

# Foraging Patterns of Tassel-Eared Squirrels in Selected Ponderosa Pine Stands<sup>1</sup>

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The tassel-eared tree squirrel (*Sciurus aberti*) and its several subspecies, has a unique and apparent obligatory association with Southwestern ponderosa pine (*Pinus ponderosa*). The dietary dependence of these squirrels on pine, including inner bark and buds of terminal twigs and both staminate and ovulate cones, identifies the squirrel as an herbivore having a potentially major influence on the growth and reproduction of ponderosa pine. Conversely, extensive harvest of pine for wood products has resulted in deterioration of the squirrel's habitat since the turn of the century (Keith 1965).

A number of studies have attempted to explain the "boom and bust" population fluctuations that seem to be characteristic of tassel-eared squirrels. In his observations

on the ecology of Abert squirrels (*S. a. aberti*), Keith (1965) attributed short term fluctuations to changes in quantity and quality of major food items assumed to be provided by pine. However, high mortality in some years apparently resulted from some factors other than food. Hall (1981), in a study of Kaibab squirrels (*S. a. kaibabensis*) also observed population fluctuations. He suggested that seasonal differences in food resources and snowfall were potential causes of declines and recovery. Availability and use of various food items have not been adequately studied.

Stephenson (1974) in a study of Abert diets discovered that fungi were a major part of the total food consumed. The fungi in Stephenson's samples were identified as belonging to a subterranean group of mushrooms popularly called truffles (J. States, unpublished data), which are known to form mycorrhizal associations with pine roots. Some of these fungi were found to be new records for the Southwest (States 1983, 1984) and they were found to be primarily associated with blackjack age-class ponderosa pine stands with high canopy densities (States 1985).

A telltale sign of the activity of the tassel-eared squirrel is the presence of clipped twigs on the ground under a tree after the squirrel has removed the terminal shoot from a branch. The nutritional value of the inner bark consumed by the squirrel is low. A diet comprised solely of inner

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**Abstract.**—Pine seed, primarily available in the fall, and hypogeous fungi, potentially available in all seasons, were major food items whose consumption was associated with an increase in biweekly body weights of marked squirrels. Use of alternative foods such as twigs (inner bark) and apical buds occurred when these food items were unavailable. Consumption of inner bark and buds was highest in winter (93%) and spring (86%). Although feed tree preference was noted, widespread feeding occurred in more than half of the trees in both study sites. The resulting variability in physical evidence of foraging suggests caution in its use for indexing squirrel population densities.

bark in the absence of supplemental foods could potentially threaten squirrel survival during adverse weather conditions (Patton 1974). The obvious selection of certain trees by squirrels for inner bark consumption supports the assumption that there are differences in quality of trees in the same stand. In a food preference study using captive Abert squirrels, Farentinos et al. (1981) were able to show a significant relationship between selective consumption of inner bark and low oleoresin content. However, Pederson and Welch (1987) noted a strong feeding preference for trees with inner bark that was easily peeled with no apparent relationship between inner bark oleoresin content and "feed tree" selection.

Studies on the impacts of squirrel herbivory on ponderosa pine have lead to mixed conclusions. Hall (1981) and Ffolliott and Patton (1978) found that heavy utilization of pine twigs had negligible effect on stand productivity, although Hall demonstrated significant growth decreases of individual feed trees. Soderquist (1987) reported twig clipping to decrease tree growth in ecotonal stands of ponderosa pine. Pearson (1950) and Larson and Schubert (1970) noted extensive, but seasonally variable, damage to cone crops. They were unable to determine the causes of the highly variable pattern of herbivory during several years of observation.

The tassel-eared squirrel's variety of diet and use of the forest has lead to differences of opinion regarding the best management plan for both squirrel and forest. Patton et al. (1985) considered tree density, size, and patchy distribution to be major factors constituting habitat quality since squirrels use pine for cover and nesting as well as for food.

