Landscape Models to Predict the Influence of Forest Structure on Tassel-Eared Squirrel Populations

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Abstract

*The tassel-eared squirrel (*Sciurus aberti*) is often used as an indicator species in southwestern ponderosa pine (*Pinus ponderosa*) forests. Because of more than a century of fire suppression, grazing, and timber harvest, these forests have become increasingly prone to catastrophic wildfire, resulting in pressure to implement large-scale treatments to reduce fire threat and restore ecosystem function. However, such treatments could have dramatic effects on tassel-eared squirrels and other wildlife. Because of emerging plans for thinning southwestern forests to reduce fire threat, we undertook a modeling effort to produce spatial data to examine the results of proposed management actions on squirrel habitat. We used squirrel density and recruitment data from 9 study areas located in the Flagstaff region of northern Arizona, USA, linked with spatial data on forest structure developed from remote-sensing imagery. We used a multiscale approach to analyze relationships between forest structure and squirrel density and recruitment. We then used an information-theoretic approach to identify the most parsimonious models for both squirrel density and recruitment. The most strongly supported models of squirrel density included local-scale basal area and >60% canopy cover at the 65-ha spatial scale. For squirrel recruitment, 4 different models that included both local-scale basal area (m^2/ha) and variations of canopy cover over extents of approximately 160–305 ha were strongly supported. Using the most parsimonious models, we created spatial data layers representing both squirrel density and recruitment across an 800,000-ha landscape in northern Arizona. Our approach resulted in spatially explicit models that can be used in efforts to predict the effects of forest management on squirrel populations.*

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Key words

Akaike's Information Criterion, Arizona, density, forest structure, information theory, recruitment, Sciurus aberti*, spatial modeling, tassel-eared squirrel.*

The tassel-eared squirrel (*Sciurus aberti*) is a ponderosa pine *(Pinus ponderosa)*–obligate species, endemic to the southwestern United States (Keith 1965). It plays an important role in these systems, where it facilitates essential symbiotic interactions of mycorrhizal fungi with ponderosa pine through consumption of fruiting bodies and dispersal of spores (States and Gaud 1997, States and Wettstein 1998). It also serves as an important prey for the southwestern subspecies of the northern goshawk (*Accipiter gentilis*; Reynolds et al. 1992, Beier and Drennan 1997). Previous research has suggested that squirrel population parameters are highly dependent on forest structure, particularly canopy cover and ponderosa pine basal area (Ratcliff et al. 1975, Patton 1984, Patton et al. 1985, Dodd et al. 1998, 2003, Dodd 2003). For these reasons, the tassel-eared squirrel is considered an important management indicator species in southwestern forests.

Changes in forest structure over the past 100 years, decreases in forest health, and associated increases in the frequency of catastrophic wildfire, have resulted in a call for intensive forest restoration treatments over hundreds of thousands of hectares of southwestern dry coniferous forests (Covington and Moore 1994, Allen et al. 2002, Zimmerman 2003). Since the late 1800s, timber harvest, fire suppression, and livestock grazing have contributed to substantial changes in the structure of ponderosa pine–dominated forests in this region. Presettlement forests were generally savannah-like and were often dominated by patches of large, old trees (Cooper 1960, Covington and Moore 1994, Belesky and Blumenthal 1997), whereas today's forests are often more homogenous and dominated by smaller-diameter trees (Johnson 1994, Covington et al. 1997, Mast et al. 1999). As these conditions have resulted in increased potential for catastrophic wildfire and disease and decreased ecosystem health (Covington and Moore 1994, Covington et al. 1997), restoration initiatives (e.g., Moore et al. 1999) have advocated aggressive thinning and prescribed fire to return forests to a structural condition closer to presettlement conditions (Covington and Moore 1994, Covington et al. 1997). However, these treatments are often very intensive (Covington et al. 1997, Fulé et al. 1997, Mast et al. 1999) and may result in rapid and dramatic changes in forest structure within treated areas. Such treatments have the potential to adversely affect many wildlife species (Wagner et al. 2000, Allen et al. 2002, Chambers and Germaine 2003), including tassel-eared squirrels, though few studies have specifically addressed potential impacts.

Spatially explicit models linking population parameters for sensitive species with forest structural conditions would aid forest management planning in the Southwest by allowing land managers to predict the effects of management scenarios on sensitive taxa. As

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a key management indicator species (Chambers and Germaine 2003), the tassel-eared squirrel is a prime candidate species for habitat modeling. Prior work on the relationships between squirrel populations and forest structure has indicated that squirrel populations are affected by both local forest structural conditions and structure over larger spatial extents (Dodd 2003, Dodd et al. 2006). These studies used forest structural characteristics measured on 24-ha ground plots, along with a measure of the ratio of optimal-to-marginal habitat (ROMPA; Krohne 1997) derived from Enhanced Thematic Mapper (ETM) imagery over a 500-ha area around each plot. Using these predictor variables, they were able to document strong relationships between forest structure and squirrel populations, and they were able to identify forest structural characteristics that could be used to define optimal and marginal habitat. However, they did not create spatially explicit models, nor did they identify the spatial extents over which forest structure influences tassel-eared squirrel populations.

