Tree Selection by Tassel-eared Squirrels of the Ponderosa Pine Forests of the Colorado Plateau

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Abstract. Three subspecies of tassel-eared squirrels (*Sciurus aberti*) are endemic to the ponderosa pine (*Pinus ponderosa*) forests of the Colorado Plateau, including several national parks and monuments. In foraging for inner bark, squirrels have removed as many as 1,078 shoots from a single ponderosa pine tree in one 6-month period. Most trees, however, escape such herbivory entirely. A stand contains relatively few feed trees among all trees present. The larger the tree, however, the more likely it will be a feed tree more than once. In spite of the opportunity to return time after time to the same favorite trees, only one-fourth of all the feed trees could be so classified in more than one census period. The variation in the number of shoots removed in any census period was largely explained by the availability of pine seed.

Key words: Feed tree, *Pinus ponderosa*, plant–herbivore interaction, ponderosa pine, *Sciurus aberti*, squirrel.

Tassel-eared squirrels (Abert's squirrel, *Sciurus aberti*) obtain much of their food from ponderosa pine (*Pinus ponderosa*). The consumption of ponderosa pine by tree squirrels is one of the important vertebrate–tree interactions in the ponderosa pine forest. The relation between the tree and the squirrel is critical to understanding the ecology of the herbivore and has other implications relating to effect on canopy architecture, reproduction potential, and tree survival (Allred 1989).

One of the most obvious signs of squirrel feeding is the layer of shoots that are dropped. Fewer than 10 clips were under most of the trees visited by squirrels. Some of the trees, however, seem to be favorites for feeding, and squirrels remove large numbers of shoots from these feed trees.

Keith (1965), Larson and Schubert (1970), and Hall (1981) suggested that squirrels return to feed trees year after year. On the other hand, it is possible that after considerable defoliation, the tree responds with the production of chemical compounds that alter its taste (Farentinos et al. 1981; Zhang and States 1991). Subsequently, squirrels may concentrate on different feed trees in different years (Ffolliott and Patton 1978).

We collected information for 3.5 years on the feeding activities of the tassel-eared squirrel around Flagstaff, Arizona, and on the north rim of the Grand Canyon. Our purpose was to clarify the pattern of clipping by the squirrel in the ponderosa pine forest.

Methods

We observed squirrel herbivory on the North Kaibab Plateau, both inside and outside Grand Canyon National Park, and in Walnut Canyon National Monument 16 km east of Flagstaff. We censused the number of shoots clipped from ponderosa pine trees on a 5.6-ha site located on property of Lowell Observatory in Flagstaff. No logging had been permitted, and the site had not experienced fire in more than 40 years. A few clumps of Gambel's oak (*Quercus gambelii*) were within the mixed-age stand of ponderosa pine.

All trees in the stand were measured for diameter at breast height (DBH) and evaluated for characteristics of health and vigor—mistletoe (*Phoradendron* sp.) and damage to the trunk. All trees experiencing herbivory were tagged, and individual histories of herbivory were kept on each. Every 2–3 weeks from 28 November 1986 through 24 May 1990, we counted all evidence of squirrel feeding and associated each piece of evidence (e.g., shoots on the ground) with an individual tree. Terminal shoots removed by squirrels were referred to as clips. Clips were distinguished from shoots blown down after having been weakened by insect burrowing or broken off by hail storms or by the weight of accumulated snow.

The 3.5 years were divided into 6-month periods for the analysis of herbivory. If a tree experienced a loss of 40 or more clips in one of these periods, it was classified in that period as a feed tree during the entire study. A tree that was a feed tree in one of the census periods, but not in the other six, would have an average clip loss less than 40.

Results

Squirrels removed an average of 4 shoots from the nonfeed trees and 22 shoots from the feed trees ($P < 0.05$) in each census period over the 3.5 years of observation. Feed trees had greater DBH on the average (32.09 ± 12.51) than nonfeed trees (23.31 ± 8.02; Fig. 1).

