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LANDSCAPE-SCALE HABITAT RELATIONSHIPS TO TASSEL-EARED SQUIRREL POPULATION DYNAMICS IN NORTH-CENTRAL ARIZONA

Guidelines for Ponderosa Pine Forest Ecosystem Management

**Federal Aid in Wildlife Restoration
Project W-78-R**

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INTRODUCTION

A dramatic evolution in forest management has occurred in the Southwest during the last decade toward forest ecosystem restoration (Covington and Moore 1994). Pre-European settlement (ca. 1870) ponderosa pine (*Pinus ponderosa*) forests generally consisted of older trees and were more open and park-like (Cooper 1960, Covington and Moore 1994, Belsky and Blumenthal 1997). Today, younger trees dominate southwestern forests (Johnson 1994, Mast et al. 1999), often with >3,000 stems/ha (Mast 2003). These unnatural conditions present increased potential for catastrophic wildfire, disease, and decreased ecosystem health (Covington and Moore 1994, Covington et al. 1997). These problems have spawned restoration initiatives (Moore et al. 1999) that advocate aggressive thinning and prescribed fire to reduce the risk of catastrophic wildfire and promote ecosystem health and old-growth forest conditions (Covington and Moore 1994, Covington et al. 1997).

Though widespread agreement exists as to the need and urgency for ponderosa pine forest ecosystem restoration, similar agreement has not been achieved on the manner in which restoration goals should be pursued, particularly with regard to restoring forest processes and natural ranges of variability (Allen et al. 2002). **Treatments based on reconstruction of presettlement forest density (Fulé et al. 1997) have resulted in large reductions in tree density, up to 98%, with resultant densities of 60 trees/ha or less (Mast et al. 1999).** Though some wildlife species may benefit from such treatments, forest canopy-dependent species may be adversely affected (Wagner et al. 2000, Allen et al. 2002, Chambers and Germaine 2003). Few studies have specifically addressed potential impacts of restoration on wildlife or provided insights on how to balance treatments to address multiple species' needs.

Ponderosa pine forest restoration activities in the Southwest are anticipated to increase dramatically, potentially affecting millions of hectares of forest (Allen et al. 2002, Zimmerman 2003). As restoration activities are pursued at the landscape scale, the combined influence of patch- and landscape-scale habitat alteration on wildlife is of increasing interest and concern.

Why focus on the tassel-eared squirrel?

The tassel-eared squirrel (*Sciurus aberti*) is an obligate species of the Southwest's ponderosa pine forests. It is a popular small game and unteachable species, and important prey for the northern goshawk (*Accipiter gentilis*; Remolds et al. 1992). Squirrels play a key role in facilitating essential symbiotic interactions of root-inhabiting (mycorrhizal) fungi with ponderosa pine through consumption of fruiting bodies and dispersal of spores (Stales and Gaud 1997, Stales and Wettslein 1998). Tree squirrels in general are well suited for research since they are sufficiently abundant to yield statistically meaningful population data and sensitive enough to structural habitat condition changes to allow for forest management inferences (Carey 2000). The tassel-eared squirrel is an indicator species useful to managers in assessing ponderosa pine restoration activities (Chambers and Germaine 2003).

Areas recently treated under forest restoration prescriptions to achieve presettlement reference conditions (Mast et al. 1999, Mast 2003) are structurally similar to areas subjected to past intensive even-aged management (Dodd et al. 2003). **Even-aged treatments that have reduced forest canopy closure and interlocking canopy trees, tree density, and patchiness have been demonstrated to be detrimental to tassel-eared squirrel populations (Pederson et al. 1976, 1987; Patton 1984; Patton et al. 1985; Dodd et al. 2003).**

Intensive thinning alters microhabitats where hypogeous (subsurface) fungi grow, reducing fungi production (States and Gaud 1997) and disrupting symbiotic relationships among fungi, pines, and squirrels (Pederson et al. 1987, States et al. 1988, States and Gaud 1997). Mycelia and fruiting bodies of both hypogeous and epigeous (above-ground) fungi constitute an important seasonal food for tassel-eared squirrels (Stephenson 1975, States et al. 1988) and strongly influence juvenile squirrel recruitment (Dodd et al. 2003).

Restoration activities may add to cumulative impact from past even-aged management of southwestern forests (Dodd and Adams 1989), including already-reduced stand, patch, and landscape diversity (Patton 1992). Extensive forest restoration may diminish remaining high quality squirrel habitat (Patton 1984, Dodd et al. 1998), potentially reducing suitable habitat below threshold levels, with exaggerated effects on squirrel populations (Andren 1994, Andren and Delin 1994). Conversely, squirrels may benefit from creation of a landscape-scale mosaic of structural habitat conditions and patch sizes (Patton 1975a, 1992; Lema 2001; Dodd et al. 2003).

Study Objectives

Forest managers currently have a limited understanding of the relationships of landscape-scale habitat composition to tassel-eared squirrel populations and other ponderosa pine-dependent wildlife. There is a particular need for information on how best to design restoration projects that reflect the varied habitat needs of wildlife, balanced with forest health and wildfire risk reduction objectives. For this reason, coupled with the escalating emphasis on forest restoration that will increasingly affect forest landscapes, I initiated a research project with the following objectives:

- 1) estimate tassel-eared squirrel density, juvenile recruitment, and survival across a gradient of landscape-scale forest habitat conditions,
- 2) quantify patch- and landscape-scale habitat structure and composition and evaluate relationships to squirrel populations,
- 3) evaluate the presence of thresholds in squirrel population response along gradients of landscape-scale habitat composition, and
- 4) develop landscape-scale forest habitat management guidelines that reflect squirrel habitat needs.

Rationale for Landscape Approach

Various approaches have been used to quantify landscape-scale heterogeneity (Wiens et al. 1993, Bowers and Matter 1997). Most approaches typically described patch area, spatial dispersion (e.g., isolation, connectedness), degree of pure habitat loss (Andren 1994), or proportion of suitable habitat. Bowers and Matter (1997) stressed the problem associated with variable interactions in limiting induction from patch area relationship studies. They found that population response (density) did not vary by patch area for 20 of 32 species and suggested that no consistent density-area relationship operates across landscapes.

Andren (1994) described non-linearity in landscape patterns and the relative importance of differences in habitat loss (proportion of suitable habitat), patch area, and isolation under varying degrees of habitat fragmentation. Like Kareiva and Wennergren (1995), Krohne (1997), and Bowers and Matter (1997), he concluded that there are important thresholds associated with reductions in suitable habitat.

At some threshold, typically around 30% suitable habitat, effects of patch area and isolation on populations accelerate and strengthen the effect of suitable habitat loss

(Andren 1994). Up until this point, influences of patch area and isolation at the landscape level are secondary to the proportion of suitable habitat present (Andren 1994). Gardner et al. (1987) reported that proportion of suitable habitat at landscape-scale might fundamentally change density-patch area relationships. These findings represent a compelling argument for structuring my landscape-scale assessment to focus on relationships of suitable habitat to squirrel populations. Therefore, I focused my assessment on the proportion of suitable habitat, or **Ratio of Optimum to Marginal Patch Area (=ROMPA; Lidicker 1988, Krohne 1997).**

Landscape-scale habitat evaluations and assessments of fragmentation often have employed island biographic theory (MacArthur and Wilson 1967, Harris 1984). Typically, suitable habitat surrounded by modified or unsuitable habitat is treated as "patches as islands" of suitable habitat surrounded by unsuitable habitat (Bowers 1997), with dispersal and movements influenced by the nature of dispersal barriers and corridors. My approach was to orient study sites along a gradient of landscapes with varying ratios of "optimum" habitat within a mosaic of intensively managed "marginal" habitat.

Description and quantification of high quality ("optimum") squirrel habitat exhibiting characteristics of source areas (Pulliam 1988) by Dodd et al. (1998, 2003) facilitated this landscape-scale assessment; such habitats exhibited stable density and consistent recruitment. Conversely, intensively thinned ("marginal") habitats displayed characteristics of sink habitats (Pulliam 1988), with large seasonal fluctuations in nonresident (immigrant) squirrel density (especially in proximity to optimum habitats) and poor recruitment (Dodd et al. 1998, 2003). I endeavored to select study sites along a ROMPA (Lidicker 1988, Krohne 1997) gradient of relatively consistent structural habitat condition for the extremes of optimum and marginal habitat.

STUDY AREAS

From 1999-2002, I conducted my study at 9 sites in north-central Arizona, located on the Coconino National Forest (Fig. 1). All of my 280-ha sites were within the ponderosa pine association of the montane coniferous forest community (Brown 1994), between 2,050-2,400 m elevation, and within the range of the Abert squirrel (*S. a. aberti*).

I employed a geographic information system (GIS) supervised classification using spectral signatures from LANDSAT satellite imagery and IMAGINE remote sensing software (ERDAS 1994) to identify 280-ha study sites composed of optimum and marginal habitats. The 280-ha size was considered adequate to investigate landscape relationships for the tassel-eared squirrel, and exceeded the 125-ha study areas used by Swihart and Nupp (1998) to examine landscape relationships for 4 species of tree squirrels. Aerial photography and ground validation were used to aid in selection of sites. My target minimum patch size within study sites was 31 ha, the size needed to accommodate my population sampling plots.

What's "ROMPA"?

ROMPA, or the ratio of optimum to marginal patch area (Lidicker 1988, Krohne 1997), was used as the basis for conducting my landscape-scale assessment. ROMPA is simply a measure of the relative proportions of a given area composed of 2 classes in a given mosaic of optimum and marginal habitat. For example, an area with 40% ROMPA is comprised of optimum habitat patches accounting for 40% of the total area, with the remaining 60% composed of marginal habitat patches. Thus, ROMPA is a means to characterize the proportion of suitable (e.g., optimum) habitat in an area of interest.

