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Life History, Status, & Effect of Hunting
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**LIFE HISTORY, STATUS, AND EFFECT OF HUNTING
ON ABERT'S SQUIRRELS IN COLORADO**

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ABERT'S SQUIRREL

Abert's squirrels (Sciurus aberti) are also known as tassel-eared, tuft-eared, and Kaibab squirrels. They are distinguished by 2.5-cm long tufted ears, which are especially noticeable in winter. Males and females are similar in size. Ranges of external measurements are: total length, 463 to 584 mm; length of tail, 195 to 255 mm; and length of hind foot, 65 to 80 mm (Hall and Kelson 1959). Weights vary from a high in October with males and females averaging 715 and 690 g, respectively, to a corresponding 613 and 699 g in April and May (Patton et al. 1976). Keith (1965) reported males weighing 589 g and females 602 g.

DESCRIPTION

Several color phases of Abert's squirrel occur, with the most common being grizzled iron gray above with a broad reddish brown band down the back and white underparts (Flyger and Gates 1982). A melanistic color phase is black all over, and others are sable brown to cinnamon in color. The Kaibab squirrel (S. a. kaibabensis) is dark bodied except for a distinct white tail. Color is genetically controlled, but it is not considered an important taxonomic feature (Hoffmeister and Diersing 1978). Females have mixed litters of gray and melanistic forms (Ramey 1972, Nash and Seaman 1977).

Flyger and Gates (1982) described nine subspecies: S. a. aberti, S. a. barberi, S. a. chuscensis, S. a. durangi, S. a. ferreus, S. a. mimus, S. a. navajo, S. a. phaeurus, and S. a. kaibabensis. Hoffmeister and Diersing (1978) describe six subspecies, including S. a. kaibabensis. Subspecies

variation is based primarily on the extent and color of the median stripe on the back, as well as some minor differences in the shape of the skull (Nash and Ramey 1970). Isolating barriers appear to have caused separation among the subspecies, which McKee (1941) considers an example of evolution in its first stages.

Two subspecies of Abert's squirrel, S. a. mimus and S. a. ferreus, occur in Colorado and are similar in appearance. The typical gray form of S. a. mimus is characterized by a brownish-red patch or irregular stripe on the back; the tail is a mixed gray on both sides. S. a. ferreus is paler and the red patch is either much reduced in size or lacking entirely (Nash and Ramey 1970). The black melanistic phase predominates in northern Colorado and the gray phase is found primarily in the southern part of the state.

Abert's squirrels are heterothermous with body temperatures varying with behavior from 35.2° to 41.1°C (Golightly and Ohmart 1978). Patton et al. (1976) measured temperatures of 38.5 to 42.7°C.

DISTRIBUTION

Abert's squirrels are found in ponderosa pine (Pinus ponderosa) forests in the foothills of the Rocky Mountains and the Colorado plateau in the United States (Flyger and Gates 1982), and in the Sierra Madre Occidental from Northern Sonora and Chihuahua to southern Durango in Mexico (Nash and Seaman 1977). They occur in Colorado, New Mexico, Arizona, a small portion of central Utah, and in southern Wyoming (Hall and Kelson 1959, Flyger and Gates 1982). Absence north of southern Wyoming suggests that these squirrels may not be able to exist in more northern climates (Davis and Brown 1989).

Armstrong (1972) reported Abert's squirrels are found in Colorado in the

foothills and lower mountains of the Eastern Slope, and in the San Juan Mountains to the border with Wyoming. Extensions of their known range have occurred in recent years in southeastern (Mellott and Choate 1984) and western Colorado (Davis and Bissel 1989). They are common in ponderosa pine forests in the southern and central regions of the state, with S. a. mimus occurring in southwestern Colorado, and S. a. ferreus in the Front Range, Sangre de Cristos, and Wet Mountains (Fitzgerald et al. In press).

Rockwell (1916) reported that Abert's squirrels were formerly much more abundant in Colorado, and he predicted extinction of the species unless it was adequately protected. However, more recent writers do not indicate that populations are low.