Squirrels removed at least one shoot from each of 2,765 trees. Of these, 393 were feed trees in at least one of the 6-month census periods (Fig. 2). A majority (76%) of the trees was classified as feed trees in only 1 of the 7

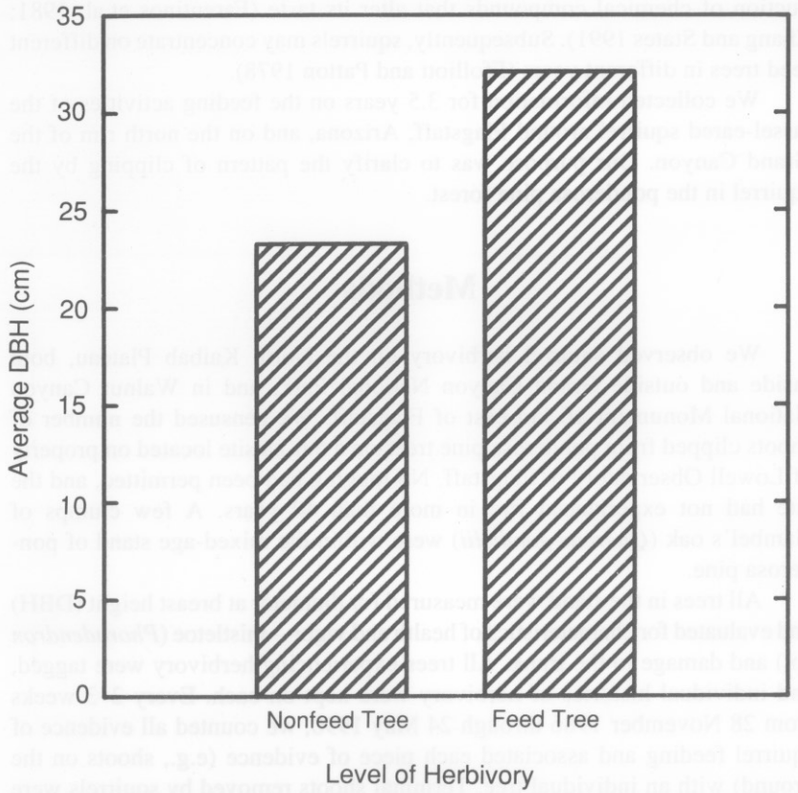

Fig. 1. The average diameter-at-breast-height (DBH) of feed trees and nonfeed trees ($n = 2{,}765$; $P < 0.001$).

census periods. Only five trees (1%) lost 40 or more shoots in each of four census periods.

Trees that were most often selected as feed trees had the greatest average DBH (Fig. 2). The least clipped trees within the stand tended to have smaller DBH.

As clipping intensity increased, more trees were clipped heavily enough to be classified as feed trees. The number of feed trees varied from a low of 8 (period 4) to a high of 55 (period 1) when the total number of clips in a census period was less than 20,000. However, as the number of clips approached 40,000, the number of feed trees continued to rise. In fact, there seemed to be a proportional relation between the number of shoots clipped and the number of trees with more than 40 clips removed (Fig. 3).

Both the number of cones produced by the pine trees and the number of cones taken and consumed by the squirrels varied (Fig. 4). As the number of cones taken decreased, the amount of clipping by the squirrels increased more than a proportional amount.