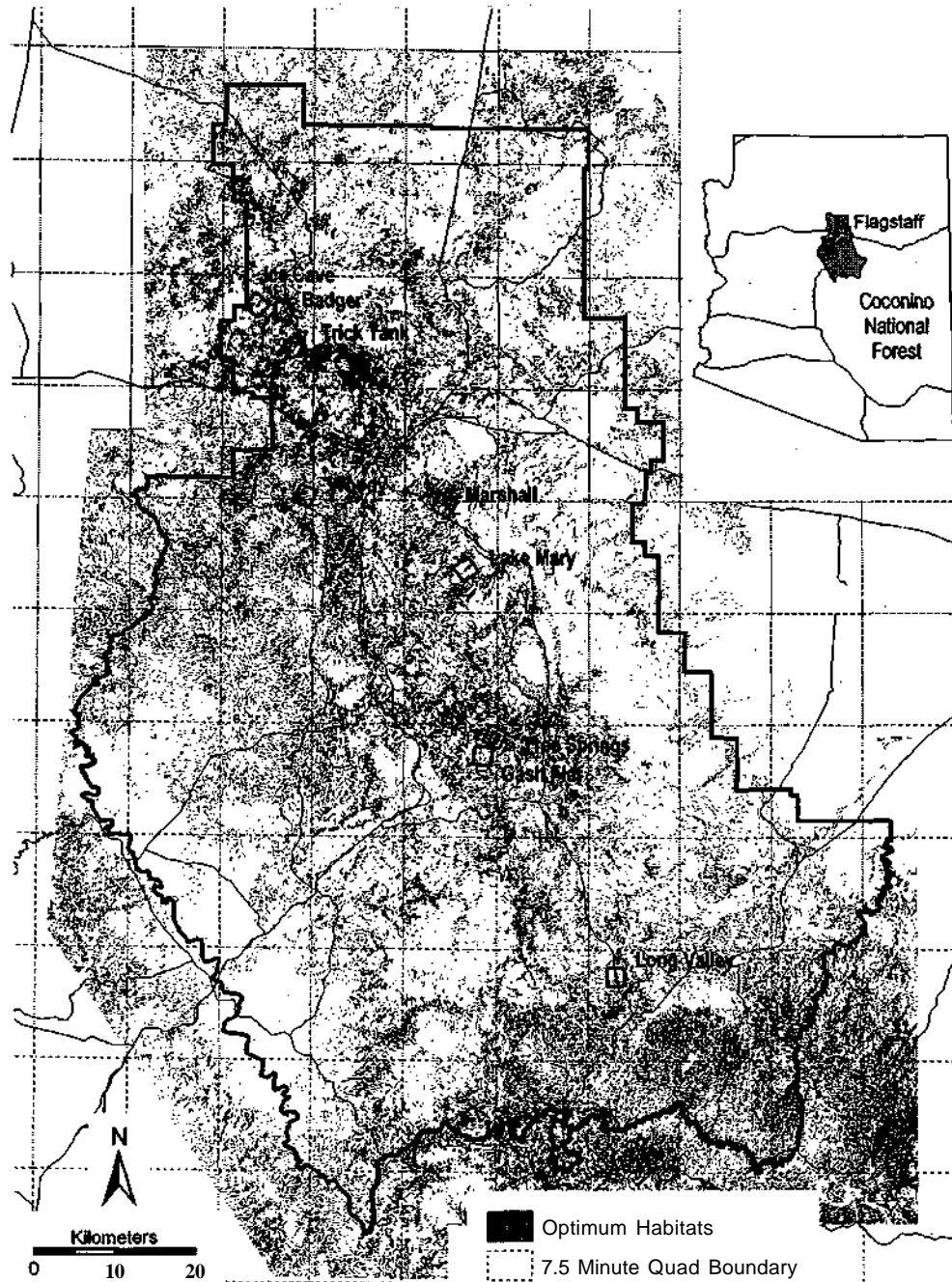


Figure 1. Location of 9 study sites on the Coconino National Forest, north-central Arizona, at which tassel-eared squirrel population dynamics and landscape-scale habitat condition were assessed 1999-2002. The shaded area corresponds to optimum habitats identified by GIS supervised classification using spectral signatures¹ from LANDSAT satellite imagery.

Optimum habitats exhibited multiple age classes with a large tree component (>50 trees/ha $45+$ cm diameter at breast height [dbh]), basal area >35 m²/ha, and $>50\%$ canopy closure with interlocking canopies. Optimum habitats generally were patchy and exhibited uneven-aged structure, with old growth or mature forest characteristics reflecting limited or no past logging (Fig. 2a). Conversely, marginal habitats had relatively few large trees, basal area <18 m²/ha, and $<30\%$ canopy closure. Marginal patches had been subjected to intensive snelterwood harvest (Schubert 1974) in the past (all >5 years prior to my study) and were predominately even-aged (Fig. 2b).

ROMPA for my sites, expressed as a percentage, ranged from 4.6 to 99.2% optimum habitat (Fig. 3). A disproportionate number of my sites (6) had a ROMPA near or below 50% to facilitate assessment of potential thresholds in squirrel population response along the gradient, which has occurred around 30% ROMPA for other species (Andren 1994).

SQUIRREL POPULATION DYNAMICS

I estimated tassel-eared squirrel density, juvenile recruitment, and survival at each study site. Separate estimates for each were derived for optimum and marginal habitat sampling plots and all sampling plots combined. Also, I computed mean study site population estimates from the sum of proportional area-weighted estimates for optimum and marginal habitats.

I used analysis of covariance (ANCOVA) to assess differences in mean squirrel density, recruitment, and survival rates between marginal and optimum habitat sampling plots. In my ANCOVAs, I controlled for study site effects (Hays 1981). Also for density, I used 90% prediction intervals derived from the feeding sign index regression model to assess differences in

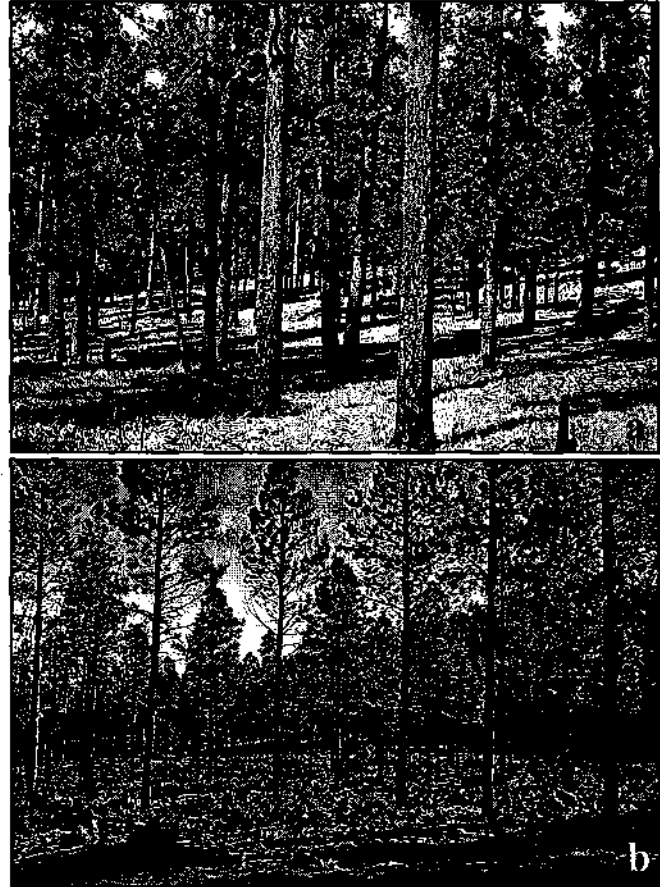


Figure 2. Typical structural habitat condition of optimum (a) and marginal (b) habitats associated with 9 study sites in north-central Arizona.

density estimates among study sites; non-overlapping intervals indicated differences.

Density

Depending on study site ROMPA, I located 2-4 density sampling plots 24 ha in size in marginal ($n = 13$ plots) and optimum ($n = 12$ plots) habitats, proportional to the area of each habitat class (Fig. 3). I estimated squirrel density using the feeding sign index technique developed by Dodd et al. (1998) and validated by Dodd and Rosenstock (*In prep*). This index provides for efficient and reliable estimation of squirrel density on numerous sampling plots which otherwise would be impractical with costly, labor-intensive capture-recapture techniques to