RANGE EXPANSIONS

Several range extensions for Abert's squirrels have been reported. They appeared in the Animas River area, Colorado, not long before 1938 (Coughlin 1938). The first specimen of Abert's squirrel was recorded in Utah in 1947, in La Sal National Forest, San Juan County (Durrant 1947). Brown (1965) reported an extension of the known geographic range of Abert's squirrel into Wyoming at a locality 1.2 km north of the Colorado-Wyoming state line.

Abert's squirrels were observed in the Spanish Peaks State Wildlife Area, which is a southward extension of the Sangre de Cristo Range. This extended the known range of S. a. ferreus in Colorado approximately 72 km to the southeast (Mellott and Choate 1984). Observational records of Abert's squirrels since 1972 expand the range in Colorado by 11 more counties than reported by Armstrong (1972) (Davis and Bissel 1989). Extensions of the distribution of the species are thought to either reflect increased

observations by additional researchers (Nash and Seaman 1977), or extensions, unassisted by transplantings, of the actual range of the species (Davis and Bissel 1989).

These range expansions during the past 50 to 75 years may simply be a small part of a more general northern expansion of the range of this species. This process may have been occurring continuously during the past several thousand years as Abert's squirrels followed the northward, post-Pleistocene expansion of ponderosa pines into Colorado (Davis and Bissel 1989). Abert's squirrels apparently can cross barriers of unsuitable (non-ponderosa pine) habitat (Cooper 1987, Davis and Brown 1989).

TRANSPLANTS

Abert's squirrels have been transplanted in Arizona, New Mexico and Utah, but not in Colorado (Davis and Brown 1988). There has been a high success rate, indicating that the species is able to establish populations from small propagules (Davis and Brown 1988).

REPRODUCTION

Male and female Abert's squirrels probably first breed at 10 to 12 months (Flyger and Gates 1982). Mating takes place in spring and early summer, following complex chases that usually involve one female and several males. After 38 to 46 days of gestation (Keith 1965, Farentinos 1972b), a litter ranging from two to five young and averaging 3.4 (Keith 1965) and 3.2 (Farentinos 1972b) young is born.

Young usually are born in May, June, and July in Colorado (Nash and Ramey 1970, Farentinos 1972b, Flyger and Gates 1982, Fitzgerald et al. In press).

Although Stephenson (1975) reported that litters could be born as late as mid-August in Arizona, most litters were born from June to mid-July. In the southern part of the range, there may be more than one litter each year (Hall and Kelson 1959), but single litters were reported in Colorado (Nash and Ramey 1970) and Arizona (Keith 1965, Stephenson 1975).

Most nests are built in ponderosa pine trees, but natural hollows in Gambel oak trees are occasionally used (Nash and Seaman 1977). The nests are constructed from intertwined twigs, lined with pine needles and grasses, and usually have a single opening. In addition to nests used for rearing young, each squirrel has a nest for protection from severe winter weather, but for females this may be the same nest (Harju 1978).

Newborn squirrels weigh 12 g and are 60 mm long (Keith 1965). At birth, their eyes and ears are covered by thin membranes and they are hairless but with vibrissae and claws (Keith 1965). Snyder and Linhart (1993) reported that young remain in the nest for the first six to seven weeks after birth. They stay in, or very close to, their nest tree for the first few weeks after emerging from the nest. When the young are about six weeks old the mothers start to bring food to the nests (Keith 1956). Keith (1965) reported that squirrels in captivity were weaned at 10 weeks, and probably could survive without the care of the mother (Fitzgerald et al. In press). The duration of dependency of young on adults in the wild is unknown. The young reach mature size at 15 to 16 weeks. Their weights averaged 170 g at five weeks, 195 g at six weeks, 242 g at seven weeks, and 355 g at nine weeks of age (Keith 1965).

NATURAL MORTALITY FACTORS

Reported mortality factors are few (Flyger and Gates 1982), apart from

road kills (Coughlin 1938, Dodge 1965, Hoffmeister 1971) and predation by redtail hawks (Buteo jamaicensis), goshawks (Accipiter gentilis) (Reynolds 1963, Dodge 1965, Keith 1965), and great horned owls (Bubo virginianus) (Farentinos 1972b). Other hawks which occur in the range are also capable of taking the squirrels (Keith 1956). Reynolds (1963) believed that goshawks may be a regulatory mechanism for stabilizing fluctuating populations of Abert's squirrels, and Bailey and Niedrach (1965) found that one of the goshawk's main foods in Colorado ponderosa pine forests was Abert's squirrels.

