

TASSEL-EARED SQUIRREL POPULATION, HABITAT CONDITION, AND DIETARY RELATIONSHIPS IN NORTH-CENTRAL ARIZONA

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Abstract: We examined the seasonal population dynamics of tassel-eared squirrels (*Sciurus aberti*) in north-central Arizona, USA, during 1996–1997 to assess relationships with forest structural habitat condition and dietary fungi use. Our 8 study sites averaged 66 ha and exhibited considerable variation in ponderosa pine (*Pinus ponderosa*) habitat structure. We conducted capture–recapture trapping during 3 seasons each year, for a total of 56,016 trap days and 2,542 captures of 450 squirrels. We attained population estimates with mean standard error $\pm 10\%$. Density across periods ranged from 0.05 to 1.03 squirrels/ha, and fluctuated widely at half our study sites, particularly between April and August trapping periods. Indices of recruitment averaged 0.14 juveniles/female. Survival rates averaged 0.78, with winter survival (0.63) significantly lower than other periods. We analyzed 382 fecal samples for seasonal hypogeous and epigeous fungi, of which 21 taxa were detected. Mean fecal fungal content was significantly higher in August (70.8% relative frequency) than in January (28.2%) and April (9.4%). Recruitment was strongly and positively related to both the number of interlocking canopy trees and August fungal content in fecal samples. August fecal fungal content was positively related to basal area for all tree species. Across all periods, squirrel density was positively related to fecal fungal diversity. Winter squirrel survival was inversely related to snow cover duration and positively related to dietary fungal diversity. Squirrel density fluctuations between April and August were positively tied to pine quadratic mean diameter. Forest management and restoration practices emphasizing intensive, widespread thinning may adversely impact tassel-eared squirrels and the fungi that provide food. Integrating squirrel habitat needs of interlocking canopies and other structural attributes in forest management will benefit squirrel populations.

JOURNAL OF WILDLIFE MANAGEMENT 67(3):622–633

Key words: Arizona, diets, forest management, fungi, habitat relationships, *Pinus ponderosa*, ponderosa pine, population dynamics, *Sciurus aberti*, tassel-eared squirrels.

The tassel-eared squirrel is an obligate species of Arizona's extensive ponderosa pine forests. It is a popular small-game and watchable species and an important prey for the northern goshawk (*Accipiter gentilis*; Reynolds et al. 1992). Squirrels play a key role in facilitating 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).

Timber harvest, long-term fire suppression, and livestock grazing have contributed to substantial changes in southwestern ponderosa pine forests since European settlement. Pre-settlement forests were more open and parklike (Cooper 1960, Covington and Moore 1992, 1994; Belsky and Blumenthal 1997), whereas a proliferation of younger age-class trees dominates forests today (Johnson 1994, Mast et al. 1999). Current conditions present increased potential for catastrophic fire, disease, and decreased ecosystem health (Covington and Moore 1994, Covington et al.

1997). These problems have spawned forest health restoration initiatives (Moore et al. 1999, Wagner et al. 2000) that advocate using aggressive thinning and prescribed fire to promote ecosystem health and old-growth forest conditions (Covington and Moore 1994, Covington et al. 1997).

Intensive timber harvest associated with forest ecosystem restoration may reduce short-term canopy closure, tree density, diversity, and patchiness. Such modifications are structurally similar to past even-aged management practices shown to be detrimental to tassel-eared squirrels (Pederson et al. 1976, 1987; Patton 1984; Patton et al. 1985). Extensive and repeated even-aged timber harvest in Arizona since 1980 has cumulatively impacted squirrel habitat (Dodd and Adams 1989), to which forest restoration activities may further contribute. Intensive timber harvest also alters microhabitats where hypogeous fungi grow, reducing fungi production (States and Gaud 1997) and potentially disrupting the symbiotic relationship between fungi, pines, and squirrels (States 1985, Pederson et al. 1987, States et al. 1988). Mycelia and fruiting bodies of both hypogeous and epigeous fungi constitute an impor-

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tant seasonal food source for tassel-eared squirrels (Stephenson 1975, States 1985).

To address forest management impact to wildlife, including the growing emphasis on forest restoration, we initiated a tassel-eared squirrel research project. Squirrels are well suited for such research as they are sufficiently abundant to yield statistically meaningful population data yet sensitive enough to structural habitat condition change to allow for forest management inferences (Carey 2000). Our objectives were to (1) estimate seasonal squirrel density, survival, and recruitment across a structural habitat gradient; (2) quantify forest habitat characteristics and their relationships to squirrel population dynamics; and (3) determine seasonal squirrel diets and their relationships to habitat and population dynamics.

STUDY AREAS

We conducted our study during 1996 and 1997 at 8 sites in north-central Arizona, USA, located on the Coconino and Kaibab national forests. All sites were within the ponderosa pine association of the montane coniferous forest community (Brown 1994), between 2,075 and 2,375 m elevation, and within the range of the Abert squirrel subspecies (*S. a. aberti*). Study sites were oriented along gradients of forest structural conditions that were relatively homogeneous across approximately 60 ha and free from overstory tree habitat modification for at least 3 years prior to our study.