The purpose of this study was to determine the seasonal patterns of food resource utilization by Abert squirrels in selected ponderosa pine stands and to relate the results to squirrel population levels within the stands. The use of fungi and inner bark as major food items is discussed as it pertains to stand characteristics and the potential impact of herbivory on ponderosa pine.

### Study Areas and Methods

Two sites in clumped, uneven-aged ponderosa pine stands were studied in areas that had not been disturbed by fire and timber harvest for the past 35 years. A 9.3 ha site was located on the property of the Lowell Observatory and adjacent to the Coconino National Forest. The other site of 2.5 ha was located in the Mount Edden Environmental Study area of the Coconino National Forest. The elevation of both sites was 2150 m, and they were within 10 km of the Flagstaff airport where weather data used in the study was collected (NOAA 1987).

Squirrels were captured, marked, and released at the observatory site. At this location there were 90 plots, 625 m<sup>2</sup> each, in a nested trapping grid similar to the one described by Patton et al. (1985). The grid contained 42 systematically spaced Tomahawk live-traps baited and set for eight daylight hours once each week. Trapping was conducted from September 1985 through June 1987 and squirrel body weight was recorded. Fecal pellets deposited in traps were collected and analyzed to

Table 1.—Estimated food availability for Abert squirrels.

Year	Truffles kg/ha	Seed cones/tree x n=25	Acorns/tree x n=20	Mushroom abundance
1983	2.88	144	552	high
1984	0.86	10	83	low
1985	0.39	10	123	very low
1986	0.72	137 <sup>a</sup>	20 <sup>b</sup>	very high
1987	0.65	10	10 <sup>b</sup>	moderate

<sup>a</sup>Cone crop 21% aborted due to insect damage; 31% of total cone crop harvested by September.

<sup>b</sup>Acorn production low due to early frost.