Mites, ticks and the common flea (Opisodasys obustus) usually were present on all squirrels examined by Keith (1965) in Arizona. Mange was prevalent in the spring and an unidentified nematode was found in one squirrel examined by Keith (1965). The effect of parasites and diseases on survival or reproduction of Abert's squirrel is unknown.

Keith (1965) reported that Abert's squirrels frequently exhibited stress, and several animals died after exhibiting severe spasms and convulsions when removed from traps and held or restricted for more than a few minutes. Animals released at the first signs of this condition did not have normal muscular coordination.

The effect of supplemental feeding on survival of Abert's squirrels is unknown. One survey participant (S. Casey, Evergreen, Colo., personal communication) suggested that sunflower seeds may be detrimental to Abert's squirrels, whereas C. A. Ramey (Denver Wildlife Research Center, personal communication) speculated that supplemental feeding might benefit squirrel populations.

DENSITY AND POPULATION DYNAMICS

Abert's squirrel populations fluctuate over time and from area to area (Goldman 1928; Keith 1956, 1965; Nash and Ramey 1970; Hoffmeister 1971; Armstrong 1972; Hall 1981). Ramey (1973) estimated Abert's squirrel densities of 30/km² in the Black Forest of Colorado in the summer of 1970 and 12/km² in the spring of 1973. Farentinos (1972b) reported 33 Abert's squirrels/km² in an area immediately west of Boulder, Colorado during the spring of 1970, and 56 squirrels/km² during the autumn. The increase probably represents recruitment of juveniles, but during the winter the population declined to 31 squirrels/km² by the spring of 1971. Predation and emigration of some squirrels to adjacent forested areas may be factors that contributed to the decline. Neither a severe winter nor a food shortage appear to have contributed, however data are lacking. Ovulate cone production of ponderosa pines during 1970 was relatively high and the nutritional value of the inner bark and bud tissues following the cone production would be reduced.

Keith (1965) reported densities of only 2.5 to 5 Abert's squirrels/km² in 1954 in Arizona, yet in the same region, densities of 30 squirrels/km² had been reported in 1941 (Trowbridge and Lawson 1942, cited by Nash and Seaman 1977). Patton (1975b) estimated a density of 247 squirrels/km² (1/acre) in a small part of Coconino National Forest, Arizona.

Because Abert's squirrels are so dependent on ponderosa pine, population fluctuations may be a response to cycles of cone production (Nash and Ramey 1970, Flyger and Gates 1982) and the quality of bark and bud tissue (Keith 1965, Farentinos 1972b). Heavy seed crops are thought to exhaust the supply of foods stored in the stems of trees, and it may require a number of years for the trees to replenish these food reserves and to produce another good seed crop (Keith 1965). Keith (1965) suggested that during the winter,

Abert's squirrels struggled to survive, as they actively fed throughout the day, even in heavy snowstorms and very few animals had any body fat. If squirrels receive a nutritious diet during winter, they probably survive the winter in better condition, breed more successfully, and may increase in number (Keith 1965). Nixon et al. (1975) concluded that survival and reproductive rates of gray squirrels (Sciurus carolinensis) and fox squirrels (Sciurus niger) improved with good nutrition.

Stephenson and Brown (1980) reported that annual mortality of Abert's squirrels in Arizona ranged from 22 to 66%, and can be related to the number of days with 10 cm or more of snow cover. Brown (1982) reported declines in squirrel activity in spring 1973, which followed heavy snows during winter 1972-73. Although snow cover is not likely to be directly responsible for this mortality, it probably acts to reduce the availability of high quality foods, such as hypogeous fungi. Also, delayed production of ponderosa pine staminate flowers and fungi may result from long periods of snow cover or related climatological factors (Stephenson and Brown 1980). Stephenson and Brown (1980) observed squirrels in poor physical condition in spring, particularly after winters of heavy snowfall.