Our study sites included 3 sites with patchy, uneven-aged stand structure (Clints Well, Marshall Mesa, Parks) and 5 sites that were intensively logged and predominantly even-aged (Fort Tuthill, Gash Flat, Long Valley, Mormon Lake, Pumphouse). The uneven-aged sites had old-growth or mature forest characteristics reflecting either no past logging or light, individual tree selection harvest, with mean basal area (41.5 m²/ha) twice that of the 5 even-aged sites (19.6 m²/ha). The Parks site, although uneven-aged in nature, was open with basal area (26.8 m²/ha) more approximating our thinned, uneven-aged sites; this site was also surrounded by relatively dense managed forest. Half of our sites had measurable Gambel oak (*Quercus gambelii*) as an overstory component (Clints Well, Gash Flat, Marshall Mesa, and Mormon Lake). Forest structural parameters varied considerably among sites with mean total basal area ranging from 16.2 to 57.7 m²/ha and canopy closure from 27.5 to 59.4%. Dodd et al. (1998) employed principal compo-

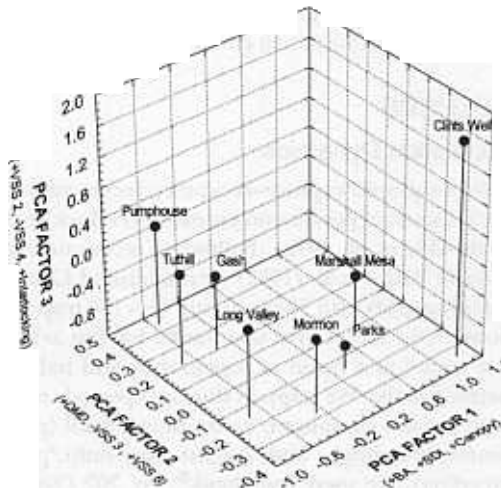


Fig. 1. Principal components analysis (PCA) ordination of habitat characteristics measured in 1997 for 8 study sites in north-central Arizona, USA (Dodd et al. 1998). The ordination diagram reflects mean study site scores for the first 3 components (factors) describing 71% of total variance. Factor 1 describes basal area, stand density index (SDI), and canopy closure. Factor 2 describes quadratic mean diameter (QMD) and number of vegetation structural stage (VSS) 3 and 6 trees/ha. Factor 3 describes number of VSS 2 and 4 trees/ha and number of interlocking canopy trees per point.

nents analysis (PCA) to ordinate the 8 study sites along gradients of habitat structural condition. This analysis separated 4 PCA factors accounting for 82% of the total variance in the original habitat data set. The first 3 PCA factors (Fig. 1) account for 71% of the total variance and reflect the relative positions of our study sites in multi-dimensional space along structural habitat gradients (Fig. 1).

In general, drought conditions prevailed prior to and during our study. National Weather Service records for the station nearest our study sites (Bellemont, Arizona, USA) indicated that 1995 was the seventeenth driest year on record (39.9 cm vs. 57.9 cm mean precipitation), 1996 the fourth driest (30.0 cm), and 1997 the seventh driest (35.1 cm). Despite consistent drought conditions, winter snowfall varied greatly between years. During winter 1995–1996, only 85.6 cm total snowfall was recorded, compared to the annual mean of 242.8 cm. Only 5 snow “events” occurred with accumulations ≥ 10 cm (the depth at which Stephenson and Brown [1980] reported squirrel mortality), with 12–21 days duration of snow depth ≥ 10 cm. Conversely, 338.3 cm of snowfall occurred during winter 1996–1997, with

9 events depositing ≥ 10 cm and accounting for 61–74 days duration ≥ 10 cm depth.

METHODS

Population Dynamics

We employed capture–recapture techniques to obtain squirrel population estimates (Pollock et al. 1990, Otis et al. 1978). Following recommendations in White et al. (1982) we established 12×12 trapping grids with 70-m spacing ($n = 144$ trap stations). Our target grid size was 60 ha, but actual size varied as a result of topography and habitat heterogeneity. We trapped during 3 periods each year: January (post-hunt/early winter), April (post-winter/breeding), and August (pre-hunt/post-breeding). We used Tomahawk® No. 202 (Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) traps baited with unshelled peanuts (Patton et al. 1976). All sites were trapped simultaneously a minimum of 8 days during each period. Additional trapping (up to 4 days) was done at individual sites as needed to attain population estimates with target standard error (SE) below $\pm 10\%$.

We immobilized captured squirrels using Metofan® (Pitman-Moore, Mundelein, Illinois, USA; Patton et al. 1976, Pederson et al. 1987). We affixed a numbered metal ear tag (Monel No. 3; National Band and Tag Co, Newport, Kentucky, USA) and a colored plastic collar to each squirrel. We visually determined sex and obtained body mass with a 1,000-g spring scale. We relied on differential body mass and morphological characteristics to separate juveniles from adults (Farentinos 1972, Keith 1965).

Population and Density.—We computed population estimates using the program CAPTURE (White et al. 1982, Rexstad and Burnham 1991). We used this program to test assumptions, to select appropriate models that minimized capture-related sources of variation in capture probabilities, and to derive population estimates, 95% confidence intervals (CI), and standard errors (SE). We calculated densities by dividing population estimates by study-site size (ha).