In 2003, the Forest Ecosystem Restoration Analysis (ForestERA) project finished developing highly accurate spatial data representing basic forest structural characteristics, such as basal area (m^2/ha), tree density (stems/ha), and percentage of canopy cover, in the region of the aforementioned tassel-eared squirrel studies. Thus, the opportunity arose to reanalyze these squirrel population data along with new spatial data within a Geographic Information System (GIS). The purpose of our research was to 1) assess which forest structural characteristics were the best for modeling tassel-eared squirrel density and recruitment, 2) assess the spatial extent over which those variables affect squirrel populations, 3) model squirrel density and recruitment using forest structure at multiple spatial scales, 4) use an information-theoretic approach to determine the best models for prediction of squirrel density and recruitment, and 5) produce spatially explicit models of squirrel density and recruitment. Spatially explicit data layers can be vital to achieving effective integration of landscape- and patch-scale management prescriptions with the rapidly escalating emphasis on ponderosa pine restoration in the Southwest that will occur over large contiguous areas (Allen et al. 2002, Zimmerman 2003) and with our increased understanding of landscape-scale habitat influences on squirrel populations (Dodd 2003, Dodd et al. 2006). Our research addresses the difficulty in conceptualizing the complexities of tassel-eared squirrel population response at multiple spatial scales.

Study Area

Our study area for this habitat mapping effort encompassed approximately 800,000 ha of forested land on the western Mogollon Plateau extending from just north and west of Flagstaff, Arizona, USA, southeast to the western edge of the 180,000-ha Rodeo-Chediski burn of 2002 (Fig. 1). Elevations ranged from approximately 1,500 m in deeper canyons on the edge of the plateau to more than 3,600 m on the San Francisco Peaks. The vegetation in the region was dominated by stands of nearly pure ponderosa pine and pine mixed with Gambel oak (*Quercus gambelii*). Smaller stands of mixed-conifer, dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and white pine (*Pinus strobiformis*), pinyon-juniper (*Pinus edulis* and *Juniperus* spp.) woodlands, aspen (*Populus tremuloides*) groves, and open grasslands were also common (Fig. 1). The primary land manager in the region was the U.S. Department of Agriculture, Forest Service, with parts of 4 national forests (Coconino, Kaibab, Tonto, and Apache–Sitgreaves) comprising more than 75% of the study area. The remaining land was owned by various private, state, and federal entities.

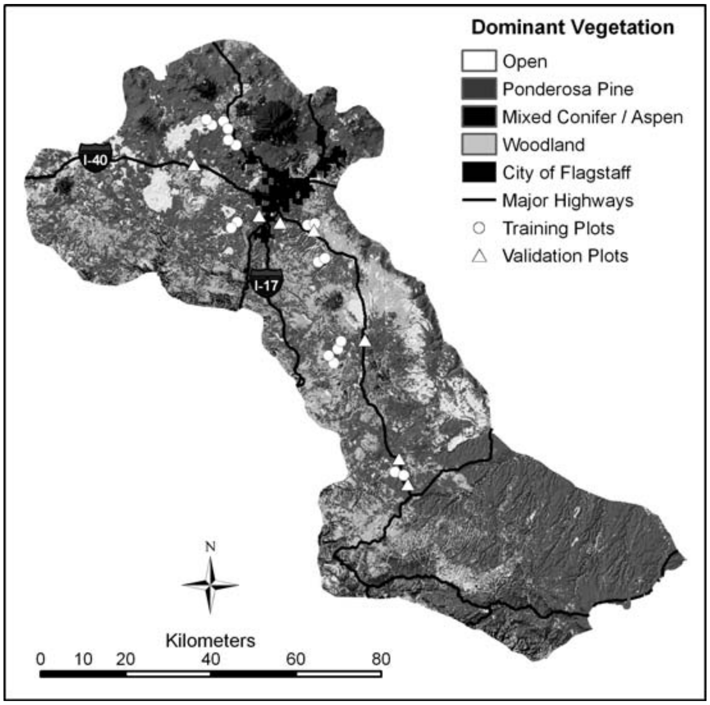

Figure 1. Map of the 800,000-ha study area on the western Mogollon Plateau in northern Ariz., USA, showing dominant vegetation types, major highways, the city of Flagstaff, and the location of study sites where both training (1999–2002) and validation (1996–1997) data on tassel-eared squirrel density and recruitment were measured.

Methods

Squirrel Population Data

We measured squirrel density and recruitment on 2 plots, each 24 ha in size, from each of 9 280-ha study sites ($n = 18$ sampling plots; Fig. 1) on the Coconino National Forest in north-central Arizona, USA. For each plot, we averaged density and recruitment values from the 4 consecutive years (1999–2002) of the field study. Although the 2 study plots within a site were occasionally in close proximity, they usually differed considerably in structure (see Dodd 2003, Dodd et al. 2006). In addition, of the 696 individual tassel-eared squirrels trapped during the study, only 7 ever occurred on >1 plot. Thus, we considered the plots to be independent sampling units.