Pederson and Welch (1985) maintained that protein deficiency is the probable cause of high winter mortality of Abert's squirrels, particularly during winters with deep and lasting snow cover. This also helps to explain the distribution of Abert's squirrels. Frequent deep snow would account for the absence from ponderosa pine forests in the Sierra Nevada, most of the Great Basin, and much of the northern Rocky Mountains. Furthermore, heavy snow cover may also explain the great fluctuations in population levels at the climatic limits of the species range, such as, the North Kaibab Plateau

(Stephenson and Brown 1980). It seems likely that a less nutritious diet, caused by natural fluctuations in seed production and stem nutrient content, ~~combined with heavy snowfall which would prevent access to foods such as~~ fungi, would cause fluctuations in the populations.

Stephenson and Brown (1980) found no relationship between recruitment and changes in population levels, and they assumed mortality was the principal factor influencing annual population fluctuations. Keith (1956) observed no mortality of young and concluded that their mortality rate probably was low.

In Arizona, Kufeld (1966) found that tree squirrels, which included a large percentage of Abert's squirrels, showed little variation in population age structure, even though there was large variation in the number of squirrels. He concluded that factors other than annual production seem to influence population levels. Keith (1965) suggested short-term fluctuation in squirrel abundance, superimposed on a long-term decrease in Arizona, probably related to logging of ponderosa pines.

Dodge (1965) reported that in Arizona, a number of Kaibab squirrels had been found dead with no marks indicating cause of death. He estimated the population of Kaibab squirrels to be between 550 and 1,650 in 1965 and expressed concern for the continuation of the subspecies. However, the estimated harvest for Kaibab squirrels in 1992 was 1,672 (Ron Engel-Wilson, Arizona Game and Fish Department, personal communication), which indicates that either the population estimates by Dodge (1965) were erroneous, or there has been a dramatic population increase rather than a decrease from 1965 to 1992. Hall (1967) reported evidence from tree-ring measurements suggesting a gradual decline in forest vigor and concluded that this was causing a decline in number of squirrels on the Kaibab plateau.

Male Abert's squirrels seem to predominate in the population, with ratios of 1.4:1 (Keith 1965, Farentinos 1972b). Adults comprised 53 and 65% of populations near Boulder (Fitzgerald et al. In press). Thirty squirrels provide a minimum viable population and would require 174 ha of optimal habitat (Towry 1984).

ACTIVITY AND HOME RANGE

Abert's squirrels are diurnal and return to their nests before sunset. Golightly (1976) reported that they are usually active all winter and rarely stay in the nest for longer than 24 hours even in bad weather. In contrast, Harju (1978) reported that they may remain in the nest for as long as two weeks in bad weather. Golightly and Ohmart (1978) reported that squirrels were seldom outside of nests at temperatures below -10°C .

In Boulder County, Colorado, Farentinos (1979) found that the mean home range of males was 5.3 ha in winter and 2.6 ha in summer. Female home ranges averaged 4.9 ha in winter and 1.3 ha in summer. According to Fitzgerald et al. (In press) home ranges can be as much as 20 ha in Colorado. The average home range of five Arizona Abert's squirrels was 7.3 ha, but was only 2.0 ha when snow cover was present (Keith 1965). Patton (1975b) found home ranges of three squirrels were 4.0, 12.2, and 34.4 ha in Arizona. Golightly and Ohmart (1978) reported that fresh snow restricted their movements. Farentinos (1979) reported that prolonged dry periods may force squirrels out of their usual home ranges in search of new water sources. However, Keith (1956) reported that Abert's squirrels drink water daily in captivity, but do not require open water in the wild.

Abert's squirrels are rather solitary animals and generally are not

territorial (Keith 1965, Farentinos 1972a). However, males may defend a territory from intrusion by other males during the mating season (Rice 1957, Nash and Ramey 1970). They seem to be social only during mating and when caring for offspring (Austin 1990). Occasionally, a mother may allow one of her young to remain with her during its first winter (Keith 1956).