Survival Rates.—To estimate squirrel survival between trapping periods, we used the “robust design” (Pollock 1982, Pollock et al. 1990). The robust design combined pooled closed population capture–recapture histories and the open population Jolly–Seber model. Survival rates, 95% CI, and SE were derived for intervals between trapping efforts using the program JOLLY (Jolly 1965, Pollock et al. 1990). We deter-

mined the cumulative duration (days) of total snow cover ≥ 10 cm at our study sites during winter 1996–1997 by periodic observation throughout the winter, and evaluated the relationship to survival estimates using Spearman rank correlation.

Recruitment.—Emergence of juveniles from maternal nests generally occurs in late August (Brown 1984). Our August trapping periods occurred too early to reliably capture juveniles following their emergence from maternal nests. Therefore, we used the number of juvenile squirrels caught during our January trapping periods as a relative index of recruitment, measured as juveniles/adult female (Brown 1984). We assumed that squirrels were juveniles if body mass was ≤ 550 g, compared to a mean January mass of 697 g (± 17.5 SE, $n = 69$) for known adults (Dodd et al. 1998). We recognize the limitations of this index and the potential for bias associated with differential juvenile mortality, emigration, or immigration.

Habitat Assessment

Habitat Measurements.—We measured habitat characteristics reported to influence tassel-eared squirrel populations (Ratcliff et al. 1975; Pederson et al. 1976, 1987; Patton 1984) and that are pertinent to forest management. At each study site, 25 of the interior 100 trapping stations were randomly selected; outer trapping stations were not selected because some study sites were not adequately buffered from adjacent areas of different habitat condition. We then located a 0.10-ha circular plot in a random direction and distance ≤ 35 m from the trapping station. We measured habitat variables during fall 1997 while deciduous species were still leafed. Within each plot, we measured diameter at breast height (dbh) for pine and Gambel oak ≥ 2.5 cm dbh.

We estimated canopy cover by vertical projection, using a staff-mounted, self-leveling sighting periscope (Ganey and Block 1994). Observers recorded periscope cross-hair interceptions with canopy foliage > 2 -m height at 100 points in each sampling plot ($n = 25$). We located sighting points every 1.2 m along 4 transects (15 points/transect) emanating from the plot center in cardinal directions ($n = 60$). Additional points ($n = 40$) were located every 2.4 m along 4 transects (10 points/transect) forming a square within the outer perimeter of the plot to avoid oversampling the plot center. We measured relative incidence of trees with “interlocking” canopy crowns ≤ 1.5 m of each other, which was the distance we observed squirrels readily jumping from tree to tree. We

counted continuously interlocking canopy trees >15 cm dbh starting from the closest tree at each of 5 points; 1 at the plot center and 1 each at the end of the 4 cardinal canopy closure transects.

We calculated 3 habitat variables from overstory tree measurements for each of the 25 habitat sampling plots, and averaged for each study site by tree species: (1) quadratic mean diameter (QMD; diameter of a tree with average basal area), (2) basal area by tree species, and (3) tree density corresponding to vegetation structural stage (VSS) classes. We calculated tree density by VSS diameter class (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), VSS 5 (45.7–61.0 cm dbh), and VSS 6 (>61.0 cm dbh).

Diet Assessment

During each trapping period, we collected fresh squirrel fecal samples (10–15 pellets) deposited in squirrel traps; only 1 sample was collected per individual squirrel. We collected samples proportional to the number of different squirrels captured at each study site per period.

Fecal pellets were analyzed using methodology similar to that of States et al. (1988). We calculated percentages of fungal matter based on the number of fungal units, hyphae, and spores, relative to nonfungal units counted within 10 uniform grids superimposed on a uniformly dispersed microscopic field of fecal sample particulates suspended in distilled water. We based identification of fungi on recognition of spore types, which allowed us to identify to genus. Taxonomic richness (number of fungal taxa) and diversity were measured using the Shannon-Wiener index (Shannon and Weaver 1963). We considered 7 fecal samples the minimum needed to estimate study site and seasonal fungal parameters (Carey et al. 1999).

Statistical Analysis

We performed all statistical tests using program STATISTICA® (Statsoft 1994). All mean values are reported \pm SE.

Population Dynamics and Diet Differences.—For individual study sites, we considered seasonal density and survival estimates significantly different if 95% CI were non-overlapping. We used analysis of covariance (ANCOVA) to assess differences in mean squirrel density, survival rates, recruitment among periods, and differences in diet among seasons and years. In our ANCOVAs, we controlled for study-site effects (Hays 1981). For significant ANCOVAs, we assessed pairwise differences between periods with

Sheffe's multiple comparison tests. We used $P \leq 0.05$ to identify significant relationships.

Population, Habitat, and Dietary Relationships.—We assessed interrelationships of seasonal and yearlong tassel-eared squirrel population dynamics (density, survival, recruitment, and mean change in density from Apr to Aug), seasonal and yearlong diets (fungal content, taxonomic richness, diversity), and 12 study-site habitat structural characteristics using Spearman rank correlation. We recognized that conducting the large number of comparisons from the same data sets might result in spurious results of significance (Rice 1989). To address this problem, we applied a sequential Bonferroni test for significance (Rice 1989), correcting for multiple comparisons across each population, diet, or habitat variable data set.

RESULTS

Population Dynamics

We captured 2,542 squirrels in 56,016 trap days. An average of 8.5 days of trapping was required to achieve our target SE for population estimates. We captured 450 individual squirrels (207 [46.0%] males and 243 [54.0%] females; 431 [95.8%] adults and 19 [4.2%] juveniles). Population estimate SE averaged 10.2% (± 1.0).