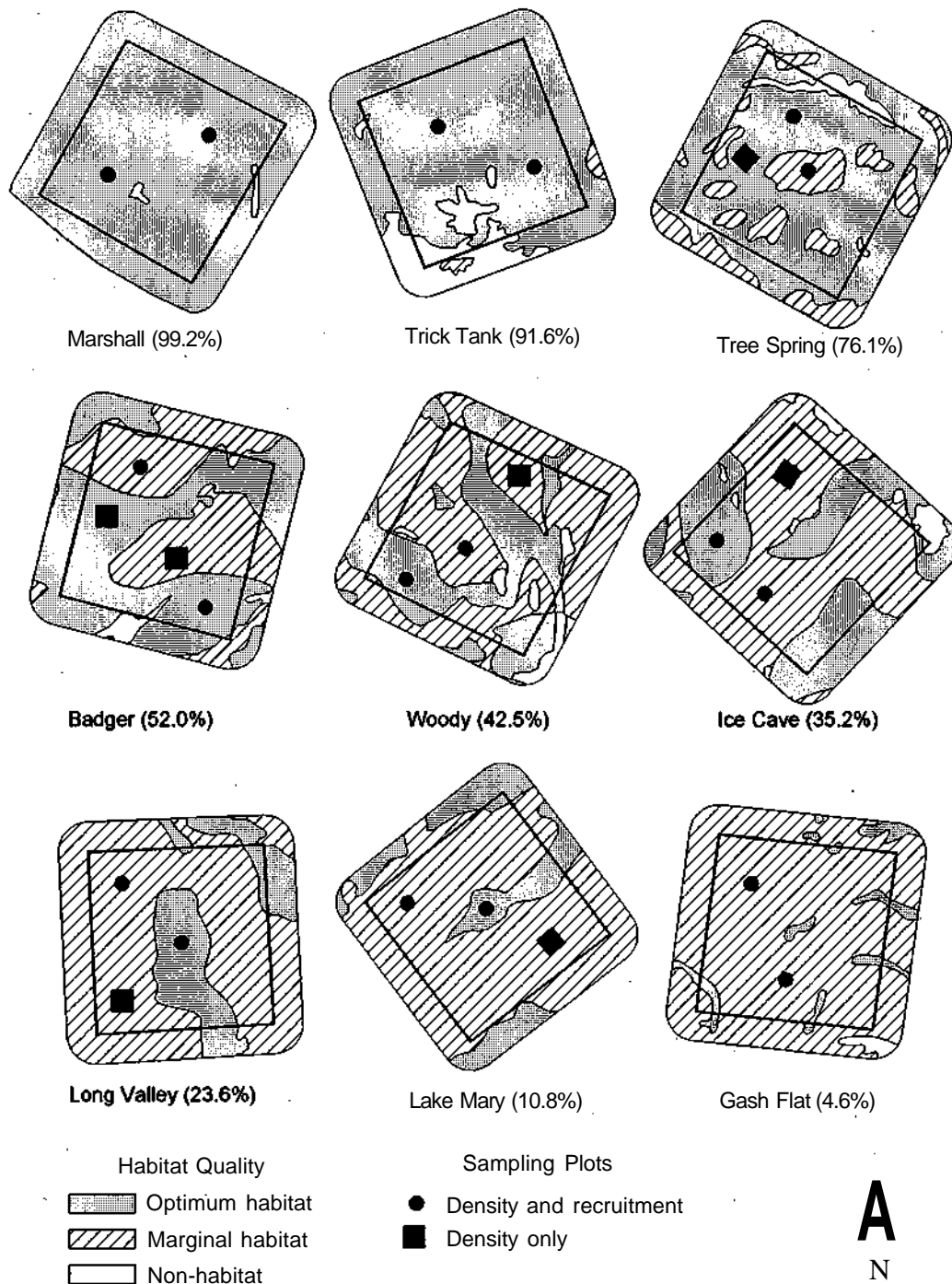


Figure 3. Landscape-scale composition of 9 280-ha study sites located in north-central Arizona. The sites were oriented along a gradient of ratio of optimum to marginal patch area (=ROMPA), with varying proportions of optimum and marginal habitats, as well as non-habitat such as meadows. The percentages refer to the proportion of optimum habitat at each study site. Dots denote the center of sampling plots where both density and recruitment were estimated, and squares denote the center of sampling plots where density only was estimated.

obtain density estimates (Pollock et al. 1990, Dodd et al. 1998).

I assessed the presence of fresh squirrel feeding sign (Rasmussen et al. 1975) that accumulated during late winter and spring on 256-m² plots located 17.5 m apart on 8 parallel transects; each transect was 70 m apart. Feeding sign counts were conducted in late-April and May each year. I entered the percentage frequency of occurrence of feeding sign on the 256-m² sampling plots and into a regression model to derive squirrel density estimates and 90% prediction intervals (Dodd et al. 1998).

Mean density on my optimum habitat plots was >2.5 times the density of squirrels on my marginal plots (Table 1). The highest mean marginal plot density occurred on study sites with intermediate (42-52%) ROMPA (Table 1). In 2000, marginal plot density for my site with 52% ROMPA (0.28 squirrels/ha) was higher than all other sites except that with 42% ROMPA, according to

the 90% prediction intervals. In 2001, marginal plot estimates for the sites with 42% and 52% ROMPA were higher than all other sites, except the site with 35% ROMPA.

The differential in density between my optimum and marginal plots was similar to that reported by Brown (1984), where unlogged sites supported 3-5 times higher density than logged sites. Patton et al. (1985) also found comparable differences in mean density at previously unlogged sites before (0.30-0.65 squirrels/ha) and after timber harvest (0.21-0.33). Mean annual density on high quality lightly logged sites (0.47 squirrels/ha) was twice that of heavily thinned sites (Dodd et al. 2003). Mean marginal plot density was highest at sites with intermediate (42-52%) ROMPA. This points to the apparent benefit of a habitat mosaic and associated edge effect, as described by Patton (1975a) and Dodd et al. (1998, 2003).

Table 1. Mean tassel-eared squirrel density estimates (\pm Standard Error; SE) from 9 study sites in north-central Arizona, 1999-2002. Estimates were derived from feeding sign index counts in April-May on 256 m² plots at marginal and optimum habitat sampling plots. Mean optimum plot density was greater than mean marginal plot density ($F = 75.0$, $df = 1, 15$, $P < 0.001$).

Study site (% ROMPA)	Mean squirrel density/ha (\pm SE)				
	Marginal plots	00	Optimum plots	in	Mean study site
Gash Flat (4.6)	0.14 (0.03)	2			0.14 (0.02)
Lake Mary (10.8)	0.09 (0.01)	2	0.40 (0.05)	1	0.15 (0.01)
Long Valley (23.6)	0.10 (0.02)	2	0.32 (0.07)	1	0.15 (0.03)
Ice Cave (35.2)	0.11 (0.03)	2	0.41 (0.06)	1	0.22 (0.03)
Woody (42.5)	0.23 (0.02)	2	0.41 (0.06)	1	0.35 (0.03)
Badger (52.0)	0.23 (0.04)	2	0.45 (0.04)	2	0.34 (0.03)
Tree Spring (76.1)	0.19 (0.04)	1	0.43 (0.06)	2	0.37 (0.05)
Trick Tank (91.6)			0.41 (0.06)	2	0.39 (0.05)
Marshall (99.2)			0.44 (0.06)	2	0.44 (0.06)
Mean	0.16 (0.01)	13	0.42 (0.02)	12	0.28 (0.02)

Landscapes, patches, classes, or plots?

In conducting research at the landscape scale, there is an inherent level of complexity associated with various habitat scales and sampling units. Our study sites were oriented along a ROMLA gradient at the *landscape-scale* (01-280 ha). Each study site landscape was composed of discrete *patches* of varying size of 2 *classes* (types) of habitat: optimum or marginal. Within 2-4 patches of 31 ha in size at each study site, squirrel density and juvenile recruitment were estimated on *sampling plots* at the *patch-scale*. To assess patch-scale habitat structural condition, observers counted trees on 12,010-ha *vegetation plots* at 2 sampling plots per Mud site.

Juvenile Recruitment

I estimated juvenile recruitment at 2 of the same sampling plots used to estimate density at each study site ($n = 8$ marginal and 10 optimum plots; Fig. 3). Incorporation of juveniles into a squirrel population is vital to its maintenance over time and to offset losses to mortality and emigration. Recruitment is also the population variable most sensitive to habitat change (Dodd et al. 2003). I established 8 x 8 trapping grids ($n = 64$ trap stations) with 70 m spacing at each sampling plot. I trapped and marked squirrels using the same techniques as Dodd et al. (1998, 2003). I relied on differences in body mass and morphological characteristics to separate juveniles from adults (Farentinos 1972, Keith 1965, Dodd et al. 2003). I assumed that squirrels were juveniles if body mass was ≤ 550 g (Dodd et al. 2003).

I conducted trapping to estimate recruitment for 5 consecutive days at each sampling plot, with all 18 plots trapped over a 12-day period in mid-late October. I expressed recruitment for marginal and optimum plots and study site means as juveniles/ha, using a buffered effective trapping area of 31 ha. This measure better

reflected variation in recruitment among plots than juveniles/adult female (Brown 1984, Dodd et al. 2003).

I captured 696 different squirrels during 23,040 trap days (Appendix 1), including 510 adults (243 females [49.1%], 252 males [50.9%], 15 unidentified) and 186 juveniles (87 female [47.5%], 96 males [52.4%], 3 unidentified). An average of 7.6 different adults were captured each year on marginal plots compared to 13.9 on optimum plots, and an average of nearly 4 times as many juveniles were trapped on optimum (3.8) versus marginal (1.0) plots (Appendix 1).

Optimum plot recruitment averaged 0.12 juveniles/ha and was significantly greater than mean recruitment on marginal plots (0.03 juveniles/ha; Table 2). Mean study site recruitment averaged 0.08 juveniles/ha, and ranged from 0.02-0.15 juveniles/ha (Table 2). Dodd et al. (2003) noted a similar difference in mean recruitment between high quality (0.24 juveniles/adult female) and intensively thinned sites (0.07 juveniles/adult female).

Survival

Tassel-eared squirrel survival is influenced by food quality and quantity (Keith 1965), habitat condition (Farentinos 1972, Dodd et al. 2003), and duration of winter snow cover (Stephenson and Brown 1980). To estimate squirrel survival rates between recruitment trapping periods, I used the "robust design" (Pollock 1982, Pollock et al. 1990). It combined pooled closed population capture-recapture histories and the open population Jolly-Seber model. Survival rates were derived for 2 intervals between trapping efforts (1999-2000 and 2000-2001) using the program JOLLY (Jolly 1965, Pollock et al. 1990).