FOOD HABITS

Although Abert's squirrels bury pine cones (Bailey 1932, States et al. 1988), they cache little food (Keith 1965) and must forage daily throughout the year (Golightly and Ohmart 1978). They have almost total dietary dependence on ponderosa pine (States et al. 1988). However, States et al. (1988) reported variability in food habits in Arizona, much of it related to precipitation patterns. They also feed on the inner bark of pinyon pine (Reynolds 1966, Ratcliff et al. 1975), and on young buds of Douglas fir trees (Ratcliff et al. 1975), pinyon pine and juniper seeds (Soderquist 1987), Douglas fir seeds (Ferner 1974), and berries of dwarf mistletoe (Stephenson 1975).

During summer and early autumn, Abert's squirrels feed heavily on the seeds of developing ovulate ponderosa pine cones, when available, as well as on a variety of fleshy fungi (Linhart et al. 1989). From autumn until well into spring, the diet is composed primarily of apical buds and inner bark (mostly phloem) stripped from ponderosa pine twigs. Stephenson (1975) found that inner bark and apical buds constituted 52 to 99% of the winter diet. In spring, staminate cones and apical buds of ponderosa pines are also important food items (Capretta and Farentinos 1979, Linhart et al. 1989). In Arizona, where Gambel oak (Quercus gambelii) is a common associate of ponderosa pine,

Stephenson (1975) reported that acorns can comprise up to 40% of the autumn diet. Gambel oak also is associated with ponderosa pine in southern Colorado. Occasional feeding on carrion and gnawing of shed antlers have been reported (Keith 1965).

Stephenson (1975) reported that fungi occurred in the diet during all seasons of the year and was the most important food item by volume and frequency of occurrence. In summer it composed as much as 92% of the diet. Hypogeous (mycorrhizal) fungi are associated with ponderosa roots, primarily of blackjack (< 100 years old [Collingwood and Brush 1974]) ponderosa pines (States et al. 1988), and complex interdependency between squirrels, pines and fungi appears to have evolved (Capretta and Farentinos 1979). Pines rely on fungi for nutrients, squirrels on the pines and fungi for food, and the fungi on the squirrels for spore dispersal (Capretta and Farentinos 1979, Kotter and Farentinos 1984). On a dry weight basis, sporocarps are generally high in protein, carbohydrates, and minerals, and low in lipids (Kotter and Farentinos 1984). Austin (1990) found that squirrels consume more fungi in years during pine seed failure. In summer and fall, squirrels place fungi in forks of trees where it dries and is later recovered. Vireday (1982) reported that the majority of fungi eaten by Abert's squirrels are hypogeous, but epigeous fungi are also eaten.

Larson and Schubert (1970) reported that in Arizona, large cone crops occurred at intervals of about 5 years. Abert's squirrels apparently prefer pine seeds to any other food (Keith 1965), and the seeds of ponderosa pine are high in nutritive value (Larson and Schubert 1970). Keith (1965) reported that in Arizona, individual squirrels ate the seed from about 75 cones a day when subsisting largely on this food. Squirrels preferred cones from certain

trees, but no reason for this preference was found (Larson and Schubert 1970).

Terminal twigs of ponderosa pine are clipped by Abert's squirrel to obtain the inner bark and apical buds. These foods apparently are substituted when other items are scarce or unavailable because of snow cover (Stephenson 1975). Pine phloem is of poor nutritional quality (Patton 1974) compared with other foods utilized by the squirrels (Linhart et al. 1989). Low in protein and fat (Patton 1974), it contains appreciable quantities of monoterpenes, a group of secondary plant metabolites with deterrent effects upon a number of herbivores (Farentinos et al. 1981). Squirrels in poor physical condition in spring have been observed, and Stephenson (1975) presented data suggesting that a prolonged diet of inner bark and apical buds may lead to physical deterioration and mortality. Soderquist (1987) noted that S. a. kaibabensis in Arizona clipped pinyon pines, which are associated with ponderosa pines, sometimes more than ponderosa pines.