All of the study sites were located within the ponderosa pine association of the montane coniferous forest community described by Brown (1994) and between elevations of 2,050 and 2,400 m. Sites were oriented along a gradient of habitat quality so that we could assess differences in forest structure in relation to squirrel population parameters (Dodd 2003, Dodd et al. 2006). Within sites, we placed each plot in an area with relatively homogenous forest structure.

On the sampling plots, we estimated squirrel density using the feeding-sign index technique developed by Dodd et al. (1998) and validated by Dodd et al. (2006). This index provided for efficient and reliable estimation of squirrel density on multiple sampling plots, which can otherwise be impractical because of the costly, labor-intensive capture–recapture techniques typically used to obtain density estimates (Pollock et al. 1990, Dodd et al. 1998). We estimated juvenile recruitment on each plot by capturing squirrels using an 8×8 trapping grid ($n = 64$ trap stations) with 70-m spacing between each sampling point. We used live traps (Tomahawk® No. 202, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with unshelled peanuts (Patton et al. 1976). We immobilized captured squirrels using Isoflurane® (Halocarbon Laboratories, River Edge, New Jersey). We affixed a numbered metal ear tag (Monel No. 3; National Band and Tag Co., Newport, Kentucky) and colored plastic collar to each squirrel. Observers visually determined sex and obtained body mass with a 1,000-g spring scale (Pesola AG, Barr, Switzerland), and we separated juvenile and adult cohorts using body mass and morphological characteristics (Keith 1965, Farentinos 1972, Dodd et al. 2003). We assumed that squirrels were juveniles if body mass was $\leq$550 g (Dodd et al. 2003). We trapped squirrels over 5 consecutive days at each sampling plot, with all 18 plots trapped over a 12-day period in mid- to late-October of each year. We expressed recruitment as juveniles/ha because this measure better reflected variation in recruitment among plots than juveniles/adult female (Brown 1984, Dodd et al. 2003). For additional details on the study sites and estimation of squirrel density and recruitment see Dodd (2003) and Dodd et al. (2006).

Spatial Data Layers

In 2003, the Forest ERA project mapped vegetation composition and structure over the study area (Hampton et al. 2003). We derived all of the vegetation layers from remote-sensing imagery using associated ground measurements of forest structure as training data. We converted the layers to GIS format using Imagine 8.6 (ERDAS Corp., Leica Geosystems, Heerbrugg, Switzerland) and ArcGIS 8.3 (ESRI Corp., Redlands, California) software. We derived the canopy-cover layer from digital orthophoto quads (primarily from the year 1997), using an advanced exploratory data-analysis method (Xu et al. 2006). We derived the dominant overstory vegetation layer from ETM (year 2001) imagery using a classification-tree methodology (Breiman et al. 1984; Hansen et al. 1996) and a machine-learning procedure known as boosting (Freund and Schapire 1995). We derived the basal area and tree-density layers from ETM imagery using a regression-tree methodology (Breiman et al. 1984) and See5/Cubist 1.7 software (Rulequest Research, St. Ives, New South Wales, Australia). The resolution of each of these layers was 90 m (90×90 m cells, 0.81 ha or 2-acre extent), and we believe this represented the most accurate spatial data available in this region. Additional details of the vegetation mapping effort and accuracy of the layers can be found in Hampton et al. (2003).

Model Development

Because we were interested in creating a landscape-level model using available spatial-data layers, we could not use all of the relationships between tassel-eared squirrel population parameters and forest structure that were documented in previous studies using these data (Dodd 2003, Dodd et al. 2006). Instead, we were limited to using those forest structural characteristics we could measure with the remotely sensed data as predictor variables in the models, namely canopy cover, basal area, and tree density. To assure that the forest structure predictions from the remote-sensing imagery did not differ significantly from actual forest structure on the ground, we assessed the correlations between data on forest structure measured at ground-based field plots and the data derived from remote sensing using a Pearson correlation coefficient ($r =$ test statistic).

Using the remotely sensed data, we developed a priori hypotheses about the influence of forest structure on squirrel density and recruitment. As squirrel populations respond to local forest conditions, particularly mature trees and cover, we hypothesized that a single, local-scale variable would be most influential in a predictive model of squirrel density and recruitment. Using the plot-level data, we chose to test this hypothesis using the local-scale variables basal area (BA), tree density, and canopy cover (CC). We combined the local-scale variable that had the most influence on squirrel density and recruitment with a landscape-scale variable (see below) to create our predictive models.

As we were interested in looking at the effects of forest structure on squirrel density and recruitment at multiple spatial scales, we also considered the effects of forest structure across multiple spatial extents. Because such an approach can result in a cumbersome number of possible models, we considered only biologically meaningful hypotheses that also minimized the total number of predictor variables. For example, Dodd (2003) and Dodd et al. (1998, 2006) found canopy cover and interlocking trees to be important forest features facilitating squirrel movement, survival, and habitat connectivity. Therefore, we hypothesized that canopy cover across multiple spatial scales would have a strong influence on squirrel density and recruitment. We constructed additional spatial data layers using 4 variations of canopy cover: 1) the number of pixels in which canopy cover exceeded 40% (CC40), 2) the number of pixels in which canopy cover exceeded 50% (CC50), 3) the number of pixels in which canopy cover exceeded 60% (CC60), and 4) mean canopy cover (CCM). Although these variations on canopy cover were not independent and were often highly correlated (r generally $>$0.5), we did not have any a priori reason to select one variant on canopy cover over another. We did not consider variations on canopy cover based on categories above 60% or below 40% because relatively few pixels had values for canopy cover in those ranges.