Density.—Mean squirrel density (squirrels/ha) across study sites did not differ significantly among the January (0.25 ± 0.05 , $n = 15$), April (0.35 ± 0.04 , $n = 15$), or August (0.44 ± 0.08 , $n = 15$) periods. Nor did mean squirrel density differ between 1996 (0.33 ± 0.04 , $n = 24$) and 1997 (0.37 ± 0.05 , $n = 21$). However, half of the study sites exhibited significant increases in mean density between January and August based on non-overlapping 95% CI (Table 1). All but 1 of these sites (Parks) were dominated by intensively logged, even-aged habitats. Parks exhibited open forest condition and basal area similar to the even-aged sites. For the 4 study sites exhibiting significant seasonal fluctuations, density increased an average of 205% from January to August compared to 17% at the other sites.

Survival.—Squirrel survival rates averaged 0.78 (± 0.03 , $n = 24$) across all periods and 7 study sites (Table 2); estimates for Gash Flat were not obtained because the site was inaccessible during January and April 1997. We found significant differences among periods ($F = 10.1$; $df = 3, 19$; $P < 0.001$). Mean winter survival (0.63, Jan–Apr 1997) was lower ($P = 0.001$ – 0.024) than in the other 3 periods. We found no differences among the other 3 periods. In the period encompassing the

Table 1. Seasonal and mean tassel-eared squirrel density estimates (squirrels/ha), from 6 capture–recapture trapping efforts in 1996–1997, at 8 study sites in north-central Arizona, USA. Letters for individual study sites denote differences among periods based on non-overlapping 95% CI, while letters for seasonal means denote differences based on analysis of covariance tests.

Study site	Density (SE)			Mean
	Jan	Apr		
Clints Well	0.22 (0.05) A	0.29 (0.04) A	0.29 ^a (0.02) A	0.26 (0.04) A
Fort Tuthill	0.19 (0.03) A	0.37 (0.04) B	0.88 (0.05) C	0.48 (0.07)
Gash Flat	0.05 ^a (0.01) A	0.16 ^a (0.02) B	0.17 (0.01) B	0.11 (0.01)
Long Valley	0.16 (0.02) A	0.20 (0.02) A	0.12 (0.01) A	0.16 (0.02)
Marshall Mesa	0.44 (0.02) A	0.50 (0.03) A	0.54 (0.03) A	0.49 (0.03)
Mormon Lake	0.16 (0.03) A	0.18 (0.02) A	0.22 (0.02) A	0.19 (0.02)
	0.14 (0.02) A	0.36 (0.03) B	0.38 (0.03) B	0.30 (0.03)
Pumphouse	0.54 (0.05) A	0.65 (0.01) A	0.79 (0.05) B	0.66 (0.04)
	0.25 (0.05) A	0.35 (0.04) A	0.44 (0.08) A	0.66 (0.04)

^a Estimates derived from only 1 trapping period.

squirrel hunting season (Aug 1996–Jan 1997), survival rates averaged 0.81. Winter survival was inversely related to duration of snow cover ≥ 10 cm at our study sites ($r_s = -0.867$, $P = 0.011$, $n = 7$).

Recruitment.—Eight juveniles (8.0% of total squirrels) were caught in January 1996, and 11 (8.7%) in 1997. Our index of recruitment averaged 0.15 juveniles/female (± 0.05 , $n = 7$) in 1996 and 0.13 (± 0.05 ,

$n = 7$) in 1997, and were not significantly different. Mean recruitment across sites for both years ranged from 0.02 to 0.33 juveniles/female (Table 3).

Habitat Assessment

Habitat Measurements.—Habitat structural characteristics varied greatly among study sites (Table 4). Ponderosa pine influenced study site overstory

Table 2. Tassel-eared squirrel survival rates for 4 periods 1996–1997, at 7 study sites in north-central Arizona, USA, derived from the robust design using program JOLLY. Letters for individual study sites denote differences among periods based on non-overlapping 95% CI, while letters for seasonal means denote differences based on analysis of covariance tests.

Study site	Survival rate (SE)				Mean
	Apr 1996–Aug 1996	Aug 1996–Jan 1997	Jan 1997–Apr 1997	Apr 1997–Aug 1997	
Clints Well	0.75 (0.12) A	0.66 (0.15) A	0.66 (0.12) A	— ^a	0.69 (0.07)
Ft. Tuthill	— ^b	0.82 (0.09) A	0.71 (0.08) A	0.89 (0.08) A	0.81 (0.04)
Long Valley	0.86 (0.16) A	0.63 (0.16) A, B	0.54 (0.15) B	— ^b	0.68 (0.04)
Marshall Mesa	0.96 (0.05) A	0.81 (0.08) A, B	0.69 (0.07) B	0.97 (0.06) A	0.86 (0.03)
Mormon Lake	0.71 (0.17) A, B	0.88 (0.10) A	0.42 (0.14) B	0.93 (0.17) A	0.73 (0.05)
Parks	— ^b	0.92 (0.08) A	0.69 (0.12) A	0.74 (0.17) A	0.85 (0.04)
Pumphouse	0.77 (0.08) A	0.97 (0.05) B	0.70 (0.07) A	0.84 (0.06) A	0.82 (0.03)
Mean	0.81 (0.12) A	0.81 (0.10) A	0.63 (0.10) B	0.91 (0.11) A	0.78 (0.03)

^a Trapping suspended—no estimate available.