Across all study sites, mean squirrel survival rates averaged 0.47 on marginal plots and 0.53 on optimum plots (Table 3), which were not significantly different. Mean study site survival averaged 0.49.

Table 2. Mean tassel-eared squirrel juvenile recruitment estimates (juveniles/ha) for 1999-2002, at 9 study sites in north-central Arizona. Estimates were derived from live trapping with 64 traps on 31 ha for 5 consecutive days in October. Mean optimum plot recruitment was greater than marginal plot recruitment ($F = 8.09$, $df = 1, 15$, $P < 0.012$).

Study site (% ROMPA)	Mean juvenile squirrel recruitment (\pm SE)					Mean study site
	Marginal plots	(\ll)	Optimum plots	(\ll)		
Gash Flat (4.6)	0.02 (0.01)	.2				0.02 (0.01)
Lake Mary (10.8)	0.02 (0.02)	1	0.03 (0.02)	1		0.02 (0.02)
Long Valley (23.6)	0.02 (0.01)	1	0.02 (0.01)	1		0.03 (0.01)
Ice Cave (35.2)	0.01 (0.01)	1	0.18 (0.09)	1		0.07 (0.03)
Woody (42.5)	0.04 (0.02)	1	0.16 (0.07)	1		0.09 (0.05)
Badger (52.0)	0.10 (0.07)	1	0.16 (0.07)	1		0.12 (0.06)
Tree Spring (76.1)	0.02 (0.01)	1	0.10 (0.05)	1		0.07 (0.03)
Trick Tank (91.6)			0.16 (0.09)	2		0.15 (0.08)
Marshall (99.2)			0.13 (0.07)	2		0.13 (0.07)
Mean	0.03 (0.01)	8	0.12 (0.02)	10		0.08 (0.02)

Table 3. Mean tassel-eared squirrel survival rates for 1999-2000 and 2000-2001, at 9 study sites in north-central Arizona. Estimates were derived from the robust design and program JOLLY capture using histories associated with trapping to estimate juvenile recruitment 1999-2002.

Study site (% ROMPA)	Mean squirrel survival rate (\pm SE)					Mean study site
	Marginal plots	($\bullet\bullet$)	Optimum plots	(\gg)		
Gash Flat (4.6)	0.51 (0.16)	2				0.49 (0.15)
Lake Mary (10.8)	0.39 (0.30)	1	0.58 (0.08)	1		0.36 (0.28)
Long Valley (23.6)	0.25 (0.14)	1	0.27 (0.09)	1		0.25 (0.13)
Ice Cave (35.2)	0.76 (0.12)	1	0.76 (0.08)	1		0.76 (0.11)
Woody (42.5)	0.75 (0.30)	1	0.44 (0.16)	1		0.62 (0.24)
Badger (52.0)	0.32 (0.10)	1	0.76 (0.09)	1		0.55 (0.10)
Tree Spring (76.1)	0.30 (0.15)	1	0.30 (0.07)	1		0.30 (0.09)
Trick Tank (91.6)			0.53 (0.09)	2		0.49 (0.08)
Marshall (99.2)			0.55 (0.13)	2		0.55 (0.13)
Mean	0.47 (0.07)	8	0.53 (0.16)	10		0.49 (0.14)

My estimates of mean annual squirrel survival fell within the range of 0.44-0.78 over 8 years reported by Stephenson and Brown (1980). However, it is well below the estimate for adult squirrel survival of 0.74 (Lema 2001) or the average survival of 0.78 reported by Dodd et al. (2003).

HABITAT ASSESSMENT

Landscape-Scale Analysis

I delineated all marginal and optimum habitats, as well as non-habitat (e.g., meadows) patches on LANDSAT satellite imagery and aerial photos, and then digitized and entered them onto GIS. I employed FRAGSTATS spatial analysis software (McGarigal and Marks 1995) to quantify landscape structure and composition. Landscape variables were computed at both the class (marginal and optimum habitats) and landscape scales. I computed 8 class-scale variables (Appendix 2) and 18 landscape-scale variables (Appendix 3) with FRAGSTATS for my 280-ha study sites (McGarigal and Marks 1995).

Patch-Scale Analysis

I measured habitat characteristics reported to influence tassel-eared squirrel populations (Ratcliff et al. 1975, Pederson et al. 1987, Patton 1984, Dodd et al. 2003). At each recruitment-sampling plot, I randomly selected 12 trapping stations and randomly located 0.01-ha circular vegetation plots in the same manner as Dodd et al. (2003).

Within each vegetation plot, I measured dbh for ponderosa pine ≥ 2.5 cm dbh. I estimated canopy cover by vertical projection with a staff-mounted, self-leveling sighting periscope (Ganey and Block 1994), using 100 periscope sighting points/plot as per Dodd et al. (1998, 2003). I measured the relative incidence of trees with "interlocking" canopy crowns ≤ 1.5 m of each other, the distance I observed squirrels readily jumping

from tree to tree. I counted continuously interlocking canopy trees >15 cm dbh at 5 points at each vegetation plot in the same manner as Dodd et al. (2003). I calculated basal area and tree density corresponding to vegetation structural stage (VSS) diameter classes (Reynolds et al. 1992): VSS 2 (2.5-12.5 cm dbh), VSS 3 (12.6-30.3 cm dbh), VSS 4 (30.4-45.6 cm dbh), and VSS 5 and 6 combined (>45.7 cm dbh).

Patch-scale structural characteristics for optimum and marginal habitats are summarized in Appendix 4. Mean basal area of my optimum patches (29.0 m²/ha) was nearly twice that of marginal patches (15.9 m²/ha). Optimum patch canopy closure averaged 54.2% versus 31.6% for marginal patches. The number of interlocking canopy trees per point averaged 26.6 and 4.6, respectively for optimum and marginal plots. Optimum patches averaged 532.0 ponderosa pine stems/ha compared to 226.0 at marginal patches. Optimum patches exhibited more large trees/ha >45 cm dbh, 146.4 versus 88.0, as well as small trees 2.5-22.8 cm dbh, 324.8 compared to 104.9, respectively.

My goal of orienting study sites along a ROMPA gradient of marginal and optimum habitats of consistent structural condition was not met fully. Though marginal sampling plots exhibited clustering along gradients of structural habitat condition (Fig. 4), these plots combined with the optimum sampling plots reflect considerable variation in structural habitat condition (Fig. 4, Appendix 4). As such, structural habitat condition was not controlled sufficiently to limit its potential influence on squirrel population response in conjunction with landscape composition.

POPULATION AND HABITAT RELATIONSHIPS

I used forward stepwise multiple regression to assess relationships among

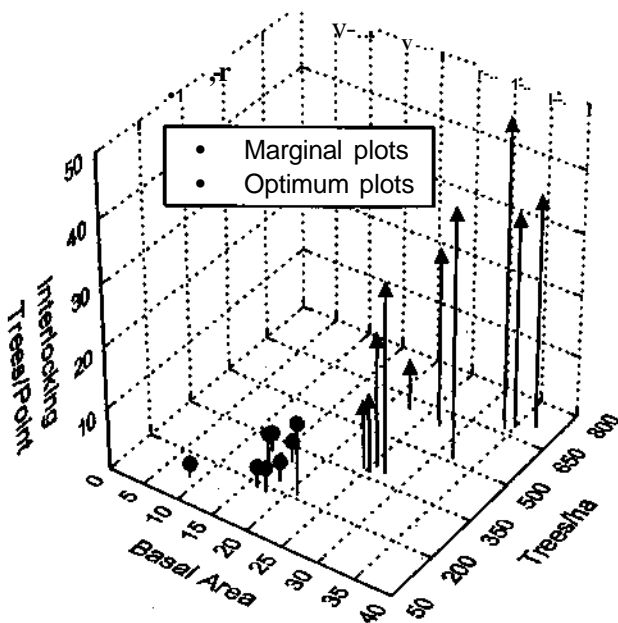


Figure 4. Ordination graph for patch-scale structural habitat variables associated with marginal ($n = 8$) and optimum ($n = 10$) sampling plots at 9 study sites in north-central Arizona.

mean tassel-eared squirrel population variables (density, recruitment, and survival) and habitat variables at the patch and landscape scales (Neter et al. 1996). I conducted separate regression analyses for marginal and optimum habitat sampling plots, as well as all sampling plots combined. Consistent with my plot sample sizes, I limited the number of independent variables in multiple regression models to 2 (Neter et al. 1996); otherwise, I imposed no other criterion for independent (habitat) variable selection in regression models (e.g., any combination of patch- and landscape-scale variables could be added to models). I assessed the relative importance of independent variables in the models using partial regression analysis.

Stepwise multiple regression yielded significant relationships among tassel-eared squirrel population and patch and landscape-

scale habitat variables for all sampling plot analyses, with the exception of survival for marginal and combined sampling plots (Table 4). In all 7 significant models, patch-scale structural habitat condition and landscape-scale variables were both added, underscoring their joint influence on tassel-eared squirrel populations. In most instances patch-scale structural habitat parameters had larger partial regression coefficients, indicating greater influence in the models (Table 4).

Mean squirrel density was influenced most by the number of interlocking trees/point on optimum plots, mean nearest neighbor distance to optimum patches on marginal plots (inverse relationship), and basal area on all sampling plots combined (Table 4). ROMPA was also added to models that describe the relationships to squirrel density on optimum and all plots combined, while mean canopy closure was also incorporated into the model for marginal plots (Table 4).