Using the center of the ground-based plots where squirrel density and recruitment were measured, we quantified the 4 variations on canopy cover over 4 spatial extents: 1) a 5-pixel radius ($\sim$65 ha), 2) an 8-pixel radius ($\sim$160 ha), 3) an 11-pixel radius ($\sim$305 ha), and 4) a 14-pixel radius ($\sim$430 ha). We did not assess spatial scales in between those chosen because of the high correlation among those layers (r often $>$0.8). Although canopy cover still tended to be correlated ($r > 0.4$) across spatial scales, we were interested in identifying patterns in squirrel density and recruitment based on scale, so obtaining completely independent input layers was not possible given this criterion.

Using the layers described above, we constructed multiple biologically relevant models and employed an information-theoretic approach (Anderson et al. 2000, Burnham and Anderson 2002) to select the best model from among this set of candidate models.

Model Selection and Inference

We used multiple linear regression within the fit model option in JMP Version 4.0 software (SAS Institute, Carey, North Carolina) to determine relationships between forest structural characteristics, spatial scale, and squirrel density and recruitment. We used Akaike's Information Criterion, corrected for small sample size (AICc; Akaike 1973, Burnham and Anderson 2002), to assess the overall strength of each model in the candidate set. We then ranked these models, from lowest to highest, according to their ΔAICc values. We chose those models ≤ 2 AICc of the most parsimonious model ($\Delta\text{AICc} = 0$; Anderson and Burnham 2002, Burnham and Anderson 2002), as the final set of candidate models to be used for prediction and inference. To provide a measure of model support and selection uncertainty, we calculated the Akaike weight (w_i) for each candidate model (Burnham and Anderson 2002). Finally, to assess how well the model fit the original data we calculated adjusted r^2 values for each candidate model.

Creation of Spatially Explicit Models

We used the most strongly supported candidate model, for both squirrel density and recruitment, to create spatially explicit data layers predicting these population attributes across the 800,000-ha study area (Fig. 2a,b). We created layers in ArcGIS 8.3 (ESRI Corp.) using the predictive spatial layers, the raster calculator, and the mathematical relationships from the statistical analyses. As squirrels are a ponderosa pine–obligate and not typically found outside ponderosa pine–dominated stands, we used a map of dominant overstory vegetation created from ETM imagery by the ForestERA project to identify areas of the landscape with habitat types other than ponderosa pine. In those areas, we assumed squirrels were absent, and we assumed squirrel density and recruitment was zero.

Model Validation

Because estimation of density and recruitment values for squirrels is costly and time-consuming, we were unable to validate our models using new field data. However, we were able to do a limited validation using data from 7 study sites, each approximately 60 ha in extent, where squirrel population parameters were measured during 1996 and 1997 (Dodd et al. 2003; Fig. 1). At each of these sites, we measured squirrel density and recruitment using the same techniques outlined above.

Because the locations of the 7 study sites were precisely documented using a geographic positioning system, we were able to obtain predicted values for squirrel density and recruitment on those sites using our models. We determined these values by taking the mean value for all the 90-m pixels in the spatial model that fell within the extent of the field plots. Using simple linear regression ($r^2 = $ test statistic), we assessed the relationship between the predicted values for squirrel density and recruitment, based on the spatial model, with the estimated density and recruitment values from the field study (as reported in Dodd et al. 2003).

Results

Correlations between predicted values for forest structural variables in the spatial data layers and values for the same variables measured on the ground were 0.93 for basal area ($n = 63$), 0.87 for canopy cover ($n = 200$), and 0.91 for tree density ($n = 63$), respectively.