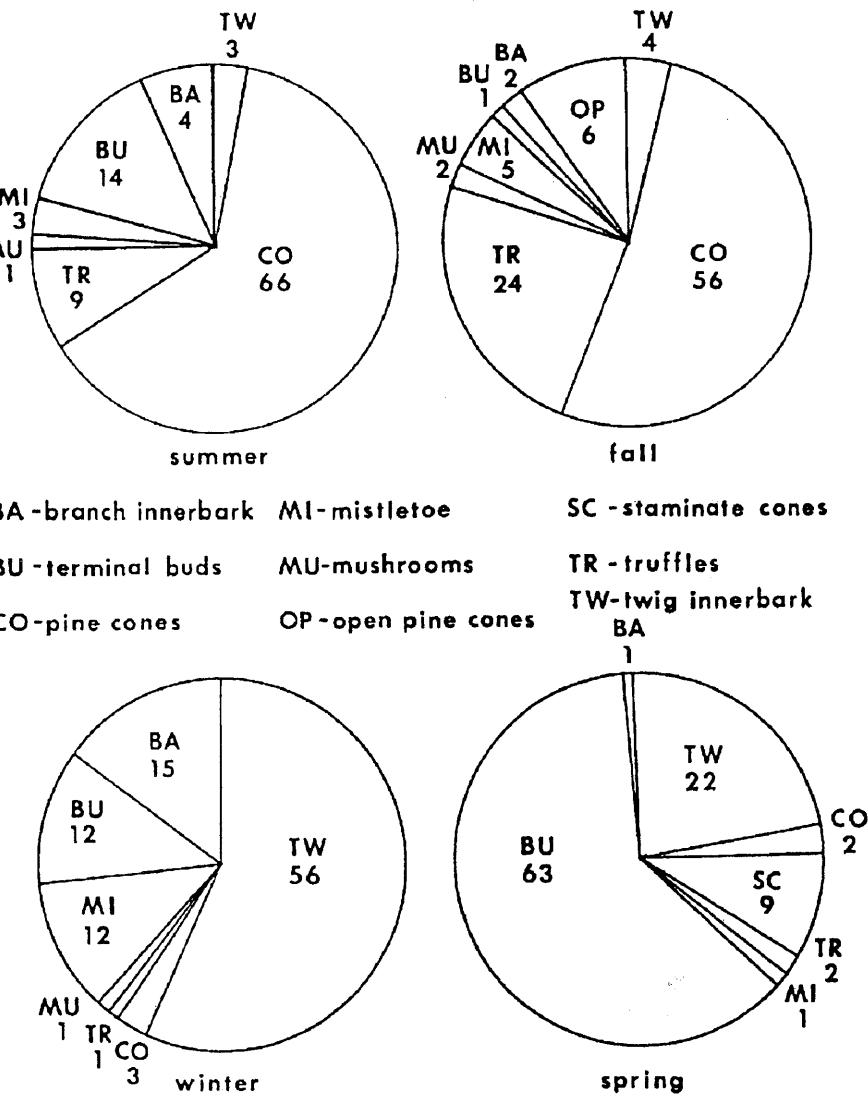


Figure 1.—Percentage of feeding time by Abert squirrels for each diet item in each season (from eighteen two-hour periods per season, Coconino National Forest, AZ).

determine the ratio of dietary fungus to plant matter and to identify the fungi through spore characteristics.

Observational data on foraging behavior was collected using focal animal sampling (Altmann 1974). We observed four individually marked males from July 1986 through November 1987 as they foraged in the study site. Data were collected in 18 two-hour observation periods in each of four "ecological" seasons. These seasons were established by combining months with similar temperature and precipitation means. The seasons correspond to periods of truffle production: Season I, December-March (winter); Season II, April-June

(spring); Season III, July-August (summer); Season IV, September-November (fall).

Resource availability and physical signs of foraging activity were recorded over a 20-month period (June 1986 through January 1988). Cone consumption, twig clipping, and digging activity were documented on 26 contiguous 625 m<sup>2</sup> plots (1.6 ha) on the observatory site. During each of the biweekly censuses, all twig remnants, cone cores, and digs (truffle excavations) were recorded with a notation of the nearest tree. Trees were characterized by age-class (blackjack, or yellow pine) and diameter at breast height (DBH). The

entire 2.5 ha Mount Elden site was sampled for seasonal foraging patterns. Permanently marked pines and oaks in 20 plots were censused yearly in September for acorn and cone production. Cones and acorns were counted on a quarter of the tree and multiplied by four to obtain a production estimate. Truffle production estimates were made according to States (1985). Relative mushroom abundance was determined by counting numbers of mushrooms present within 10 randomly placed 50 m<sup>2</sup> quadrats sampled in the fall.

## Results

Resources available as food for tassel-eared squirrels showed considerable annual variability (table 1). The four food items were all relatively abundant in 1983, but availability subsequently dropped. Production of cones and mushrooms was relatively high again in 1986, but there were considerably fewer truffles and acorns present than in 1983. In general, the quantity of truffle production was more consistent than it was for the other foods.

Seasonal foraging behavior of the squirrels (fig. 1) reflected changes in availability of food items. The animals heavily utilized a large cone crop in 1986 before the seeds were mature, and continued to utilize it into November when the remaining seeds were released. Cone and truffle use dropped abruptly from a fall high of 80% feeding time when the squirrels switched to intensive feeding on buds and inner bark of twigs. This behavior comprised 85% of the spring feeding time. Collectively, pine products constituted the largest portion of the diet through winter and spring. Seasonal patterns were apparent in the use of different parts of the tree.

