC model selection results for estimating survival, recruitment, and capture probabilities of northern flying squirrels in dry forests of eastern Washington (*Ecological Archives* A016-025-A4).