Mean juvenile recruitment on optimum plots was inversely related to the number of small sapling-sized trees, and secondarily to landscape edge density (Table 4). The number of interlocking canopy trees most influenced recruitment on marginal sampling plots, along with ROMPA, whereas ROMPA had the larger partial regression in the model for combined sampling plots (Table 4).

Like optimum plot recruitment, optimum plot survival was primarily related (inversely) to the number of small sapling-sized (VSS 2) trees/ha; ROMPA was also added to the model (Table 4). No simple or multiple regression relationships were established for survival on marginal or combined plots.

Patch-Scale Relationships

Tassel-eared squirrels have relatively low mobility. Home ranges for squirrels vary by season, sex, age, habitat condition, and food

Table 4. Results for forward stepwise multiple regression of tassel-eared squirrel population parameters and patch- and landscape-scale habitat variables measured 1999-2002, at 9 study sites in north-central Arizona, including coefficient of multiple determination (R^2), intercept (fio), independent variables (patch and landscape habitat) included in the regression models and their partial regression coefficients (P_i and fa).

Population parameter	Sample plots	Stepwise Multiple Regression Results								
		Multiple R^2	P	β_0	Patch variable	P_i	P	Landscape variable	β_2	P
Density	Optimum	0.808	0.003	0.298	Interlocking trees	0.841	0.001	ROMPA (\sin^{-1})	0.418	0.040
	Marginal	0.819	0.014	-0.101	Canopy closure (\sin^{-1})	0.538	0.043	Nearest neighbor	-0.573	0.036
	All	0.886	0.001	-0.109	Basal area	0.790	0.001	ROMPA (\sin^{-1})	0.301	0.006
Recruitment	Optimum	0.848	0.001	0.150	VSS 2 trees/ha	-1.038	0.001	Edge density	0.700	0.004
	Marginal	0.923	0.006	-0.014	Interlocking trees	0.832	0.008	ROMPA (\sin^{-1})	0.193	0.084
	All	0.597	0.002	-0.008	Interlocking trees	0.363	0.070	ROMPA (\sin^{-1})	0.551	0.019
Survival	Optimum	0.823	0.002	1.061	VSS 2 trees/ha	-1.134	0.001	ROMPA (\sin^{-1})	-0.688	0.011
	Marginal	No significant relationships established								
	All	No significant relationships established								

availability, and have been reported as ranging from 1.3 ha (Farentinos 1979) to 26.0 ha (Lema 2001). Sieg (2002) found that squirrel home ranges on 6 of my 9 sites ranged from 7.8 to 14.2 ha for juvenile females ($n = 25$) and 7.8 to 12.7 ha for adult females ($n = 14$). Given such home range sizes, it is not surprising that squirrels responded primarily to patch-scale habitat influences and only secondarily to landscape, based on partial regression coefficients (Table 4).

Patton et al. (1985) and Pederson et al. (1987) stressed the importance of overstory tree dumpiness and canopy closure to tassel-eared squirrels. The number of interlocking canopy trees/point was the patch-scale attribute most frequently added to multiple regression models for squirrel density (optimum plot) and recruitment (marginal and all plots). Percentage canopy closure was incorporated into another model (marginal plot density). These results complement the findings of Dodd et al. (2003) where the number of interlocking trees was strongly related to squirrel recruitment at the patch scale. Patton (19756) reported that 92% of squirrel nests were found in trees growing inside a group, with 75% having 3 or more interlocking canopy trees. Aside from nest placement, interlocking canopies are needed for juveniles (and adults) traveling from maternal nests and as cover for protection from aerial and ground predators (Austin 1990). States and Gaud (1997) found that hypogeous fungi fruiting body production was strongly and positively correlated with canopy cover and basal area in ponderosa pine forests, and fecal fungi content was strongly tied to squirrel recruitment (Dodd et al. 2003).

Basal area was incorporated into the density model for all sampling plots. Other studies found basal area to affect tassel-eared squirrel populations. Ratcliff et al. (1975)

found a significant positive relationship between density and basal area. Patton et al. (1985) and Pederson et al. (1987) reported lower squirrel density, recruitment, and fungi associated with reduced basal area and canopy closure.

Sapling-sized VSS 2 trees, considered to be far more prevalent today than under presettlement forest conditions (Johnson 1994, Mast et al. 1999, Allen et al. 2002) contribute to decreased forest health and increased risk of catastrophic crown fire (Covington and Moore 1994, Zimmerman 2003). Stands with high densities of saplings exhibited low productivity of fungal sporocarps (fruiting bodies), reported to be a consequence of competition among trees that reduces nutrients available for mycorrhizal fungi (States and Gaud 1997). Such competition and reduced production of fungal sporocarps likely accounts for the inverse relationship between sapling tree density and optimum plot recruitment, consistent with Dodd et al. (2003), as well as the relationship with optimum plot survival.

Landscape-Scale Relationships

With 26 total landscape variables available for regression analysis, ROMPA - was the landscape-scale variable added in the stepwise procedures for 5 of the 7 significant models (Table 4). This indicates greater success in my attempt to focus on this landscape parameter compared to my attempt to control patch-scale structural habitat condition. ROMPA, or the proportion of suitable habitat in the landscape was considered important in describing wildlife response by Andren (1994), Andren and Delin (1994), and Gardner et al. (1987). In the other 2 significant models, mean nearest neighbor distance (to optimum patch) and edge density were incorporated in the stepwise procedure (Table 4). Edge density is the sum of the lengths for all edge segments within my 280-ha study sites

divided by the area (McGarigal and Marks 1995). Highest edge density and peak recruitment on optimum plots occurred on intermediate ROMPA (35-76%) sites, pointing to the influence and importance of edge effect and patch mosaic pattern.

The inverse relationship between mean optimum patch nearest neighbor distance and marginal plot squirrel density may reflect the influence of proximity to high quality source habitats from which squirrels immigrate to marginal habitats (Van Horn 1983, Pulliam 1988). It may also reflect the indirect influence of edge effect where marginal patch squirrels benefit from the juxtaposition of optimum and marginal habitats, as described by Lema (2001) and Dodd et al. (2003). In the latter case, squirrels are able to efficiently use both marginal and optimum habitats at sites with lower mean nearest neighbor distances and capitalize on seasonally available food sources found in marginal patches (e.g., pine cone seed) while at the same time taking advantage of cover associated with optimum patches (Dodd et al. 1998).

POPULATION RESPONSE THRESHOLDS

I evaluated the existence of thresholds in squirrel population response along the ROMPA gradient using piecewise linear regression (Neter et al. 1996). With this technique, linear regression lines are broken into 2 separate regression lines at a breakpoint, as either continuous or discontinuous lines. I applied a lack of fit F -test to assess whether the piecewise regression model provided a significantly better fit to the relationships between population response and ROMPA (R. St. Laurent, Northern Arizona University, *personal communication*). This test compared the loss functions for each technique.

Where piecewise linear regression models were determined to provide a better fit over linear regression models, I evaluated where the independent variable (ROMPA) breakpoint occurred by comparing loss functions associated with each ROMPA interval between study sites. I determined the breakpoint (= threshold) to occur where the loss function for the ROMPA intervals was minimized.

Of the 9 comparisons made between linear and piecewise linear regression techniques for squirrel population parameters and ROMPA at optimum and marginal plots and mean study sites, the piecewise linear relationship constituted a better fit for 3 (Fig. 5). For the 2 multiple regression models to which ROMPA was not added (Table 4), nonlinear thresholds in population response to ROMPA were identified for both. Though the linear relationship between mean study site squirrel density and ROMPA itself was significant ($r^2 = 0.847$, $P < 0.001$, $n = 9$), the discontinuous piecewise linear relationship accounted for 13% more variation in density (97.6%) and constituted a better fit ($F_{3,4} = 7.08$). The discontinuous piecewise linear regression relationship between mean marginal plot density and ROMPA (Fig. 3) explained 152% more variation (98.0%) over the linear relationship and provided a better fit ($F_{3,2} = 22.42$). The breakpoint for both piecewise density relationships occurred between 35-42% ROMPA (Fig. 5).

Piecewise linear regression explained 278% more variation in mean juvenile recruitment on optimum plots than linear regression ($F^* = 18.20$). This discontinuous relationship exhibited a breakpoint in juvenile recruitment between 24-35% ROMPA, with negligible recruitment below this threshold (Fig. 5).