The physical evidence left in the forest by the squirrels verified a seasonal progression of food item availability (fig. 2). Numbers of digs

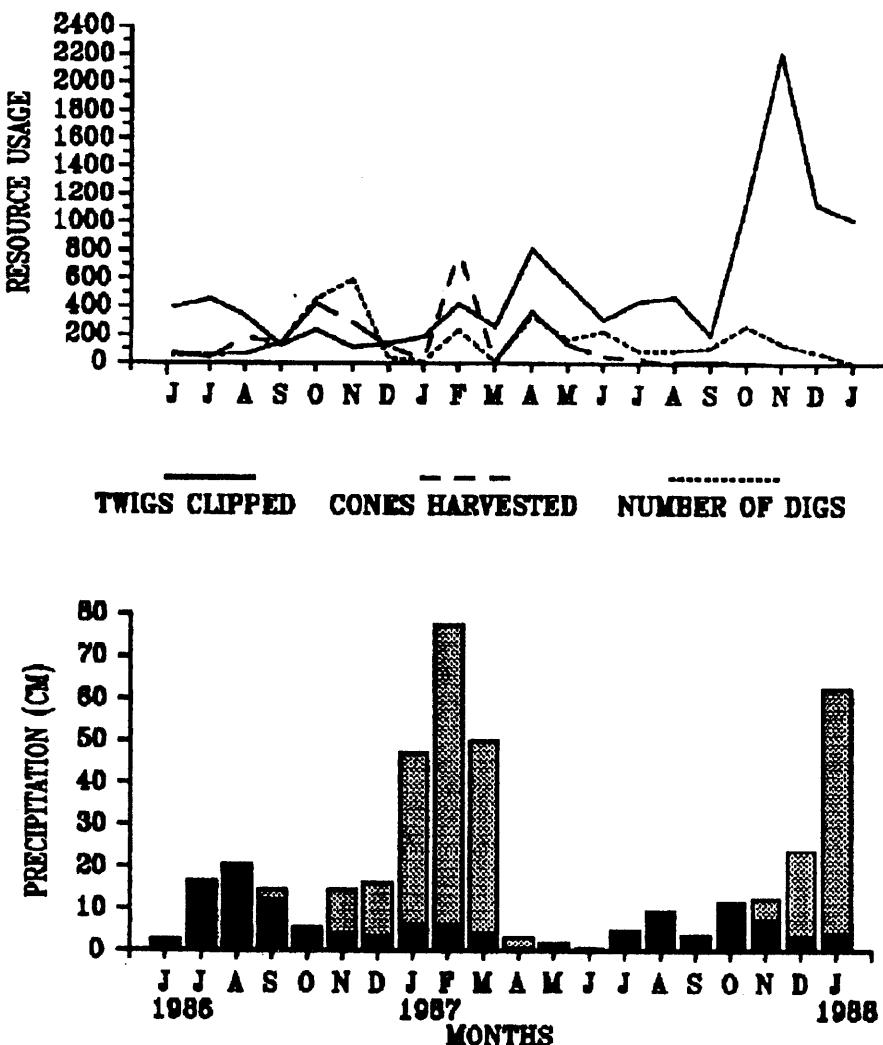


Figure 2.—Monthly resource usage by Abert squirrels compared to total precipitation (solid bar) and snow depth (shaded bar), Coconino National Forest, AZ.

peaked in late fall and dropped in the winter, a pattern which corresponds to foraging time percentages for truffles (fig. 1). Subsequent digs during winter and early spring represented retrieval of cones buried the previous fall. Numbers of cone cores left after seed removal increased as the cones matured. Numbers of cone cores subsequently decreased in the winter months. As the use of cones and truffles declined, numbers of clipped twigs increased. Twig clips decreased to a moderate level in summer but again reached a high level the following winter. This peak was coincident with increased snow depth, a decrease in availability of truffles, and the absence of seed cones. By the end of January 1988, a majority of the 1114 trees (67.9%) in the observatory site had been clipped at least once with an average of almost 10 clips per tree.