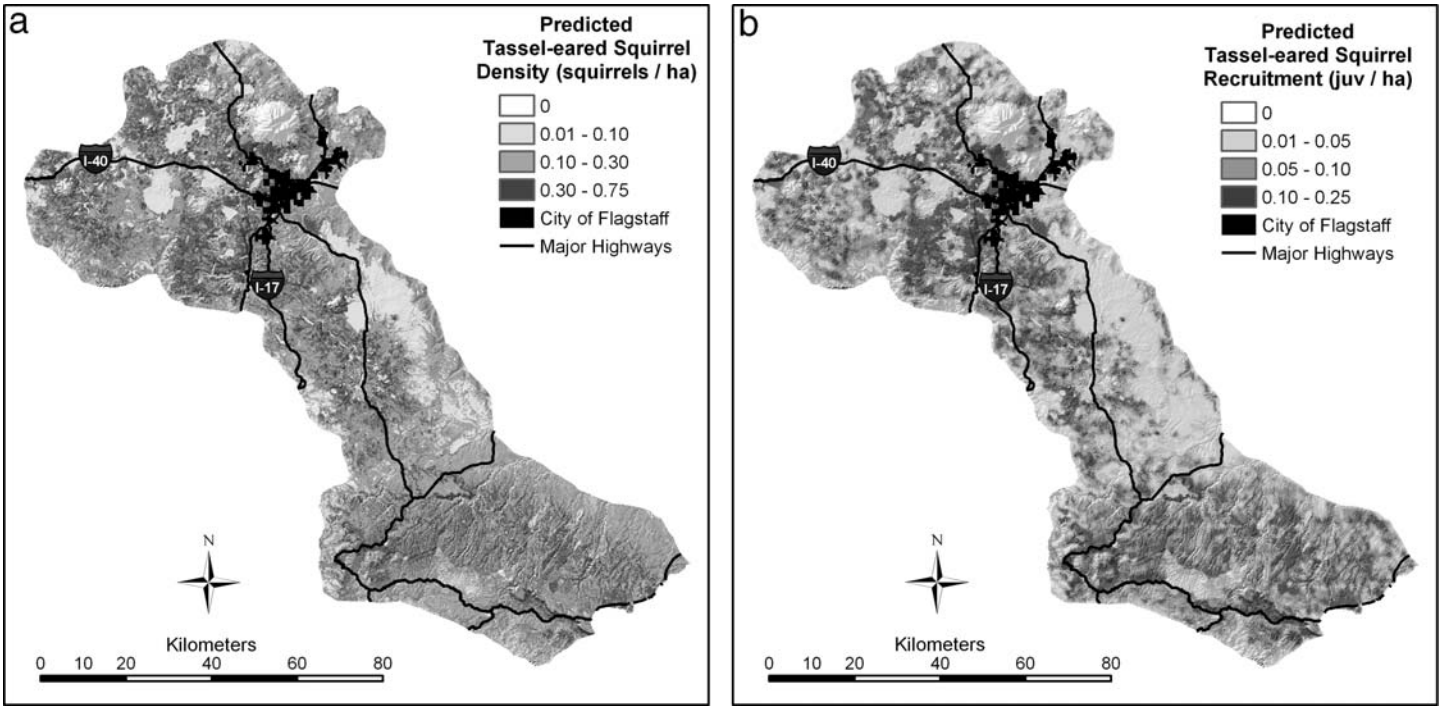

Figure 2. (a) Map of predicted squirrel density (individuals/ha) across the 800,000-ha study area on the western Mogollon Plateau in Ariz., USA; (b) Map of predicted squirrel recruitment (juveniles/ha) across the same study area. Maps are based on field data collected on squirrel density and recruitment from 1999–2002 and predicted forest structural characteristics derived from years 1999–2000 Enhanced Thematic Mapper satellite imagery and year 1997 digital orthophotos.

Table 1. Delta Akaike's Information Criterion, corrected for small sample size (ΔAICc) for 3 simple linear-regression models predicting tassel-eared squirrel density (individuals/ha) and recruitment (juveniles/ha) on the western Mogollon Rim, Ariz., USA. All models contain an intercept and error term in addition to the listed parameters ($K = 3$ for all models). From this model set, we chose the best local-scale (24-ha plot) variable to use in the creation of our set of candidate multiple linear-regression models for prediction of squirrel density and recruitment.

	Density		**Recruitment**	
Model parameters	**AICc**	**ΔAICc**	**AICc**	**ΔAICc**
Basal area (m^2/ha)	−100.06	0.00	−107.59	0.00
Tree density (stems/ha)	−95.79	4.27	−105.36	2.23
Canopy cover (%)	−83.00	17.06	−99.35	8.24

Because of the strength of these correlations, we felt confident that we could use the spatial data layers to model squirrel population parameters across the full extent of our study area.

Based on our initial analysis, using only a local-scale variable, basal area showed the strongest relationships with both squirrel density and recruitment (Table 1). We chose to use basal area as the only local-scale variable in further model development because the tree density and canopy cover models were only weakly supported by the data and because the 3 local-scale variables were highly correlated ($r > 0.7$).

For prediction of both squirrel density and recruitment, our methodology resulted in a final set of 17 candidate models for analysis. This set included 1 model with a plot-level variable (basal area) only and 16 additional models that included basal area at the plot level, a canopy cover variant over a specific spatial extent (4 variations on canopy cover at 4 spatial extents = 16 variations), and an interaction effect (see Table 2 for variables used in the models). Although we could have included models without an interaction effect, we believed that an interaction effect was likely because squirrels require both mature trees (high basal area) and overhead cover (canopy). It is likely these factors work in combination, rather than independently, to influence squirrel population parameters.

Table 2. Variables used to model and predict tassel-eared squirrel density (individuals/ha) and recruitment (juveniles/ha) in relation to forest structure and spatial scale on the western Mogollon Rim, Ariz., USA.