Abert's squirrels tend to feed on the inner bark of particular ponderosa pine trees, also referred to as feed trees. Squirrels usually feed on cone-bearing trees between 28.0 and 76.0 cm in diameter (Patton and Green 1970), although within this range, it is variable which trees are chosen (Farentinos et al. 1981). Gaud et al. (1993) found that trees most often selected as feed trees had the greatest average diameter breast height (dbh) and the least clipped trees tended to have smaller dbh. Once a tree with palatable inner bark is found, it may be used as a food source season after season (States et al. 1988). However, there are cases where an apparent change in palatability of a certain tree may occur on a seasonal basis (Capretta and Farentinos 1979). Wild and captive born squirrels prefer feeding on twigs from feed trees more than non-feed trees in a laboratory environment (Capretta et al.

1980). According to Gaud et al. (1993) clipped trees did not seem to die from squirrel herbivory, but Heidmann (1972) reported that occasionally trees were so defoliated that they died.

Capretta and Farentinos (1979) reported that their preliminary data showed no apparent differences in sugar content between feed and non-feed tree phloem, but suggested that feed tree phloem may contain significantly higher amounts of proteins and lower levels of monoterpene hydrocarbons (Zhang and States 1991). Farentinos et al. (1981) reported that twigs from feed trees contained smaller amounts of monoterpenes, and that captive squirrels avoided food laced with high amounts of monoterpene. Pederson and Welch (1985) found no difference between monoterpene levels in feed and non-feed trees, and crude protein levels were not significantly higher in feed trees than non-feed trees. Pederson and Welch (1985) suggested that squirrels prefer trees with inner bark that is easily peeled from twigs. Hall (1981) analyzed oleoresin for monoterpene composition, and found no significant differences in amounts of individual monoterpenes between feed and non-feed trees. Snyder (1992) reported that nonstructural carbohydrates and sodium were significantly higher in the phloem of feed trees, and iron and mercury were significantly lower than non-feed trees.

Feed tree selection also depends on other factors such as alternative foods, canopy cover, squirrel behavioral patterns (Zhang and States 1991), and location relative to squirrel nests (Gaud et al. 1993).

HABITAT REQUIREMENTS

Abert's squirrels are restricted to ponderosa pine stands between 1,800 and 3,000 m in elevation (Nash and Seaman 1977), where annual precipitation is

less than 63.5 cm (Patton 1975a). Cooper (1987) reported a squirrel at 3,850 m in alpine tundra vegetation of the San Francisco Peaks Natural Area, Coconino County, Arizona.

The pines provide nest sites, nest building materials, and food resources for Abert's squirrels (Patton and Green 1970). Forests with open understories are preferred (Hall 1972). Nest trees usually are pines with a crown comprising 35 to 55% of the total tree height, and a diameter of 36 to 41 cm (Patton 1975a). Adjacent trees are of similar size with touching crowns which provide escape routes (Patton 1975a). Keith (1965) noted in Arizona that trees with nests varied from 30 to 100 cm dbh and that the nests were built 4.9 to 27 m above ground in trees that were 6 to 34 m in height. Patton and Green (1970), and Patton (1975a) concluded that the most important components of nest cover were tree density, diameter, and a grouped distribution of trees. Nests usually were located on a limb or against the tree trunk 5.3 to 17.5 m above ground, and often on the south side of trees, possibly to take advantage of the warming effects of the sun (Farentinos 1972c). Snyder and Linhart (1994) reported that the phloem of nest trees had lower concentrations of copper, iron, and silicon and higher levels of sodium and nonstructural carbohydrates, than phloem of control trees.

The best cover for Abert's squirrels is found in uneven-aged ponderosa pine stands with trees spaced in small even-aged groups within the stand (Patton 1975a). Patton (1977) defined a stand as a community of trees that has sufficient uniformity of composition, age, spatial arrangement, or condition to be distinguishable from adjacent communities, and forms a silvicultural or management entity (<20 ha). These pine stands have densities between 497 and 618 trees per hectare and average tree diameter of 28 to 33 cm

dbh, but small groups of larger trees are present which produces a mosaic of height groups (Patton 1975a). Trees over 51 cm dbh are the best cone producers (Patton 1977). In Arizona, healthy, mature ponderosa pines with exposed crowns and large diameters (61 to 71 cm) are usually the best cone producers in terms of seed quantity, quality, and frequency of bearing (Larson and Schubert 1970). One or two Gambel oaks (*Q. gambelii*) in the 30 to 36 cm dbh size class should be present, in areas where this plant community occurs (Patton 1977).