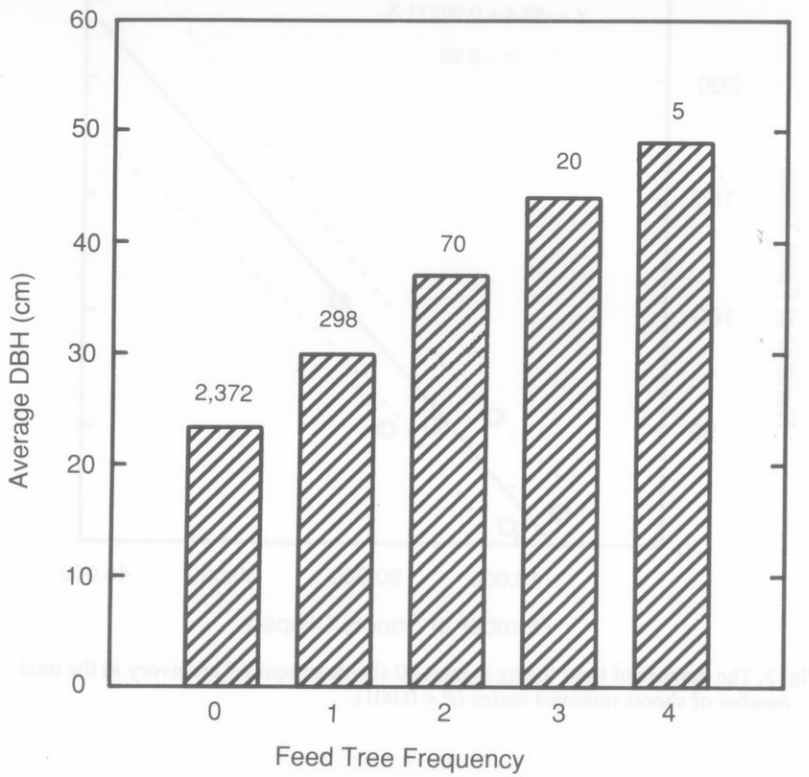

Fig. 2. The average size of trees from which squirrels removed at least one shoot. *Numbers above the bars* are the numbers of trees in each category. Averages differed significantly ($P < 0.001$).

Discussion

The definition of a feed tree has varied (Patton and Green 1970; Ffolliott and Patton 1978; Soderquist 1987). We used 40 clips per tree because it was the overall average number of clips per tree of all trees fed on in the first 2.5 years of these observations (Allred 1989).

Squirrel herbivory affects only a small percentage of the pine trees. However, the trees that are chosen by the squirrels and classified by us as feed trees may suffer a significant reduction in photosynthetic capacity and perhaps an altered canopy architecture.

Repeated depredations by squirrels on feed trees occurred on only a few trees and occurred within the period when trees had a chance to recover their foliage. The trees from which squirrels removed the most shoots were among those in the forest having the greatest DBH and did not seem to be subject to death from squirrel herbivory.

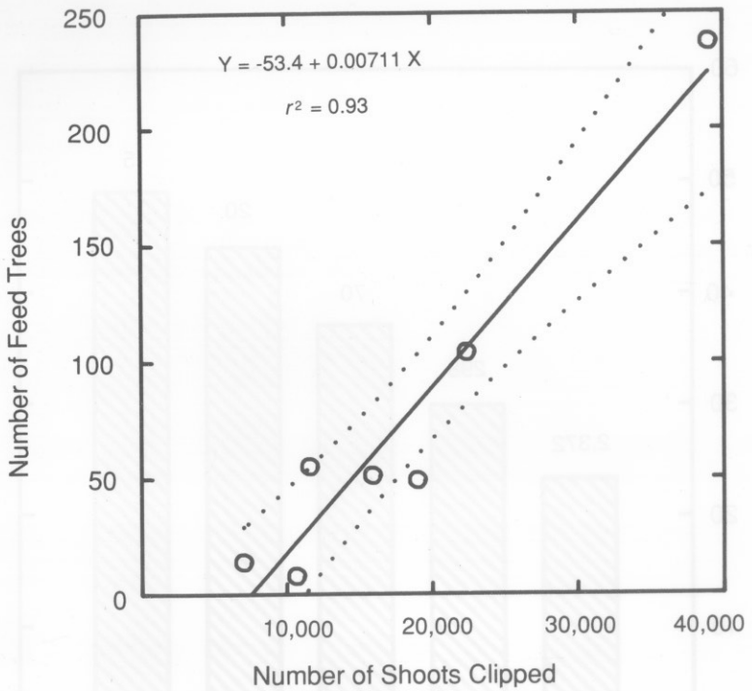

Fig. 3. The number of trees losing at least 40 shoots to squirrel herbivory as the total number of shoots removed varies ($P < 0.001$).

Some researchers have inferred that squirrels choose feed trees based on the presence of chemicals that affect the taste of the shoot (Farentinos et al. 1981; Zhang and States 1991; Snyder 1992). If squirrels proportionally increase their consumption of inner bark in some years (Fig. 3), perhaps they have also increased their tolerance of such chemicals. Conversely, perhaps the conditions that have resulted in heavier than average clipping may have also contributed to a decrease in the concentration of these chemicals.