My determination of landscape thresholds in ROMPA with regard to both density and recruitment parallel those reported by Andren (1994), Bowers and

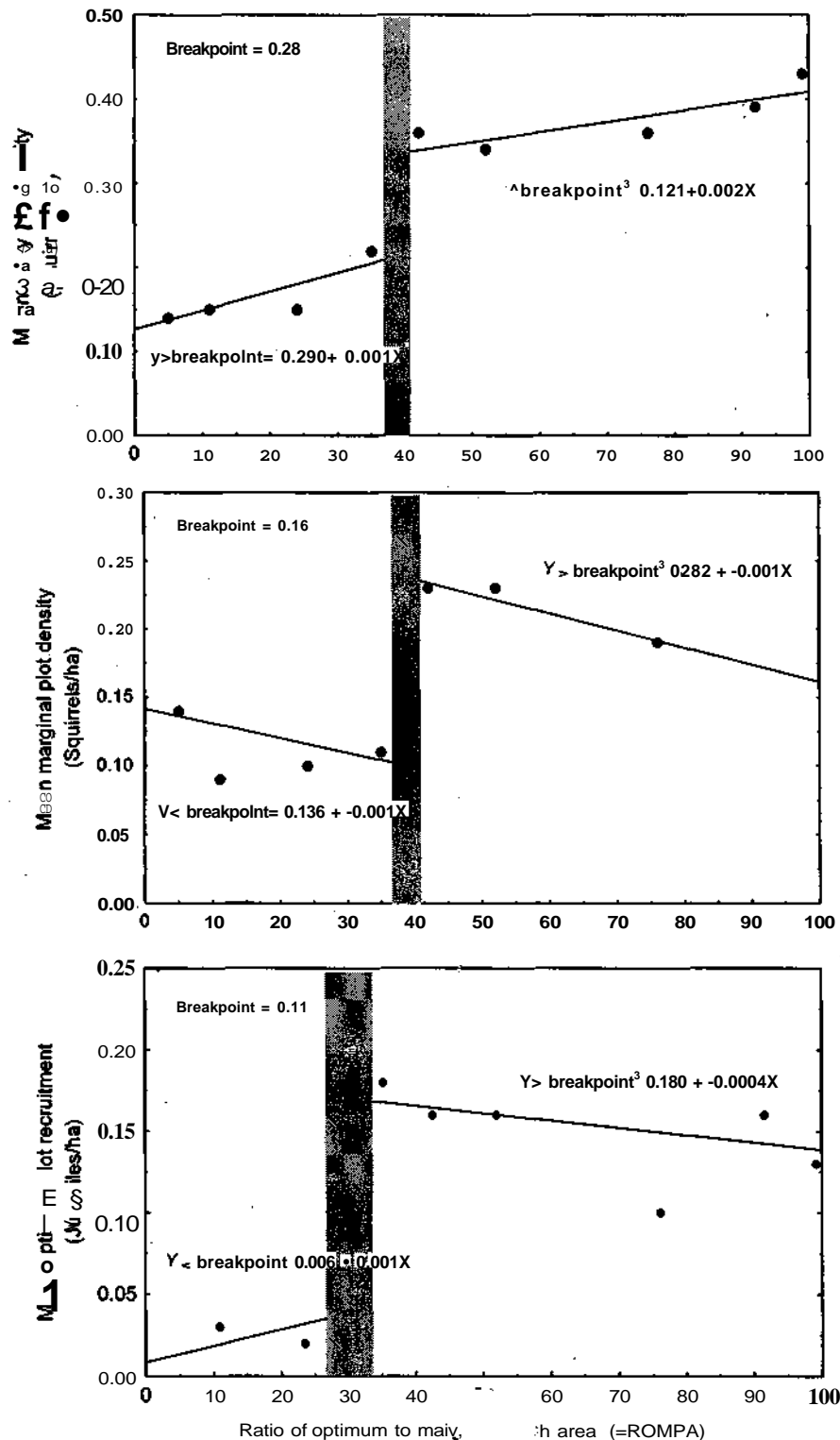


Figure 5. Piecewise linear regression relationships between tassel-eared squirrel mean study site density (top), mean marginal plot density (middle), and mean optimum plot recruitment (bottom) and landscape-scale ratio of optimum to marginal patch area (ROMPA) for 9 study sites in north-central Arizona, 1999-2002. The lines and regression equations reflect different linear relationships above and below breakpoints in the dependent variable (density or recruitment). The shaded areas correspond to the intervals in which thresholds in ROMPA occur.

Matter (1997), Krohne (1997), and Mönkkönen and Reunanen (1999). Andren (1994) illustrated through modeling how the relative importance of habitat loss (proportion of suitable habitat), patch area, and isolation differ under varying degrees of habitat fragmentation. At 60% suitable habitat, his continuous landscape began to break into patches, yet all patches shared common edges; hence patch isolation was nonexistent. Between 60% and 50% suitable habitat, maximum patch area declined rapidly (by 95%) as there were fewer and smaller patches, but isolation remained relatively low. Patch isolation did not occur to a high degree until suitable habitat was reduced to 40%. Once the proportion of suitable habitat dropped below 20%, further reductions resulted in an exponential increase in the distance between patches and isolation.

In reviewing 35 bird and mammal studies, Andren (1994) reported that thresholds in population response generally occurred around 30% suitable habitat, and possibly even as low as 10% depending on the relative mobility of the species and condition of surrounding matrix habitats (Lindenmayer and Franklin 2002). Kareiva and Wennergren (1995), Mönkkönen and Reunanen (1999), and Lindenmayer and Franklin (2003) stressed that effects of habitat loss below such thresholds could be delayed and irreversible even after first realized.

Indeed, Patton (1984:412) cautioned 20 years ago that "optimum habitats (for tassel-eared squirrels) likely do not exist in many areas due to the intensity of timber harvest in Arizona." Management that focuses on the lower threshold level established for optimum plot recruitment (24-35% ROMPA) compared to those for density (35-42%) could lead to delayed cascading fragmentation effects (Lindenmayer and Franklin 2002), particularly since recruitment typically is more sensitive to habitat change

(Dodd et al. 2003). As such, I suggest that thresholds in tassel-eared squirrel population response occur in the neighborhood of 35 % ROMPA.

With presettlement forest conditions generally described as being much more open and park-like than contemporary forests (Covington and Moore 1994, Mast et al. 1999) including tree densities of 62-100/ha, basal areas of 9-15 m²/ha, and canopy closures of 17-22% (Mast 2003), why do thresholds in squirrel populations exist today along a gradient of optimum habitat conditions of considerably greater tree density, basal area, and canopy closure? There is considerable debate regarding the natural range of variability in presettlement forest conditions, as well as the uncertainties associated with reconstruction techniques (Allen et al. 2002). Most accounts of presettlement forest structure stress the high degree of variability on the landscape (Cooper 1960, White 1985).

This high variability is best illustrated by Fulé et al. (2002) for several ponderosa pine reference sites in northern Arizona. Though reconstructed basal area averaged 16.0 m²/ha, it ranged from 4.0-45.7 m²/ha. Reconstructed tree density/ha averaged 96 trees/ha, yet ranged from 20.1-409.6 trees/ha. Though the extent of relatively dense forest conditions approximating (or even exceeding) my optimum habitat conditions is unknown, it is apparent that patches of such habitat were nonetheless present on the presettlement landscape.

MANAGEMENT GUIDELINES

My results provide valuable insights into the presence of landscape-scale habitat thresholds and the importance of high quality suitable habitat reserves. However, they also corroborate recommendations of Wiens (1994), Lindenmayer and Franklin (2002), and others who stressed that emphasis must

be placed on both reserves (habitat fragments) and surrounding matrix habitats to fully understand and manage forest landscapes. Differences in ecological phenomena inherent to a variety of scales make experiments difficult (Wiens 1989, Cullinan and Thomas 1992, Lindenmayer and Franklin 2002), and selection of an appropriate scale at which to work important (Kotlair and Wiens 1990). Though I failed to fully limit patch-scale structural habitat influences on tassel-eared squirrel population response, this reflects true ecological complexity where squirrels respond to habitat at multiple scales (Patton 1992).

Lindenmayer and Franklin (2002) stressed that maintaining suitable habitat for species through a combination of reserve (including midspatial-scale "meso-reserves" comparable to my optimum patches) and matrix management at multiple scales should be the overarching objective for maintaining forest biological diversity. My results support an integrated approach to ponderosa pine forest ecosystem restoration that includes the following elements: 1) maintenance of meso-reserves, 2) thinning of the sapling (VSS 2) tree component within meso-reserves, 3) management of matrix habitats surrounding meso-reserves, and 4) integrated landscape design incorporating multiple prescriptions.

Maintenance of Meso-Reserves

My study points to the importance of maintaining patches of suitable habitat as meso-reserves (Lindenmayer and Franklin 2002) on the landscape at or above the 35% ROMPA threshold. Since I focused on squirrel population relationships to ROMPA versus patch size, my ability to make definitive recommendations on the appropriate size of meso-reserves is limited. Though the mean optimum patch size associated with my site at the 35% ROMPA threshold is 20.4 ha (Appendix 3), the largest

What's a "Meso-Reserve"?

Preservation of large ecological reserves has been a cornerstone of conservation biology for decades. Such reserves may encompass entire watersheds, national parks, wilderness areas, or other similar protected areas. Lindenmayer and Franklin (2002) termed smaller, midspatial-scale protected areas "meso-reserves." In my case, meso-reserves correspond to the patch scale. Though smaller in size than reserves, they are larger than aggregated humps of interlocking trees exhibiting variable basal areas, hence the reference to "meso," or middle. Such meso-reserves are integral to maintaining squirrel populations above the KOMPA threshold of 35%.

patch index (LPI) must also be considered. LPI, or the area of the largest optimum patch divided by total landscape area (McGarigal and Marks 1995), for the site corresponding to the 35% threshold is 13.0% (Appendix 2), yielding a patch size of 36.4 ha.

As such, I recommend that at least 1 meso-reserve should be 36 ha in size while at least 3 others should approximate the 20 ha mean patch size for each 280-ha planning area (Fig. 6), consistent with reserve design principles (Lindenmayer and Franklin 2002).

Within a landscape project area, habitats that best approximate my optimum habitat plots should be designated and managed as meso-reserves. Meso-reserves should be comprised of multi-aged habitat patches best exhibiting: 1) basal area $>35 \text{ m}^2/\text{ha}$, 2) $>50\%$ canopy closure with interlocking canopies, and 3) a well-defined large tree component with >50 VSS 5-6 ($>45 \text{ cm dbh}$) trees/ha.