In spite of relatively low food availability in the year from September 1985 through August 1986 (table 1), resident squirrels maintained a fairly constant weight throughout the winter (table 2). The average weight of four male squirrels dropped 6% during spring and early summer from the previous fall's high. Subsequent weight gains, 5%, occurred concurrently with maturation of the 1986 fall cone crop. Winter weight loss paralleled the decrease in availability of fungi, as evidenced by their presence in fecal contents (fig. 3).

The number of terminal shoots removed by squirrels in the Mt. Elden site from 1984-1987 was apparently related to snowfall (table 3). Squirrel densities remained relatively constant, but the number of trees clipped increased by 30% and the average number of clips per tree decreased by 81%. Total snowfall was greater in 1985 than in either 1986 and 1987. The map of clipping behavior shows marked shifts in areas of heaviest clipping in the 2.5 ha site (fig. 4). The smallest area of clipping intensity (46% of the site) occurred in 1985, and it also had the highest

Table 2.—Mean body weight (grams) and standard deviation of individual male squirrels in each season from September 1985 through November 1986. The numbers of captures per season are in parentheses.

Squirrel	IV Fall	I Winter	II Spring	III Summer	IV Fall
1	614 + 11.7 (11)	632 + 30.1 (12)	610 + 12.7 (3)	587 + 27.9 (7)	610 + 27.6 (9)
2	748 + 37.0 (5)	680 + 34.3 (7)	723 + (1)	703 + 18.6 (5)	769 + 20.9 (5)
3	655 + 20.4 (13)	681 + 15.2 (12)	671 + 18.0 (7)	648 + 29.8 (5)	674 + 16.9 (8)
4	737 + 24.7 (6)	688 + 31.5 (5)	669 (1)	662 + 33.6 (7)	674 + 33.8 (11)
x	689	670	668	650	682

number of clips per tree. The area of clipping expanded in 1986 and 1987 to 67% and 64%, respectively. Of the 604 trees clipped in the three years, 45% were clipped once while 23%

were clipped every year. Yellow pine constituted 10% of the stand and 82% of these were clipped. Most yellow pines not clipped were isolated in open areas. Sixty-one percent of all

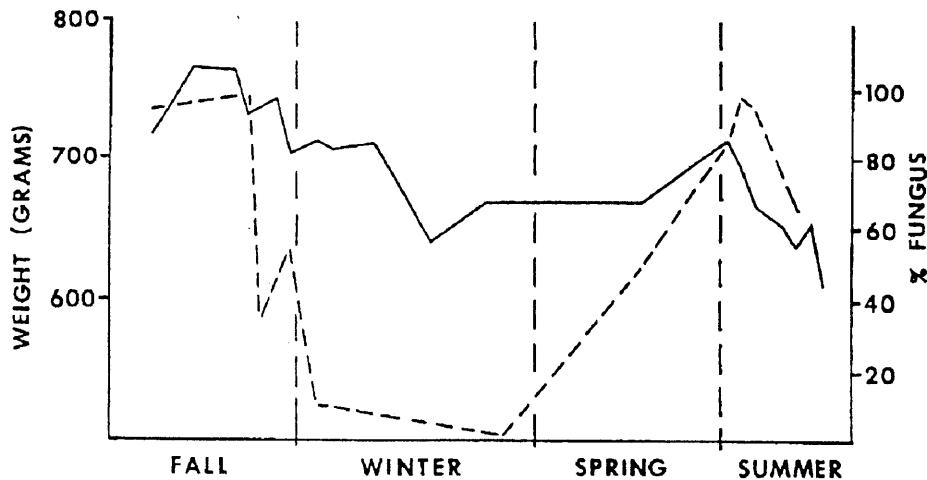


Figure 3.—Weight loss (solid line) by Abert squirrels as compared to fungal content of feces (dotted line) during the period September 1985 to August 1986, Coconino National Forest, AZ.

Table 3.—Twig clipping data for Yellowpine (YP) and Blackjack (BJ) age-class trees over three successive winter seasons in the Mount Elden study area.