Variable code	**Variable description**
BA	Basal area (m^2/ha) at the 24-ha plot level
65CC40	Cells with canopy cover >40% at the 65-ha spatial extent
160CC40	Cells with canopy cover >40% at the 160-ha spatial extent
305CC40	Cells with canopy cover >40% at the 305-ha spatial extent
430CC40	Cells with canopy cover >40% at the 430-ha spatial extent
65CC50	Cells with canopy cover >50% at the 65-ha spatial extent
160CC50	Cells with canopy cover >50% at the 160-ha spatial extent
305CC50	Cells with canopy cover >50% at the 305-ha spatial extent
430CC50	Cells with canopy cover >50% at the 430-ha spatial extent
65CC60	Cells with canopy cover >60% at the 65-ha spatial extent
160CC60	Cells with canopy cover >60% at the 160-ha spatial extent
305CC60	Cells with canopy cover >60% at the 305-ha spatial extent
430CC60	Cells with canopy cover >60% at the 430-ha spatial extent
65CCM	Mean percent canopy cover at the 65-ha spatial extent
160CCM	Mean percent canopy cover at the 160-ha spatial extent
305CCM	Mean percent canopy cover at the 305-ha spatial extent
430CCM	Mean percent canopy cover at the 430-ha spatial extent
INT	Interaction effect (e.g., BA × 160CC50)

Table 3. Statistics for the set of 17 candidate multiple linear-regression models used to predict squirrel density (individuals/ha) on the western Mogollon Plateau, Ariz., USA. Results for the intercept-only (null) model provided for comparison.

Model parameters[a]	***K***[b]	**AICc**[c]	**ΔAICc**[d]	**(w_i)**[e]
BA	3	−100.06	0.00	0.302
BA, 65CC60, INT	5	−99.99	0.07	0.291
BA, 160CC40, INT	5	−97.72	2.34	0.094
BA, 160CCM, INT	5	−96.96	3.10	0.064
BA, 65CC50, INT	5	−96.54	3.52	0.052
BA, 305CC40, INT	5	−96.32	3.74	0.047
BA, 65CC40, INT	5	−94.88	5.18	0.023
BA, 305CCM, INT	5	−94.80	5.26	0.022
BA, 65CCM, INT	5	−94.59	5.47	0.020
BA, 430CC40, INT	5	−94.35	5.71	0.017
BA, 305CC50, INT	5	−93.52	6.54	0.011
BA, 160CC50, INT	5	−93.45	6.61	0.011
BA, 430CC60, INT	5	−93.24	6.82	0.010
BA, 160CC60, INT	5	−93.18	6.88	0.010
BA, 430CCM, INT	5	−93.11	6.95	0.009
BA, 430CC50, INT	5	−93.00	7.06	0.009
BA, 305CC60, INT	5	−92.99	7.07	0.008
Intercept only	2	−69.17	30.89	0.000

[a] See Table 2 for a description of model parameters.

[b] Number of parameters in the model (including intercept and error terms).

[c] Akaike's Information Criterion values adjusted for small sample size (AICc).

[d] Delta AICc values.

[e] Akaike weights.

From among our candidate set, the two best models of squirrel density included BA with or without a landscape-level variable and >60% canopy cover at the 65-ha spatial scale (Table 3). These models represented 59% of the total weight among all possible models, and the maximum adjusted r^2 value from among these models was 0.90, also indicating a good fit with the data. All other models were less supported by the data ($\Delta AICc > 2.3$; Burnham and Anderson, 2002). Nevertheless, other models that included canopy cover at smaller spatial extents (65 and 160 ha) accounted for 38% of the total weight. All of the models in the candidate set received considerably higher support than the intercept-only model (Table 3).

Unlike squirrel density, there was greater model selection uncertainty associated with predicted squirrel recruitment and 4 models had ΔAICc values ≤2 (Table 4). We included the model with CCM at the 160-ha spatial scale among our final set of models selected for inference because its ΔAICc value was 2.02. In general, there was strongest support for models containing landscape-level variables with 160- or 305-ha spatial extents and less support for models containing variables at the largest and smallest spatial extents. This was a consistent pattern for models containing each of the 4 variations of canopy cover. Akaike weights indicated that the top 2 models, both of which included canopy cover variations at the 160-ha spatial extent, received about 46% of the overall support among the set of candidate models. As with squirrel density, all of the models in the candidate set received considerably higher support than the intercept-only model (Table 4). In total, the top 5 models in the set received

Table 4. Statistics for the set of 17 candidate models used to predict squirrel recruitment (juveniles/ha) on the western Mogollon Plateau, Ariz., USA. Results for the intercept-only (null) model provided for comparison.