Thinning Within Meso-Reserves

Given the negative relationship between small, sapling-sized VSS 2 trees and squirrel recruitment and survival in optimum habitats, thinning of sapling-sized trees within the forest understory of meso-reserves is

warranted. Thinning will not only yield benefit to squirrels, but also will benefit hypogeous fungi on which they feed (States and Gaud 1997), improve forest health and tree growing conditions (Mast 2003), and reduce the risk of wildfire (Zimmerman 2003). I recommend use of "thinning-from-below" prescriptions or prescribed fire within meso-reserves to target sapling-sized trees.

Matrix Management

Patch-scale structural habitat condition within the matrix surrounding meso-reserves has a strong influence on species occurrence within the landscape, and even partially suitable habitat may lessen the impact of fragmentation (Lindenmayer and Franklin 2002). This was true with my study, as squirrel population response was influenced most by patch-scale habitat condition. Even within marginal habitats, patch-scale structural habitat parameters including the number of interlocking trees, basal area, and canopy closure influence squirrel density and recruitment regardless of ROMPA.

Aggregated retention of clumps of overstory trees providing interlocking canopies and variable basal areas throughout the matrix will provide for small, distributed refugia (Lindenmayer and Franklin 2002). Harvest prescriptions that provide variable-density thinning will retain or enhance structural heterogeneity (Carey and Johnson 1996, Chambers and Germaine 2003).

Compared to basal areas associated with reference condition-based full restoration prescriptions of approximately 15 m²/ha (Mast 2003), I recommend variable thinning within matrix habitats to retain a minimum average basal area of 25 m²/ha. Such an average basal area should provide for sufficient interlocking canopies as well.

Integrated Landscape Design

Mast (2003) stressed that no single prescription or model should be applied in

forest restoration, owing to the inherent variability of ponderosa pine forest ecosystems. Allen et al. (2002) and Chambers and Germaine (2003) recommended use of prescriptions that achieve incremental forest restoration under multiple harvest entries to minimize short-term impact and preserve critical processes.

I modeled mean squirrel density and recruitment under different proportions of the landscape under optimum habitat meso-reserves, a full restoration prescription employing reconstruction techniques (Fulé et al. 1997, Mast 2003), and a matrix prescription with aggregated retention of more interlocking trees and higher variable basal area (Table 5). Juvenile recruitment increased incrementally under a 10% meso-reserve (ROMPA) scenario and increasing proportions of remaining area in matrix prescription. At 35% of the area in meso-reserves and equal amounts (32.5%) of remaining habitat in full restoration and matrix prescriptions, recruitment plateaued even with higher ROMPA and a greater proportion of matrix habitat (Table 5). Density increased up to the point that 50% each of the habitat was incorporated in meso-reserves and matrix prescriptions. However, density associated with a landscape design with 35% ROMPA and equal amounts (32.5%) of full restoration and matrix management accounted for nearly 90% of the peak density (Table 5).

Thus, benefits to tassel-eared squirrel populations are relatively minor above a landscape prescription with approximately one third each of the area in meso-reserves, full restoration, and matrix prescriptions. Such a prescription (Fig. 6) optimizes attainment of squirrel needs (both in meso-reserves and matrix habitats) and treatment of priority areas to achieve full restoration objectives and wildfire risk reduction, while preserving forest processes and reducing short-term impact on treated matrix areas.

Table 5. Modeling projections of tassel-eared squirrel density and recruitment under varying proportions of landscapes within different management prescriptions, including optimum habitat meso-reserves, full restoration (Mast et al. 1999), and intermediate variable thinning matrix prescriptions. Projections determined by multiple regression models (see Table 4) for optimum (meso-reserve) and marginal habitats with varying ROMPA, basal area (density), and number of interlocking trees (recruitment).

Proportion of landscape under different prescriptions				
% area in optimum habitat meso-reserves ^a	% area under full restoration R _x ^b	% area under matrix management R _x ^c	Mean density (squirrels/ha)	Mean recruitment (juveniles/ha)
10.0	90.0	0	0.17	0.02
10.0	45.0	45.0	0.18	0.03
10.0	0	90.0	0.27	0.03
35.0	65.0	0	0.25	0.05
35.0	32.5	32.5	0.32	0.07
35.0	0	65.0	0.35	0.07
50.0	50.0	0	0.31	0.07
50.0	25.0	25.0	0.34	0.07
50.0	0	50.0	0.37	0.07

^aDensity model basal area = 40m²/ha; recruitment model interlocking trees = 135 trees/point

^bDensity model basal area = 15m²/ha; recruitment model interlocking trees = 20 trees/point

^cDensity model basal area = 25m²/ha; recruitment model interlocking trees = 50 trees/point

CONCLUSIONS

In pursuing my research objectives, I added substantially to the understanding of the joint role of patch- and landscape-scale habitat in influencing tassel-eared squirrel populations. Given the immense task of restoring ponderosa pine forest ecosystems in the Southwest, my findings underscore the potential to maintain and even benefit wildlife while pursuing forest restoration goals. **Patch-size meso-reserves of high quality habitat at or above threshold levels of 35% ROMPA are critical to maintaining squirrel populations, and will benefit other wildlife species and forest processes.** Recognizing the benefits associated with

thinning the sapling-sized VSS 2 component of meso-reserves to squirrels, forest health, and wildfire risk reduction enhances the likelihood for meso-reserve designation and application within an overall forest restoration and wildfire risk reduction context.

Application of a variety of prescriptions within matrix areas surrounding meso-reserves is also important to maintaining or enhancing squirrel populations, short-term forest function and processes, and forest biological diversity. Effective integration of prescriptions employing aggregated retention of forest structure important to squirrels and other wildlife, reconstruction-based restoration prescriptions, and meso-reserves

has the potential to optimize attainment of ponderosa pine forest ecosystem restoration and wildlife population goals.

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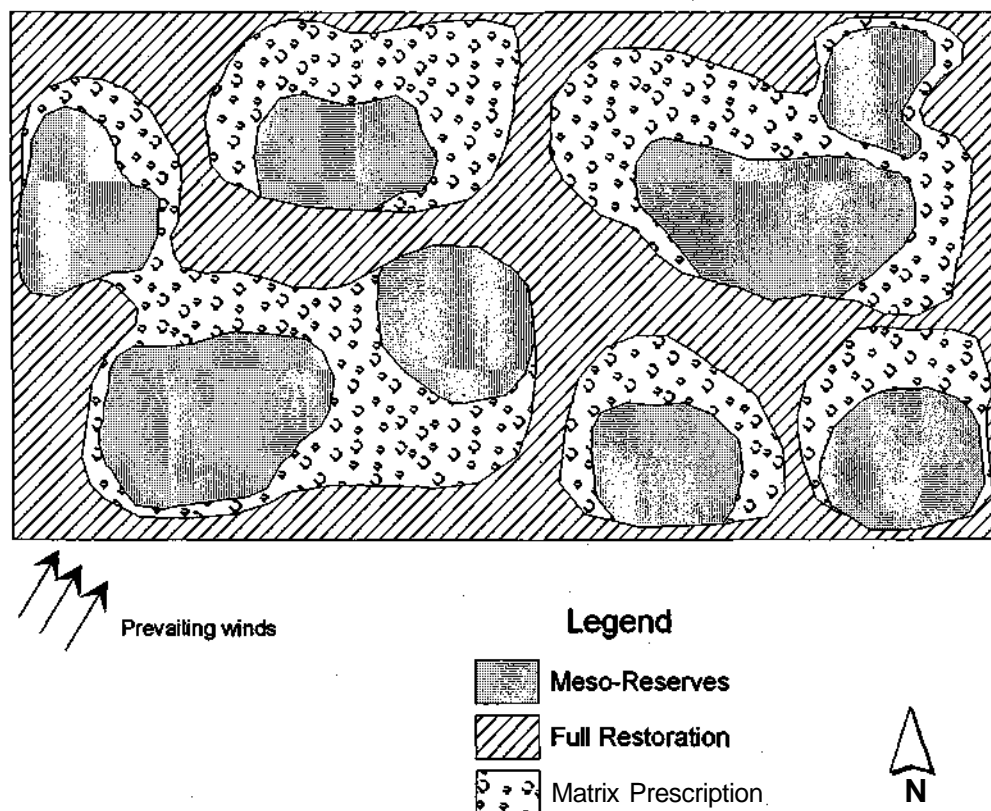


Figure 6. Integrated landscape design which optimizes tassel-eared squirrel density and recruitment, comprised of 75% each of the area under meso-reserve, variable thinning matrix management, and full restoration (Mast 2003) prescriptions. The integrated design addresses prevailing wind patterns and wildfire risk reduction, as well as reserve design principles (Lindenmayer and Franklin 2002).

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Metric to English Unit Conversions			
Measure	Metric	By	= English
Unsal area	m ² /IKI	X4.2X	ly/ae
Tree density	stems/ha	4.2.47	stems/ae
Diameter at breast height	cm Jbh	X 0.43	in dhh
Area	IKI	X 2.47	tic
Elevation/ distance	m	X3.28	ft

Appendix 1. Number of different tassel-eared squirrels captured and juvenile recruitment estimates on marginal ($n = 8$) and optimum ($n = 10$) plots during live trapping conducted in October 1999-2002 to estimate juvenile recruitment at 9 study sites in north-central Arizona.