Year	Snow cm.	Squirrel number	Number YP	Trees BJ	Clipped total	Clips/tree	Total clips	Dry wt. kg
1984-85	345.4	6	38	155	193	124.7	24,061	295
1985-86	266.7	8	52	268	320	65.4	20,640	253
1986-87	217.7	6	58	533	591	24.2	14,288	175

blackjack pine with a DBH greater than 10 cm were clipped. Eleven of these and one yellow pine died following virtually total canopy removal by squirrels. The average number of twigs clipped in yellow pine was greater than in blackjack pine but their mean dry weight, 11.2 • 8.7 g, was less than that of blackjack pine, 13.2 • 4.8 g. Five of the yellow pines in 1985 had more than 1000 twigs removed from each. A majority of the trees clipped only once before 1987 were also clipped in 1987 and were located in an area with little previous squirrel use (fig. 4).

## Discussion

The tassel-eared squirrel is a whole forest species in the sense that essentially all age classes of trees are utilized. Although pine provides much of the squirrel's food, the various items are taken by the squirrel from different age classes of trees (table 3). The largest number of cones is pro-

duced by mature yellow pines (Larson and Schubert 1970), while truffles tend to be associated with pole sized blackjack pines (States 1985). Thus, prime squirrel habitat provides optimal food in stands containing a combination of tree age classes whose size, density, and grouping provides cover and nesting sites as well (Patton 1984).

Major shifts in foraging by the tassel-eared squirrel are apparently associated with variations in the availability of food resources in the forest. In 1986 squirrels relied heavily on pine seeds with moderate utilization of truffles and the inner bark of twigs (fig. 2). Cone and acorn failure in 1987 resulted in a reversal of the relative emphasis on seeds and twigs. Observation of squirrel foraging revealed a corresponding opportunistic shift from such ephemeral foods as staminate cones and developing pine buds in the spring to mushrooms in summer to truffles in the fall. Similar opportunism in food utilization has also been reported for other tree squirrels: the European tassel-eared squirrel, *Sciurus vulgaris* (Wauters and Dhondt 1987), the American red squirrel, *Tamiasciurus hudsonicus* (Ferron et al. 1986), and the western gray squirrel, *S. griseus* (Stienecker 1977).

In spite of a seasonal emphasis on temporary supplies of certain food items, the squirrel removed terminal shoots of ponderosa pine throughout the year. When cones and truffles became scarce, as in winter and early spring, squirrels increased consumption of inner bark (figs. 1 & 2). There seemed to be a clear preference for the inner bark of certain trees to the extent that some individual trees were nearly defoliated. However, a decreasing amount of snowfall in three years (table 3) was associated with an increasing number of trees from which inner bark was taken and a decreasing average number of clips per tree. Thus, the identification of a particular tree as a favorite "feed tree" (Ffolliott and Patton 1978) seemed to depend to some extent on

other relevant environmental conditions influencing access to food supplies, e.g., mobility over snow-covered ground.

The repeated use of individual trees for inner bark was surprisingly high. We found that 23% of all clipped trees had shoots removed in each of three years, while Ffolliott and Patton (1978) reported only 2% over four years of potential use. This difference between the two studies may have resulted from differences in squirrel population densities and/or from differences in the availability of alternative foods. Nevertheless, it is important to note that a resident squirrel population may not rotate feed trees to the extent previously reported. In addition, more than half a stand's individuals may become feed trees. We expect that continued observation will increase that percentage.

The quantity of hypogeous fungi remained a fairly consistent food supply, aside from its unusual abundance in 1983 (table 1). Truffles appear to be a common component of the diet of tree squirrels (Grönwall and Pehrson 1984, Moller 1983), if not of most small herbivorous mammals (Maser et al. 1978). Judging from the analysis of gut contents in this (Vireday 1984) and other squirrels (Grönwall and Pehrson 1984, Grachev and Fedosenko 1974, McKeever 1964), hypogeous fungi constitute one of the primary food resources. The drop in winter squirrel weight as inner bark replaced truffles in the diet (table 2 and fig. 1) is also suggestive of the importance of this fungal diet component. Kenward (1983) showed similar weight losses for gray squirrels, *S. carolinensis*, feeding heavily on inner bark.