Model parameters[a]	K[b]	AICc[c]	ΔAICc[d]	(w_i)[e]
BA, 160CC50, INT	5	−108.65	0.00	0.239
BA, 160CC40, INT	5	−108.46	0.19	0.217
BA	3	−107.59	1.06	0.141
BA, 305CC50, INT	5	−107.01	1.64	0.105
BA, 160CCM, INT	5	−106.63	2.02	0.087
BA, 305CC40, INT	5	−106.21	2.44	0.070
BA, 305CCM, INT	5	−104.45	4.20	0.029
BA, 430CC40, INT	5	−104.16	4.49	0.025
BA, 430CC50, INT	5	−104.13	4.52	0.025
BA, 65CC50, INT	5	−103.19	5.46	0.016
BA, 305CC60, INT	5	−102.07	6.58	0.009
BA, 65CC40, INT	5	−102.03	6.62	0.009
BA, 430CCM, INT	5	−101.84	6.82	0.008
BA, 65CC60, INT	5	−101.57	7.08	0.007
BA, 430CC60, INT	5	−101.42	7.23	0.006
BA, 65CCM, INT	5	−100.52	8.13	0.004
BA, 160CC60, INT	5	−100.47	8.18	0.003
Intercept only	2	−95.92	12.73	0.000

[a] See Table 2 for a description of model parameters.

[b] Number of parameters in the model (including intercept and error terms).

[c] Akaike's Information Criterion values adjusted for small sample size (AICc).

[d] Delta AICc values.

[e] Akaike weights.

about 79% of the support, based on Akaike weights. Adjusted r^2 values for these models ranged from 0.53 (BA only) to 0.66 (BA, 160CC50, interaction effect [INT]), suggesting the regression model fit was reasonably strong.

We chose to make inference about the relationships between forest structure and squirrel density and recruitment based on the most strongly supported model for squirrel density and the 5 most strongly supported models for squirrel recruitment (Table 5). Our validation suggested that the most strongly supported models for both squirrel density and recruitment accurately predicted patterns of squirrel density and recruitment on 7 independent study sites (Table 6). There were strong linear relationships between the predicted values for density and recruitment from the most strongly supported models, and the measured values for density and recruitment taken in the field (density $r^2 = 0.60$, slope $= 0.84$; recruitment $r^2 = 0.65$, slope $= 0.47$). Residuals from each relationship ranged between 0.01 and −0.01 and showed no obvious pattern in relation to predicted values.

Discussion

In this effort, we were able to link tassel-eared squirrel population characteristics with spatial data layers representing forest structure and vegetation composition and create spatially explicit models of squirrel density and recruitment (Fig. 2a,b). Our results indicate that squirrel density is best predicted using only basal area at the plot level (Table 3). Basal area is probably the best predictor, among those used in this analysis and those available for large spatial extents, of the presence of mature pines, on which squirrels depend in part for survival. The relatively weak support for some other models containing forest structure at the smaller (65 ha or 160 ha) spatial scales suggests there may be only limited influence of forest structure on squirrel densities at spatial extents larger than 24 ha.

Our models of squirrel recruitment resulted in different patterns. Although the lack of a single model that received overwhelming support (Table 4) indicates model-selection uncertainty in our candidate model set (Burnham and Anderson 2002), this result is not completely unexpected because the variables we used in the different models are not completely independent and often have moderate-to-high correlation. However, we can infer from the analysis that canopy cover threshold values of around 40–50% have a great deal of influence on squirrel recruitment. Cover values in the 40–50% range are probably indicative of the lower thresholds for connectivity in the landscape (Andren 1994). Models containing canopy cover above 60% were not strongly supported in the analysis, suggesting that lower values of canopy cover are suitable for facilitating squirrel recruitment.

Based on our results, it appears that tassel-eared squirrel recruitment is influenced by spatial extents far larger than individual home ranges, which typically do not exceed 26 ha (Farentinos 1979, Patton et al. 1985, Lema 2001). Our models suggest that canopy conditions over spatial extents of about 160–305 ha have the most influence on squirrel recruitment. Models incorporating canopy cover at spatial extents of 65 ha were not so strongly supported, suggesting that squirrels are recruited from larger areas. Likewise, there was less support for models with canopy cover at spatial extents of 430 ha suggesting that these extents may be larger than those at which squirrel recruitment typically occurs. A post hoc analysis using models with canopy cover variations over extents larger than 430 ha and smaller than 65 ha revealed that those models would receive even less support.

Table 5. Parameter estimates for each of the final multiple linear-regression models used for prediction of tassel-eared squirrel density (individuals/ha) and recruitment (juveniles/ha) on the western Mogollon Plateau, Ariz., USA (— indicates parameter not included in the model).

Model[a]	Intercept	Basal area (m^2/ha)	Canopy cover derivative	Interaction effect
Squirrel density, BA only	−0.1815	0.0206	—	—
Squirrel recruitment				
BA, 160CC50, INT	−0.1710	0.0076	0.0007	0.0001
BA, 160CC40, INT	−0.2090	0.0084	0.0006	0.0002
BA only	−0.1019	0.0079	—	—
BA, 305CC40, INT	−0.1890	0.0083	0.0003	0.0001
BA, 305CC50, INT	−0.1580	0.0073	0.0003	0.0001
BA, 160CCM, INT	−0.2568	0.0088	0.0003	0.0001

[a] See Table 2 for a description of model parameters.

Table 6. Field-measured values for tassel-eared squirrel density (individuals/ha) and recruitment (juveniles/ha), during the summers of 1996 and 1997, at 7 study sites on the western Mogollon Plateau, Ariz., USA, and predicted values for density and recruitment for the same plots, based on the most strongly supported models.