Year	Sampling plot	No. different squirrels captured				Mean recruitment	
		Adults					
		\$	♂	Unknown	Juveniles	Juveniles/ha	Juveniles/?
1999	Marginal	17	27	0	10	0.04	0.59
	Optimum	74	71	0	71	0.23	0.96
	All	91	125	0	81	0.14	0.89
2000	Marginal	50	45	3	2	0.01	0.04
	Optimum	113	113	11	6	0.02	0.05
	All	163	158	14	8	0.01	0.05
2001	Marginal	16	19	1	21	0.08	1.31
	Optimum	32	43	2	71	0.23	2.22
	All	48	62	3	92	0.16	1.92
2002	Marginal	28	36	1	0	0	0
	Optimum	44	51	1	5	0.02	0.11
	All	72	87	2	5	0.01	0.08
Total	Marginal	111	127	6	33	0.03	0.30
	Optimum	263	278	14	153	0.12	0.58
	All	374	405	20	186	0.08	0.49

Appendix 2. Landscape class metric values for marginal and optimum habitat classes for 9 280-ha study sites in north-central Arizona. Values derived from the FRAGSTATS program (McGarigal and Marks 1995).

Study site	Class	Percent ^a of landscape	No. of patches	Largest patch index	Patch density	Mean patch size (ha)	Mean edge contrast index	Mean shape index	Landscape shape index
Gash Flat	Marginal	95.4	2	94.4	0.7	133.9	28.4	1.4	0.7
	Optimum	4.6	6	1.11	2.1	2.2	29.0	1.4	3.1
Lake Mary	Marginal	89.2	1	89.2	0.3	256.8	22.3	1.6	0.6
	Optimum	10.8	3	10.0	1.0	10.4	31.5	1.6	1.6
Long Valley	Marginal	76.4	2	76.4	0.7	109.5	17.4	1.9	0.8
	Optimum	23.6	3	21.3	1.0	22.6	30.2	1.5	1.5
Ice Cave	Marginal	64.0	2	63.4	0.7	92.7	22.8	1.9	1.2
	Optimum	35.2	5	13.0	1.7	20.4	50.1	1.5	1.8
Woody	Marginal	55.1	5	27.2	1.8	31.1	7.4	1.7	2.5
	Optimum	42.5	5	37.0	1.8	24.0	2.2	1.6	2.7
Badger	Marginal	47.6	4	28.3	1.4	33.4	31.3	1.3	1.4
	Optimum	52.0	3	51.8	1.1	48.7	36.9	1.9	1.5
Tree Spring	Marginal	20.8	11	8.7	3.8	5.4	54.6	1.4	3.2
	Optimum	76.1	2	73.3	0.7	108.6	41.2	2.2	2.1
Trick Tank	Optimum	91.6	1	91.6	0.3	266.2	27.8	1.7	0.7
Marshall	Optimum	99.2	1	99.2	0.3	280.0	11.5	1.3	0.1

^aFor study sites where the combined percentage of marginal and optimum classes <100%, the balance of the landscape is composed of non-habitat (e.g., meadows).

Appendix 3. Landscape metric values derived from the FRAGSTATS program (McGarigal and Marks 1995) for 9 study sites located in north-central Arizona.

Study site	ROMPA (% optimum)	Largest patch index	Patch density	Mean patch size (m)	Mean edge contrast index	Mean shape index	Mean patch fractal dimension	Mean nearest neighbor distance (m)	Patch richness density	Shannon diversity index
Gash Flat	4.6	94.4	2.8	35.1	28.8	1.4	1.3	468.2	0.7	0.19
Lake Mary	10.8	89.2	1.4	72.0	27.5	1.6	1.5	695.0	0.7	0.34
Long Valley	23.6	76.4	1.7	57.4	25.1	1.6	1.4	372.3	0.7	0.55
Ice Cave	35.2	63.4	3.4	29.0	33.6	1.5	1.3	189.5	1.0	0.69
Woody	42.5	37.0	4.6	21.7	10.8	1.6	1.3	75.5	1.1	0.78
Badger	52.0	51.8	3.2	31.2	26.2	1.6	1.2	50.2	1.1	0.71
Tree Spring	76.1	73.3	4.9	20.4	51.3	1.6	1.3	30.0	1.1	0.64
Trick Tank	91.6	91.6	1.7	58.1	59.8	1.6	1.3	28.9	0.7	0.29
Marshall	99.2	95.4	1.0	95.4	61.6	1.3	1.3	42.2	0.7	0.05
	Simpson diversity index	Shannon evenness index	Simpson evenness index	Total edge length (m)	Edge density	Contrast- weighted edge density	Total edge contrast index	Landscape shape index	Weighted landscape shape index	
Gash Flat	0.09	0.27	0.18	3,980.9	14.2	5.5	39.1	0.7	0.2	
Lake Mary	0.19	0.49	0.39	3,206.2	11.1	8.1	57.4	0.5	0.4	
Long Valley	0.36	0.79	0.72	4,321.3	15.1	11.8	78.2	0.7	0.6	
Ice Cave	0.47	0.63	0.70	6,607.2	22.8	14.4	63.4	1.1	0.7	
Woody	0.51	0.71	0.77	11,878.8	42.0	5.4	12.7	112	0.2	
Badger	0.50	0.65	0.75	6,600.1	23.5	7.1	30.2	1.1	0.3	
Tree Spring	0.38	0.58	0.56	11,175.2	39.1	24.2	61.8	1.9	1.1	
Trick Tank	0.15	0.42	0.31	4,321.4	14.9	9.4	63.5	0.7	0.4	
Marshall	0.02	0.07	0.03	866.4	3.0	3.0	100.0	0.1	0.1	

Appendix 4. Mean ponderosa pine forest structural habitat characteristics (\pm SE) for 8 marginal and 10 optimum habitat sampling plots on 9 study sites in north-central Arizona, sampled in 2001-2002.

Study site	Plot («)	Basal area (m ² /ha)	Canopy closure (%)	Interlocking trees/point	Trees/ha by VSS class ³			
					VSS 2	VSS 3	VSS 4	VSS 5+
Gash Flat	Marginal (2)	16.6(2.0)	32.4 (2.0)	3.2 (0.5)	27.9 (12.0)	133.3 (26.4)	64.0(11.1)	21.6(4.4)
Lake Mary	Marginal (1)	17.8(1.9)	32.0 (3.0)	3.3 (0.8)	18.3(8.1)	128.3 (25.8)	57.5 (17.2)	28.3 (6.5)
	Optimum (1)	37.0 (2.9)	62.8 (3.8)	36.7 (8.4)	155.0(21.5)	376.7 (47.9)	132.5(18.6)	49.2(6.1)
Long Valley	Marginal (1)	8.6(1.7)	20.3 (3.0)	2.3 (0.6)	4.2 (2.9)	80.8 (22.2)	39.2 (8.2)	5.0 (2.3)
	Optimum (1)	22.6 (2.2)	48.7 (3.6)	7.1 (2.2)	228.3 (65.0)	304.2 (60.8)	50.8(11.4)	28.3 (7.1)
Ice Cave	Marginal (1)	13.7(1.1)	27.0 (3.3)	3.0 (0.3)	35.8 (7.0)	202.5 (29.5)	66.7 (10.5)	5.8(1.9)
	Optimum (1)	27.2(2.1)	49.0 (3.9)	27.9 (8.0)	53.3(11.0)	450.8 (66.5)	64.2 (20.2)	28.3 (6.8)
Woody	Marginal (1)	17.6(1.4)	36.5(3.1)	4.0(1.3)	14.2 (5.4)	64.2 (8.7)	68.33 (9.1)	36.7 (5.6)
	Optimum (1)	33.9 (2.4)	69.7(2.1)	48.6 (9.5)	149.2 (37.9)	325.8 (60.2)	162.5 (20.6)	32.5(4.5)
Badger	Marginal (1)	21.0(2.4)	37.2(2.7)	11.7(3.0)	7.5 (3.0)	72.5 (32.8)	106.7(15.8)	30.0 (7.2)
	Optimum (1)	25.6(2.1)	47.9 (3.0)	21.0(5.2)	84.2 (20.3)	154.2(39.1)	131.7(25.1)	24.2 (5.7)
Tree Spring	Marginal (1)	15.7(1.8)	35.0 (3.6)	6.3 (2.0)	25.8 (8.7)	127.5 (15.5)	80.0(13.3)	11.7(4.9)
	Optimum (1)	34.9 (3.5)	59.0 (3.2)	33.9 (9.0)	215.0 (45.2)	317.5(48.2)	105.0 (23.8)	49.2 (5.6)
Trick Tank	Optimum (2)	25.0(2.1)	46.7(1.3)	10.9(1.6)	43.3 (9.2)	200.8 (25.7)	87.5 (10.3)	42.1 (7.5)
Marshall	Optimum (2)	29.5 (2.2)	55.9 (2.9)	34.7 (4.9)	48.7 (10.4)	227.9 (34.2)	144.6 (20.2)	29.6(9.1)
Mean	Marginal (8)	15.9(1.3)	31.6(2.0)	4.6(1.1)	20.2 (4.5)	117.8(19.2)	67.9 (6.9)	20.1 (4.2)
	Optimum (10)	29.0(1.6)	54.2 (2.5)	26.6 (4.4)	106.9 (23.3)	278.7 (29.8)	111.1(12.6)	35.3 (3.1)

³VSS 2 = 2.5-12.4 cm dbh; VSS 3 = 12.7-30.2 cm dbh; VSS 4 = 30.5-45.5 cm dbh; VSS 5-6 = >45.7 (Reynolds et al. 1992)

For further information or a more technical presentation of methods, including statistical analyses, results, and discussion, the author refers you to the following citations, which may be obtained by contacting:

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Dodd, N. L. *In prep.* Relationships of tassel-eared squirrel juvenile recruitment to precipitation. Manuscript to be submitted to Journal of Mammalogy.

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Dodd, N. L., R. E. Schweinsburg, and S. Boe. *In review.* Landscape-scale forest habitat relationships to tassel-eared squirrel populations: forest restoration implications. Manuscript submitted to Ecological Applications.