Truffle production has been reported to be correlated with high canopy cover (States 1985), which is more characteristic of blackjack stands than of stands with a high proportion of yellow pines. This relationship between truffles and canopy cover may explain the preponder-

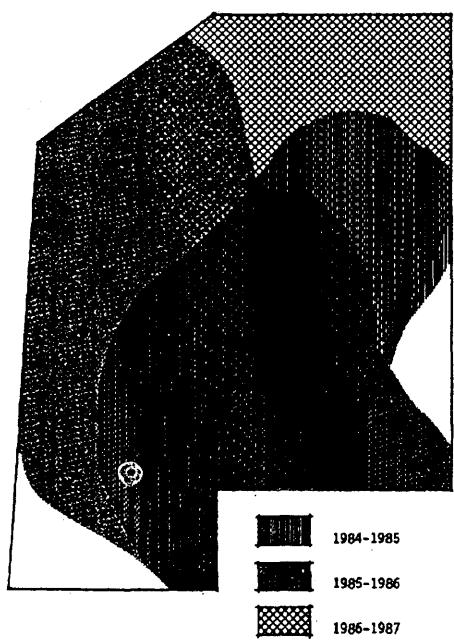


Figure 4.—Map of the 2.4 ha Mount Elden study site illustrating shifts in clipping intensity for each of three years (spring to spring), Coconino National Forest, AZ. Clipping data corresponding to these areas is presented in table 3.

ance of squirrel foraging activity observed in the blackjack stands.

Observations of food supply (table 3) and squirrel food use (fig. 2) showed considerable variability, much of it related to precipitation patterns. Consequently each year presented a different pattern of food combinations, which may take 5 to 10 years to repeat. Nevertheless, it is clear that squirrels clipped twigs to some extent every year, but greatly increased clipping when cones were scarce. Moreover, hypogeous fungi were a regularly used resource.

### Management Implications

The number of twig clips found has been suggested as an index of squirrel population density (Brown 1982, Keith 1965). However, the complex pattern of clipping observed in these three years suggests some limitations. We advocate restricting such an index to comparisons of relative population densities between different sites within the same year, when one can reasonably presume that weather conditions, pine seed abundance, and availability of alternative foods to be similar over a large area.

Maintenance of clustered stands is essential to provide the canopy cover needed for truffle production as well as cover and nesting sites for squirrels. Reduction of stand heterogeneity and removal of trees in large disjunct blocks will likely have a negative impact on Abert squirrel habitat (see also Pederson et al. 1987). Over time, squirrels utilize a majority of blackjack and yellow pine within the stands. Forest management practices that provide corridors for squirrel movement among stands will potentially reduce localized herbivory and avoid severe tree damage.