Quality of squirrel habitat increases as trees grow in diameter in a young forest, but only to a point where optimum conditions have been met. After that, tree density and grouping become self-limiting (Patton 1984).

Patton (1977) developed a system to rate habitat for Abert's squirrels in Arizona ponderosa pine. Habitat qualities rated were cone production, tree arrangement and number of tree stories (Patton 1984). Potential squirrel densities and average nest densities can then be established according to the habitat rating.

Abert's squirrels are absent from most of the ponderosa pine forests of North America. In some cases this absence can be explained by local extinction in small forests (as in the mountains of southeastern Arizona), or by excessively low dispersal rates to the more isolated forests (Davis and Brown 1989), or climatic limitations. The squirrels also have much greater resource-area requirements than ponderosa pines (Davis and Brown 1989). Although the Abert's squirrels usually are confined to ponderosa forests, Findley et al. (1975) indicated that they are common in mixed conifer forests in many New Mexican canyons.

PONDEROSA PINE HARVEST STRATEGIES TO MINIMIZE EFFECTS ON ABERT'S SQUIRRELS

Reduction of forest heterogeneity and removal of trees in large blocks likely will have a negative impact on Abert's squirrels (States et al. 1988). Patton et al. (1985) reported that Abert's squirrel density in Arizona was less in harvested than unharvested areas, and was related to the density and diameter of trees remaining for food and cover. Pederson et al. (1987) also reported that clearcut timber harvesting negatively impacted Abert's squirrels.

Patton (1984) suggested group or single-tree-selection harvests to maintain small, uneven-aged groups of ponderosa pines to provide high quality habitat for Abert's squirrels. Pederson et al. (1987) suggested cutting blocks of <8 ha to minimize impacts to Abert's squirrels. Trees left for shelter should be in groups. High quality habitat should be distributed throughout the management unit next to regenerating habitat. The best trees to leave are those in groups that have been selected by the squirrels for nest locations. Optimum habitat should have 10-13 trees providing cover around the nest tree. Several trees can be removed if necessary (e.g. mistletoe infested) without seriously affecting habitat quality, but 6 trees (2-3 must interlock the crown of the nest tree) with diameters 28-41 cm would be the minimum to leave.

Sanford (1986) reported that Abert's squirrels foraged primarily under blackjack pines for fungi and under older trees for seeds, and indicated that both age classes are needed for good squirrel habitat. Austin (1990) suggests that a sufficient number of large, cone-producing trees should be left, as well as adequate crown cover to prevent desiccation of the ground that would otherwise lead to elimination of fungal production.

Abert's squirrel have adapted to an uneven-aged forest of ponderosa pine (Patton 1977). The forest manager can create such habitat by influencing the physical characteristics of forest stands in the sapling stage, and by patterning timber harvests to keep areas of excellent or good habitat (Patton 1977). Trees that are overmature (>80 cm dbh) could be harvested without seriously affecting squirrel habitat (Allred 1989).

Hall (1972) expressed concern that protection from ground fires is causing establishment of dense forest stands which are inferior habitat for squirrels. Where fires are not recommended, thinning of trees by logging should be considered to reduce fire and pine beetle risk and to maintain a forest ecosystem closer to that under natural conditions (See Appendix 1). Forest management practices that provide corridors for squirrel movement among stands of pines will potentially reduce localized herbivory and avoid severe tree damage (States et al. 1988). Finch (1992) lists timber harvesting, fire suppression, loss of specialized habitat, and habitat fragmentation as factors jeopardizing Abert's squirrels.

HABITAT MANAGEMENT TO INCREASE ABERT'S SQUIRREL POPULATIONS

Abert's squirrel population density can be increased by providing optimum habitat conditions such as uneven-aged ponderosa pine stands with trees spaced in small even-aged groups within the stand (Patton 1975a). Trees of 28 to 76 cm dbh should be included (Patton and Green 1970). Controlled burning to reduce woody understory plants and to provide open, parklike conditions would be beneficial (Hall 1972).

Stephenson (1975) found that Abert's squirrel used artificial nest boxes for resting and breeding. These boxes were 30 cm by 30 cm by 40 cm, and were

bolted to a dominant tree in a clump of ponderosa pine at heights of 7.6 m to 14 m.