^b Insufficient sample size for previous period to compute survival rate.

Table 3. Tassel-eared squirrel recruitment indices (juveniles/female) measured in Jan 1996 and 1997, at 7 study sites in north-central Arizona, USA.

Study site	Recruitment (juveniles/female)		
	Jan 1996	Jan 1997	Mean
	0.14	0.14	0.14
	0.00	0.04	0.02
	0.00	0.10	0.05
	0.23	0.42	0.33
	0.28	0.00	0.14
	0.33	0.16	0.24
	0.08	0.06	0.07
	0.15	0.13	0.13

habitat characteristics the most, although Gambel oak also was prevalent at 4 study sites (Table 4). Density of trees <2.5 cm dbh varied greatly among sites (Table 4); 5 sites had minimal understory of trees <2.5 cm dbh, while Clints Well and Gash Flat had a substantial ponderosa pine understory. New Mexican locust (*Robinia neomexicana*) was prevalent in the understory at Fort Tuthill, with 293.2 stems/ha (±81.2).

Squirrel Diets

We collected a total of 382 squirrel fecal samples during 6 trapping periods (Table 5). We detected 21 species of hypogeous and epigeous fungi in squirrel fecal samples (Table 6). Hypogeous species of *Rhizopogon*, *Gautieria*, *Geopora*, *Hysterangium*, and *Sclerogaster* were most common and present during all periods (Table 6). Epigeous fungi, mostly fleshy agaric mushrooms, were prevalent in the January and April samples, with higher volume contributions during the former period. Significant differences occurred in mean fungal content among periods ($F = 33.1$; $df = 2, 39$; $P < 0.001$). Highest mean fungal relative frequency occurred during August ($70.8 \pm 2.9\%$, $n = 117$), which was significantly higher than January ($28.2 \pm 2.8\%$, $n = 102$, $P < 0.001$) and April ($9.4 \pm 1.1\%$, $n = 163$, $P < 0.001$) means. Mean January fungal content also was higher than that for April ($P = 0.015$). Percent fungal content during each period did not differ significantly between years. Mean yearlong fungi content in samples across study sites ranged from 9.9% to 48.6% (Table 5).

We found no significant differences in mean number of fungal taxa among periods or between years. Total number of taxa recorded in all samples across study sites was similar, ranging from 11 to 14. Fungal diversity in the squirrel diet was highest in August, although it did not differ among seasons or between years (Table 5).

Table 4. Mean forest habitat characteristics (SE) for 8 study sites in north-central Arizona, USA, sampled in 1997, including quadratic mean diameter (QMD; cm), and tree density for by vegetation structural stage (VSS) and Gambel oak >2.5 cm dbh.

	Basal area (m ² /ha)		Percent		Ponderosa pine stems/ha ^a							Gambel oak stems/ha
	All species	Gambel oak	QMD	clost	Interlocking trees/point	VSS 2	VSS 3	VSS 4	VSS 5	VSS 6		
Clints Well	39.8 (6.1)	0.6 (0.1)	16.5 (1.1)	59.4 (2.4)	3.7 (0.2)	1,619.2 (228.8)	385.6 (43.7)	59.6 (11.6)	27.6 (3.7)	20.0 (5.9)	31.6 (10.1)	
Fort Tuthill	16.2 (1.1)	—	32.8 (1.2)	31.6 (2.0)	2.2 (0.2)	21.2 (9.7)	99.2 (28.3)	85.6 (7.8)	18.8 (3.8)	1.2 (0.7)	—	
Gash Flat	22.1 (1.5)	2.4 (0.5)	32.6 (1.0)	38.8 (2.4)	3.6 (0.2)	56.8 (18.3)	84.0 (11.6)	106.0 (11.1)	22.4 (4.8)	6.8 (1.6)	58.0 (31.0)	
Long Valley	16.8 (2.1)	—	27.9 (1.0)	27.5 (3.3)	2.8 (0.2)	17.9 (5.3)	145.0 (25.3)	102.1 (16.5)	2.9 (1.2)	0.7 (0.7)	—	
Marshall Mesa	57.7 (16.8)	2.7 (0.4)	31.7 (3.5)	52.7 (2.9)	4.9 (0.2)	116.8 (16.6)	325.2 (26.7)	130.4 (15.9)	22.0 (3.1)	9.2 (2.2)	50.8 (6.7)	
Mormon Lake	24.8 (3.5)	1.0 (0.2)	29.0 (1.3)	38.6 (1.8)	3.5 (0.2)	13.2 (2.8)	224.0 (23.0)	116.0 (11.1)	8.4 (2.4)	2.0 (0.8)	48.8 (13.7)	
Parks	26.8 (2.4)	—	36.2 (2.6)	47.5 (3.6)	4.2 (0.3)	10.4 (2.0)	207.2 (37.6)	107.6 (16.6)	17.2 (3.4)	10.8 (3.6)	—	
Pumphouse	18.2 (1.7)	—	34.6 (1.9)	37.4 (3.0)	2.6 (0.2)	32.0 (8.5)	98.8 (15.4)	62.0 (8.4)	24.4 (4.9)	8.0 (1.7)	—	

^a VSS 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 = 45.7–60.7 cm dbh; VSS 6 = >61.0 cm dbh

Table 5. Seasonal and annual mean relative frequency (MRF; %) by volume of fungi and fungal diversity (FD) in tassel-eared squirrel fecal samples (*n* denotes sample size), collected 1996–1997, at 8 study sites in north-central Arizona, USA.