	Density		**Recruitment**	
Study site	**Field**	**Predicted**	**Field**	**Predicted**
Clint's Well	0.20	0.31	0.14	0.15
Fort Tuthill	0.16	0.20	0.02	0.04
Long Valley	0.07	0.07	0.05	0.01
Marshall Mesa	0.33	0.41	0.33	0.19
Mormon Lake	0.08	0.19	0.14	0.11
Parks	0.11	0.23	0.24	0.08
Pumphouse	0.27	0.20	0.07	0.04

With regard to the relationships we found between squirrel density and forest structure our results are not surprising. Previous research has consistently documented strong relationships between squirrel density and basal area (Ratcliff et al. 1975, Patton et al. 1985, Dodd 2003). Dodd (2003) and Dodd et al. (2006) found that their multiple regression model, which incorporated basal area (at the patch scale) and ROMPA (at the landscape scale) as parameters, explained 89% of the variation in squirrel density on all plots; however, basal area exhibited a substantially greater partial regression coefficient (0.79) than the landscape parameter (ROMPA; 0.30). Squirrels depend on the seeds of mature ponderosa pine and fungi associated with healthy pines, as food sources (Patton et al. 1985, States et al. 1988, Dodd et al. 2003).

Our results in regard to squirrel recruitment were also consistent with previous research. Dodd (2003) and Dodd et al. (2006) found that their multiple regression model, incorporating total number of interlocking trees (at the patch level) and ROMPA (at the landscape level), explained about 60% of the variation in squirrel recruitment across plots. However, unlike their density model, their landscape variable had a greater partial regression coefficient than the patch variable. Squirrels require cover to hide from predators and to move safely across the landscape (Austin 1990), as well as for successful recruitment (Dodd 2003, Dodd et al. 2003).

The results of our validation exercise suggest that our models can accurately predict patterns of squirrel density and recruitment on the western Mogollon Plateau. Although our validation was spatially constrained, we believe forest structural conditions on both the plots where training data and validation data were collected, encompass most of the range of conditions that would be encountered within this region. Moreover, patterns of forest composition are relatively homogenous across our study area. Thus, the patterns predicted by our models should apply across the entire study area.

Many density-independent factors, such as weather, food availability, and predation, have been shown to affect tassel-eared squirrel populations (Keith 1965). Because of this, our modeled estimates for squirrel density and recruitment may lack some degree of precision. Indeed, the relationship between squirrel recruitment, as predicted by our model, and squirrel recruitment measured on the 7 validation plots, was not one to one (slope = 0.47). Weather may be a particularly important factor in causing fluctuations in tassel-eared squirrel populations across our study area. For example, Dodd et al. (2006) found that recruitment was positively related to winter–spring precipitation. Hypogeous fungi fruiting body production and consumption during spring is vital to the onset of breeding in tassel-eared squirrels (Stephenson 1975) and may be associated with the importance of November–May precipitation in recruitment (Dodd et al. 2006). Although important, for the period of our study, the influence of precipitation on recruitment appeared secondary to that of habitat, as evidenced by poor recruitment at some sites in high-precipitation years and by the consistent response among years along a ROMPA gradient (Dodd 2003, Dodd et al. 2006). Therefore, we do not believe density-independent factors limited our ability to reliably model patterns of squirrel density and recruitment. Although our models cannot be used to predict absolute values for squirrel density and recruitment, our validation exercise suggested that the predicted patterns for these population parameters in relation to forest structure were robust (Table 6). Validation plots, where measured values for squirrel density and recruitment were higher, also had higher predicted values for these population parameters based on our models.

Management Implications

Many forest management alternatives, especially intensive thinning treatments, have been shown to result in declines in squirrel abundance, particularly where large overstory tree removal has occurred (Patton et al. 1985, Pederson et al. 1987, Sullivan et al. 1996, Carey 2000). To mediate these effects in ponderosa pine–dominated forests, we recommend that large-scale restoration or fuels-reduction efforts focus on the removal of smaller trees and maintain areas with high basal area to minimize impacts on squirrel populations. In many areas, the impact of intensive thinning on small understory trees may be lessened by the retention of large overstory trees. We further recommend that managers leave larger patches (>160 ha) of habitat with moderate-to-high canopy cover (>40%) as part of any treatment matrix. These untreated or lightly treated patches could serve as important sources for recolonization of treated areas.

Currently, the ForestERA project describes the effects of various forest restoration and fuels-reduction treatments on the structure of ponderosa pine forests. Our flexible and spatially explicit GIS-based tools will allow users to place various treatment types on a virtual landscape and assess their effects on forest structure. Because our squirrel models also link to forest structure, managers will be able to use these tools to qualitatively compare the predicted effects on squirrel populations of alternative treatments that vary in spatial extent and intensity. Several large-scale management efforts that are in the planning stages within this region intend to incorporate the findings from our study and use these models to help design their treatment plans. Once treatments are underway, there will be new opportunities to validate and revise our models.

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