Squirrels normally consume a mixed diet from ponderosa pine trees. In those years when the cone crop is low or nonexistent, squirrels concentrate much more heavily on inner bark (States et al. 1988). One possible strategy for the squirrels is to spend more time in each of the trees where they forage. The number of clips removed per tree increases proportionally as the feeding period in each tree is lengthened. We infer that this proportional relation means that the trees are graduated on a more or less continuous scale of taste.

If the squirrels pursued an alternative strategy of spending more time on their preferred trees relative to the less preferred trees, there would be a less than proportionate rise in the number of feed trees. This pattern of behavior would suggest that squirrels' acceptance of certain trees is determined by a threshold, rather than by a continuity of taste.

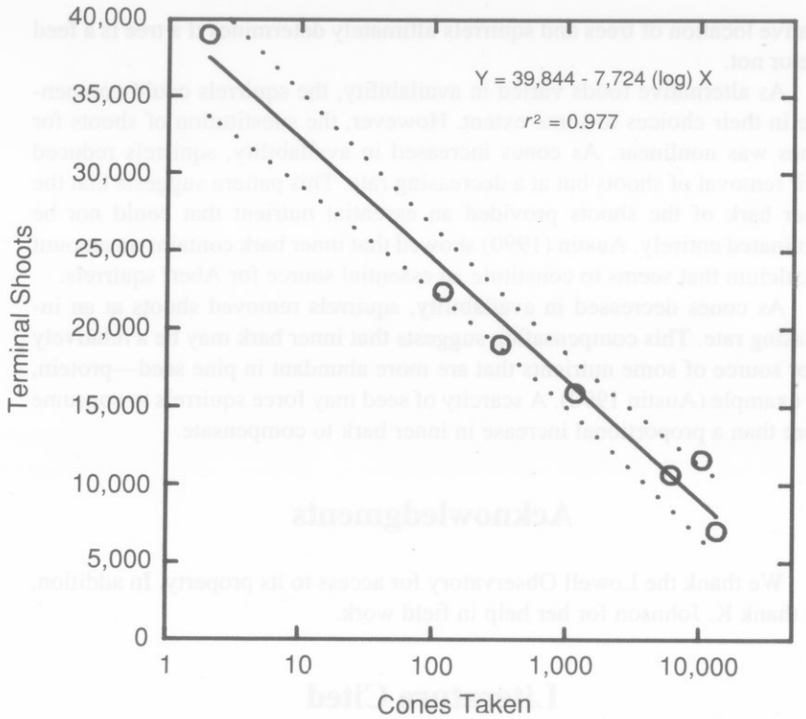

Fig. 4. Diet trade-offs: nutrition from cones and from shoots ($P < 0.001$).

Our finding of a proportional rise in the number of feed trees implies that squirrels spread their foraging for inner bark over a greater number of trees in years when the available food is of relatively low quality. Furthermore, this pattern of foraging hints that changes in chemical taste factors do not change rapidly enough in a single year to be significant. A heavily clipped tree might either increase or decrease chemical taste factors in response to squirrel foraging. Such a change would result in a nonlinear relation between the number of clips and the number of feed trees. However, the proportional relation found suggests that the attractiveness of the trees was stable within the year.

Ordinarily, one would expect the probability for a certain tree to fall into the feed tree category to be highest within a certain distance from the center of squirrel activity—that is, within a certain distance from the nests. When the cone crop fails, squirrels probably forage at greater distances from their nests; the result is that additional palatable trees in the stand suffer herbivory. The classification of these trees as nonfeed trees in cone years would then be based on their location relative to squirrel nests rather than on their chemical composition. In other words, the combination of taste chemicals and the

relative location of trees and squirrels ultimately determines if a tree is a feed tree or not.

As alternative foods varied in availability, the squirrels could compensate in their choices to some extent. However, the substitution of shoots for cones was nonlinear. As cones increased in availability, squirrels reduced their removal of shoots but at a decreasing rate. This pattern suggests that the inner bark of the shoots provided an essential nutrient that could not be eliminated entirely. Austin (1990) showed that inner bark contains an amount of calcium that seems to constitute an essential source for Abert squirrels.

As cones decreased in availability, squirrels removed shoots at an increasing rate. This compensation suggests that inner bark may be a relatively poor source of some nutrients that are more abundant in pine seed—protein, for example (Austin 1990). A scarcity of seed may force squirrels to consume more than a proportional increase in inner bark to compensate.

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