Study site	Jan			Apr			Aug			Annual		
	MRF (SE)	FD	<i>n</i>	MRF (SE)	FD	<i>n</i>	MRF (SE)	FD	<i>n</i>	MRF (SE)	FD	<i>n</i>
				13.1 (3.6)	3.51	25	73.3 (6.7)	0.95	9		6.01	42
				6.8 (2.9)	2.20	21	37.6 (6.3)	3.44	24		5.06	47
				2.8 (0.6)	1.24	9	75.0 (18.3)	0.49	9		2.24	17
				7.9 (2.6)	2.49	21	19.1 (6.8)	0.90	7		4.35	36
				15.7 (3.0)	3.32	24	92.0 (1.2)	5.96	39		12.59	96
				10.6 (3.2)	1.59	14	92.6 (1.7)	0.60	7		3.48	32
				8.1 (4.2)	1.59	21	77.4 (9.6)	1.19	10		4.47	43
				6.5 (2.4)	3.26	28	75.5 (4.4)	2.46	17		8.48	69
				9.4 (1.1)	1.36	163	70.8 (2.9)	1.89	117		1.42	382

^a Sample size insufficient to yield reliable estimate of fecal fungal content for that period

Population, Habitat, and Dietary Relationships

Squirrel Population and Habitat Relationships.—Our comparison of 12 study-site structural habitat parameters to squirrel population response variables yielded 2 significant comparisons. Indices to squirrel recruitment were strongly related to the number of interlocking canopy trees ($r_s = 1.000$, $n = 7$). Mean fluctuation in squirrel density from April to August was positively related to ponderosa pine QMD ($r_s = 0.881$, $P = 0.003$, $n = 8$). No relationships among habitat structural variables and squirrel density or survival were found to be significant.

Table 6. Hypogeous and epigeous fungi in tassel-eared squirrel fecal samples collected 1996–1997, at 8 study sites in north-central Arizona, USA.

Genera/taxa	Mean frequency of occurrence (%)			
	Jan	Apr	Aug	Total
Hypogeous fungi				
<i>Brauniellula</i>	1.0	—	—	0.3
<i>Elaphomyces</i>	6.9	17.2	32.5	19.1
<i>Endogone</i>	—	—	2.6	0.8
<i>Gautieria</i>	35.3	24.5	25.6	27.7
<i>Genabea</i>	1.0	0.6	—	0.5
<i>Geopora</i>	19.6	35.0	30.8	29.6
<i>Hymenogaster</i>	2.0	8.0	1.7	4.4
<i>Hysterangium</i>	10.8	8.0	38.5	18.1
<i>Melanogaster</i>	2.0	0.6	2.6	1.8
<i>Rhizopogon</i>	65.7	18.4	93.2	53.9
<i>Sclerogaster</i>	8.8	11.0	9.4	9.9
<i>Scleroderma</i>	—	—	3.4	1.0
<i>Tuber</i>	1.0	—	—	0.3
Epigeous fungi				
Agaric	14.7	10.4	4.3	9.7
Large agaric	9.8	6.7	—	5.5
Small agaric	64.7	29.4	1.7	30.4
<i>Russula</i>	2.9	0.6	—	1.0
Other/unidentified (4)	28.4	23.9	5.1	19.4

Dietary and Habitat Relationships.—Only 1 correlation among dietary fungal content and habitat parameters across study sites was significant: August fungal content was correlated with basal area ($r_s = 0.943$, $n = 6$, $P = 0.005$). No comparisons among fungal diversity or richness and habitat variables were found to be significant.

Dietary and Population Dynamics Relationships.—Correlations among mean seasonal and yearlong fungi content and population response variables yielded 1 significant comparison: mean August fungi content versus squirrel recruitment ($r_s = 0.943$, $n = 6$, $P = 0.005$). Winter squirrel survival for January–April 1997 was related to January 1997 fecal fungal diversity ($r_s = 0.943$, $n = 7$, $P < 0.005$). Squirrel density and fungal diversity were significantly correlated ($r_s = 0.561$, $n = 41$, $P < 0.001$) across all sampling periods. No comparisons among fungal richness and squirrel population variables were significant.

DISCUSSION

Population Dynamics

Most previous studies of tassel-eared squirrels reported dramatic fluctuations in populations between years or habitat conditions (Keith 1965, Stephenson and Brown 1980, Hall 1981, Patton et al. 1985). However, like Farentinos (1972), we found similar average densities between years and dramatic seasonal fluctuations within years. Farentinos (1972) attributed a 67% increase in density from spring to fall to recruitment of juveniles, and a 55% decline the following spring to mortality and emigration. The April–August increases in squirrel density on our study sites were apparently not a function of juvenile recruitment, which was insufficient to account for these fluctuations.