### Acknowledgments

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### Literature Cited

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227-265.
- Brown, David E. 1982. The use of "clippings" to index tassel-eared squirrel population levels. *Journal of Wildlife Management* 46:520-525.
- Farentinos, Robert C., P. J. Capretta, R. E. Kepner, and Victoria M. Littlefield. 1981. Selective herbivory in tassel-eared squirrels: role of monoterpenes in ponderosa pine chosen as feeding trees. *Science* 213:1273-1275.
- Ffolliott, Peter F. and David R. Patton. 1978. Abert squirrel use of ponderosa pine as feed trees. *USDA Forest Service Research Note RM-362*. 4 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Grachev, Uri A., and A. K. Fedosenko. 1974. On the ecology of the Teleutka squirrel (*Sciurus vulgaris exalbidus* Pall.) in the Dzungarskii Alatau. *Proceedings of the Academy of Sciences of the Kazachstan SSR, Series Biology* (6):32-39.
- Grönwall, Olavi, and Å. Pehrson. 1984. Nutrient content in fungi as a primary food of the red squirrel *Sciurus vulgaris* L. *Oecologia* (Berlin) 64:230-231.
- Hall, Joseph G. 1981. A field study of the Kaibab squirrel in Grand Canyon National Park. *Wildlife Monographs* No. 75. 54 p.
- Keith, James O. 1965. The Abert squirrel and its dependence on ponderosa pine. *Ecology* 46(1&2): 150-163.
- Kenward, Roger E. 1983. The causes of damage by red and gray squirrels. *Mammal Review* 13:159-166.
- Larson, M.M. and Gilbert H. Schubert. 1970. Cone crops of ponderosa pine in central Arizona including the influence of Abert squirrels. *USDA Forest Service Research Paper RM-58*. 15 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Maser, Chris, James M. Trappe, and Ronald A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59:799-809.
- McKeever, Sturgis. 1964. Food habits of the pine squirrel in northeastern California. *Journal of Wildlife Management* 28:402-404.
- Moller, H. 1983. Foods and foraging behavior of Red (*Sciurus vulgaris*) and Grey (*Sciurus carolinensis*) squirrels. *Mammal Review* 13:81-98.
- National Oceanic and Atmospheric Administration. 1987. Local climatological data. Annual summaries, Flagstaff, Arizona. National Climatic Data Center, Asheville, N.C.
- Patton, David R. 1974. Estimating food consumption from twigs clipped by the Abert squirrel. *USDA Forest Service Note RM-272*. 4 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Patton, David R. 1984. A model to evaluate Abert squirrel habitat in uneven-aged ponderosa pine. *Wildlife Society Bulletin* 12(4):408-414.
- Patton, David R., Richard L. Wadleigh, and Howard G. Hudak. 1985. The effects of timber harvesting on the Kaibab squirrel. *Journal of Wildlife Management* 49:14-19.
- Pearson, G.A. 1950. Management of ponderosa pine in the Southwest. *USDA Agriculture Monograph No. 6*:1-218.
- Pederson, Jordan C., R.C. Farentinos, and Victoria M. Littlefield. 1987. Effects of logging on habitat quality and feeding patterns of Abert squirrels. *Great Basin Naturalist* 47:252-258.

- Pederson, Jordan C. and Bruce L. Welch. 1987. Comparison of Ponderosa pines as feed and nonfeed trees for Abert squirrels. *Journal of Chemical Ecology* 11:149-157.
- Soderquist, Todd R. 1987. The impact of tassel-eared squirrel defoliation on ecotonal ponderosa pine. *Journal of Mammalogy* 68:398-401.
- States, Jack S. 1983. New records of hypogeous ascomycetes in Arizona. *Mycotaxon* 16:396-402.
- States, Jack S. 1984. New records of false truffles in pine forests of Arizona. *Mycotaxon* 19:352-367.
- States, Jack. 1985. Hypogeous, mycorrhizal fungi associated with ponderosa pine: sporocarp phenology. In *Proceedings of the 6th North American Conference on Mycorrhizae*. 271 p. Bend, Oregon. R. Molina (ed.)
- Stephenson, Richard L. 1974. Seasonal food habits of Abert's squirrels, *Sciurus aberti*. *Journal of Arizona Academy of Sciences* 9, 1974. Proceedings Supplement.
- Vireday, Carol C. 1982. Mycophagy in tassel-eared squirrels (*Sciurus aberti aberti* and *S. a. kaibabensis*) in northern Arizona. Masters thesis, Northern Arizona University. Flagstaff, AZ.
- Wauters, L. A., and A. A. Dhondt. 1987. Activity budget and foraging behavior of the red squirrel (*Sciurus vulgaris* L.) in a coniferous habitat. *Zeitschrift Säugetierkunde* 52:341-353.