Recruitment at our sites during both years was well below the level considered low (0.50 juveniles/female) by Brown (1984), presumably due to prevailing drought conditions. Our recruitment indices during both years were a tenth of the 12-year mean recruitment level reported by Brown (1984), suggesting that many females did not breed successfully (Farentinos 1972, Stephenson 1975). These conclusions are supported by trapping conducted October 1999–2002 at 18 sites (31 ha) on the Coconino National Forest (N. L. Dodd, Arizona Game and Fish Department, unpublished data). Annual mean indices of recruitment ranged from 0.05 to 1.90 juveniles/adult female and were strongly associated ($r^2 = 0.971$) with percentage of normal winter–spring (Nov–May) precipitation. During the 2 years of poorest recruitment and precipitation (2000 and 2002), <3% of 235 adult females captured showed evidence of having bred or nursed young.

With fluctuations in density apparently not attributable to recruitment, we postulated that fluctuations were related to (1) expanded home ranges of squirrels residing adjacent to study sites, or (2) squirrels that emigrated to study sites from population source areas. The large increases in density noted at our logged, even-aged sites coincided with the period of peak food availability, particularly pine cone seed and hypogeous fungi in late summer–fall (Stephenson 1975, Hall 1981, Brown 1984, States et al. 1988). These foods are important in determining squirrel distribution, abundance, and survival (States and Wettstein 1998).

Squirrels had left our study sites exhibiting large seasonal fluctuations by January, possibly as a result of depletion of cone crops and in search of higher quality habitat necessary for winter survival. Radiotelemetry monitoring at our Fort Tuthill site found that 27 of 28 squirrels departed the site during winter and resided in adjacent unlogged habitat (Lema et al. 1999, Lema 2001). Trapping conducted immediately adjacent to this site during late winter 1997 found that 94% of previously marked, recaptured squirrels ($n = 18$) were residing along the edge in a relatively narrow band (175 m) of quality habitat (Dodd et al. 1998). Lema (2001) also found significantly larger mean squirrel home ranges during spring and summer (15.5 ha, $n = 38$) than during winter (7.5 ha, $n = 18$), confirming that squirrels indeed exhibited expanded home ranges during the periods of increased density.

The amount and duration of winter snow cover frequently has been cited as the most important factor affecting squirrel survival (Keith 1965, Stephenson 1975, Stephenson and Brown 1980, Hall 1981). Deep, prolonged snow cover limits access to hypogeous fungi and pine cones, relegating squirrels to a diet of nutrient-deficient pine twig inner cambium on which they lose body mass and are subject to elevated mortality (Stephenson 1975, Austin 1990). Even with only a single year of data, the winter period appeared to be the most limiting period for squirrel survival at our study sites, with survival tied to snow-cover duration (Stephenson and Brown 1980).

Sport hunting's impact on tassel-eared squirrels in the Southwest and influence on annual survival is largely unknown, although sport hunting is an area of concern due to localized impact noted for other squirrel species (Nixon et al. 1974). Though we did not control for sport hunting at our study sites, the high survival rate during the period encompassing the hunting season suggests that overall impact is relatively minor, particularly compared to mortality incurred during some winters, as also reported by Brown (1984).

Dietary Fungi Assessment

Few studies have assessed tassel-eared squirrel food habits through direct analysis of diets compared to inferences made from visible feeding sign. Regardless, all studies exhibited general similarities in use of seasonally variable foods; our results were no exception. Stephenson (1975) reported that fungi comprised 38.6% of total annual stomach volume, similar to our mean relative frequency of 36.4%. Our mean August fungal content (70.8%) closely approximated his mean July–August fungi volume (73.9%), as did our April (9.4%) and his mean March–May estimates (7.8%). Seasonal fungal content closely paralleled the fecal fungi patterns reported by States et al. (1988).

States and Gaud (1997) measured hypogeous fungi sporocarp biomass and species presence over 3 years and found highest mean biomass (53.7% of total) and species (25) in fall, followed by summer (21.1% and 16 species), spring (16.8% and 13 species), and winter (8.4% and 10 species). Mycophagy at our study sites during April was relatively low compared to sporocarp biomass estimates for the spring period reported by States and Gaud (1997). Limited fungal content in the diet at this time may have reflected severe drought conditions in both 1996 and 1997, as well as high snowfall during winter 1996–1997

that possibly delayed fungal sporocarp phenology and availability.

Population, Habitat, and Dietary Relationships

Patton et al. (1985) and Pederson et al. (1987) stressed the importance of overstory tree clumpiness and canopy closure to tassel-eared squirrels. Patton (1975*a*) unsuccessfully tried to describe variation in squirrel density with an "index of patchiness." Although we too found no relationship between canopy variables and squirrel density, our strongest relationship occurred between number of interlocking canopy trees and squirrel recruitment. Study sites that had undergone intensive even-aged timber harvest and had <3 interlocking trees per sample point exhibited minimal or inconsistent squirrel recruitment. Patton (1975*b*) reported that 92% of squirrel nests were found in trees growing inside a group, with 75% having ≥ 3 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).

In addition to interlocking canopy trees, recruitment was correlated with mean fungal content in fecal samples during the August sampling periods. Mean August fungal content was in turn a function of total basal area. This is consistent with States and Gaud (1997) who found that fungal sporocarp production (and hence presence in diets) was strongly correlated with basal area and canopy cover in ponderosa pine forests. Other studies found basal area important to tassel-eared squirrels. Ratcliff et al. (1975) found a significant 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, canopy closure, and tree density.

Mycophagy increased dramatically (653%) between our April and August sampling periods, probably as a function of increased fungal availability (States et al. 1988). High fungal nutrient and caloric content (Austin 1990), coupled with high foraging efficiency (Smith 1970, Cork and Kenagy 1989), were associated with body-mass increases while tassel-eared squirrels fed on diets high in fungi (Stephenson 1975, States et al. 1988, Austin 1990, States and Wettstein 1998). Fungi availability and use by squirrels at the time of juvenile dispersal from natal nests in August probably contributed significantly to juvenile recruitment.

Though only a third of the 21 fungal taxa detected in our fecal samples exhibited >10% frequency of occurrence, the presence of other taxa nonetheless influenced squirrel density and winter survival. Fungal diversity contributes to increased diversity of phenological patterns and fungal and host tolerances to environmental extremes (Perry et al. 1989), especially important to squirrels under conditions of highly variable and seasonal precipitation.

At our intensively logged study sites, fecal fungal content was low and fungal availability was also assumed to be relatively low due to their low basal areas (States and Gaud 1997). Yet 3 of these sites (Fort Tuthill, Gash Flat, Pumphouse) exhibited dramatic seasonal fluctuations in squirrel density, peaking in August. With low fungal availability and use by squirrels, ponderosa pine seed may have acted as an attractant to squirrels. Pine cone seed production may have been enhanced as a result of the thinned, noncompeting nature of remaining trees (Schubert 1974, Buchanan et al. 1990). For example, while cone-producing (VSS 3–6) tree density at our dense Marshall Mesa site (513 trees/ha) was 150% greater than at thinned Fort Tuthill (205 trees/ha), Lema (2001) found only 30% higher pine cone availability at Marshall Mesa (6,285 cones/ha) compared to Fort Tuthill (4,830 cones/ha). Further, squirrels at Fort Tuthill exhibited a higher consumption of cones, both as a percentage of cone availability (45.0% vs. 24.5%) and by count (2,174 vs. 1,508 cones/ha). Tassel-eared squirrel population fluctuations elsewhere were attributed to pine cone abundance (Keith 1965, Hall 1981, Patton et al. 1985).

Larson and Schubert (1970) reported that ponderosa pine cone production and crop frequency were positively related to tree diameter. Patton et al. (1985) reported a significant positive correlation between squirrel density and QMD. We conclude that the relationship between seasonal density fluctuations and pine QMD appears to be a function of pine cone abundance.

MANAGEMENT IMPLICATIONS

Ponderosa pine forest restoration activities in the Southwest are anticipated to increase, with restoration targeted for 81,000 ha annually in Arizona and New Mexico over the next 10 years (Anonymous 2001). The prevailing restoration emphasis is on thinning to replicate forest tree densities existing ca. 1870, prior to European settlement (Covington et al. 1997, Fulé et al. 1997, Mast et al. 1999). Treatments emulating refer-

ence density structure have resulted in large reductions in tree density, up to 98%, with resultant densities ≤ 60 trees/ha (Mast et al. 1999).

Though it is important to recognize that our study was short-term in nature and conducted under drought conditions that resulted in relatively poor squirrel recruitment and good survival, our results nonetheless provide insights for forest restoration. Most of our study sites were influenced by past even-aged management. However, because of similarities in structural habitat characteristics between our sites and habitats treated to achieve pre-settlement reference tree densities, we think that squirrel populations and hypogeous fungi may be impacted adversely by wide-scale forest restoration treatments. Under restoration prescriptions that substantially reduce the incidence of interlocking canopy trees, squirrel recruitment will be diminished. Substantial reductions in basal area associated with restoration prescriptions will diminish fungal production (States and Gaud 1997), affecting squirrel recruitment and survival. Such impact to squirrels and fungi may be compounded with restoration treatments over large, contiguous areas.

Forest 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). Patton (1984:412) concluded that "optimum (tassel-eared squirrel) habitats likely do not exist in many areas due to the intensity of timber harvesting in the past." Extensive forest restoration may diminish remaining high-quality squirrel habitats.

Our results also suggest a potential benefit to squirrels from creation of a mosaic of structural habitat conditions and patch sizes, as described by Patton (1992). At several of our study sites, squirrels exploited seasonally available cone crops where forest thinning apparently promoted cone production, particularly where such areas were adjacent to higher-quality habitats (Dodd et al. 1998, Lema et al. 1999, Lema 2001). We found that high-quality squirrel habitats are those that exhibit basal area >35 m²/ha and VSS 5 diameter class tree density >20 trees/ha. Study sites with average or above recruitment levels had a minimum of 22 patches/ha of >5 interlocking canopy trees. As forest treatments are planned, application of variable thinning prescriptions and tree basal area within harvest areas to retain a patchy character will benefit squirrels, as well as hypogeous fungi. Last, forest treatments should pro-

mote canopy clumpiness and interlocking canopy trees to improve squirrel habitat.

ACKNOWLEDGMENTS

This project was conducted with financial support by the Federal Aid in Wildlife Restoration Act, Project W-78-R. A virtual army of 184 individuals assisted with capture-recapture trapping, far too many to acknowledge individually, yet every person's help was vital to the success of the project. A special thanks goes to the Northern Arizona University student chapter of The Wildlife Society for their tremendous volunteer support. Critical suggestions to this manuscript were provided by S. S. Germaine, R. A. Ockenfels, A. Robinson, and R. E. Schweinsburg.

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Received 27 June 2002.

Accepted 2 April 2003.

Associate Editor: Martin.