ABERT'S SQUIRREL IMPACTS ON PONDEROSA PINE FORESTS

Studies on the impacts of squirrel herbivory on ponderosa pine have led to mixed conclusions. Ffolliott and Patton (1978), and Hall (1981), found that heavy utilization of pine twigs had negligible effects on stand productivity, although Hall (1981) reported significant growth decreases of individual feed trees. Soderquist (1987) reported twig clipping decreased tree growth in ecotonal stands of ponderosa pine. Larson and Schubert (1970) noted extensive, but seasonally variable, damage to cone crops. Over a 10-year period, cone production was reduced by one-fifth. Larson and Schubert (1970) also found that trees with the least amount of squirrel damage bore the most cones, and over their 10-year study period they found that squirrels reduced cone production by 21%. Heidmann (1972) estimated that 25% of the cone crop may be destroyed. Squillace (1953) found that squirrels harvest most of the seed crop in poor and fair years. However, twig-clipping activities were less destructive to conelets than unfavorable weather and insects which were considered the major causes of conelet mortality (Larson and Schubert 1970).

No tree mortality directly attributable to Abert's squirrel feeding was observed by Ffolliott and Patton (1978), or Allred and Gaud (1993). In some years, heavy snowstorms resulted in tree mortality and induced greater amounts of green needle losses than did squirrels (Allred and Gaud 1993).

Skinner and Klemmedson (1978) noted that total nitrogen and carbon in litterfall increased by 70% because of squirrel feeding activity. This

occurred because of increased mass of litterfall and because the nitrogen concentration of clipped twigs was nearly double that of "natural" litterfall.

Despite selective pressures exerted by Abert's squirrels, it is clear that all trees that are potentially suitable sources of inner bark have not been eliminated from ponderosa pine stands, and Snyder (1992) suggests that this may be explained by selective pressures exerted by other herbivores and insects. Schmid et al. (1986) reported that abortion of seeds and insect consumption of cones were the most important factors contributing to a lack of reproductive success in ponderosa pines in Arizona. Abert's squirrels and porcupines can act as agents of natural selection, but because of their differential feeding patterns, they generate diversifying selection within stands (Linhart et al. 1989). Fire may also contribute to the maintenance of genetic variability within stands, as trees containing different amounts of oleoresin, which is highly flammable, may be differentially susceptible to destruction by fire (Snyder 1990). This may balance selective pressures exerted by Abert's squirrels and help to explain why feed tree characteristics persist within stands (Snyder 1990).

Linhart et al. (1989) maintained that genetic variability within ponderosa pine stands is essential to the health of these stands, and therefore should be a primary management objective. Since ecologically complex environments maintain genetic variability, management strategies intended to minimize the effects of phloem-feeding by Abert's squirrels and other species affecting tree fitness should recognize the potentially important role of these species in generating diversifying selection within stands (Linhart et al. 1989). In this context the feeding activities of Abert's squirrels should not be viewed as detrimental.

CONSERVATION STATUS

Meaney (1990) lists Abert's squirrel as "fairly common" in Colorado. Finch (1992) lists Abert's squirrel as a "species of concern" in the Rocky Mountain region. The reasons given for this listing are disjunct populations, special habitat needs, limited habitat, and human impacts. The Colorado Division of Wildlife lists the Abert's squirrel as a small game species.

EFFECT OF HUNTING ON ABERT'S SQUIRRELS

Abert's squirrels are game animals in Arizona, Colorado, New Mexico, and Mexico (Brown 1982), but are a protected species in Utah and Wyoming. A hunting season was established on Abert's squirrels in Colorado in 1977. Harvests and number of individuals that hunted Abert's squirrels remained low from 1977 through 1981, when permits were limited, and increased after 1981 when permits were unlimited (Fig. 1). According to Colorado Division of Wildlife harvest statistics, an average of 3,157 Abert's squirrels were harvested annually during the last 5 years (1989-1993) and 2,123 squirrels were harvested annually during the last 10 years (1982-1993, except 1985 and 1986 where data are missing) in Colorado. Hunting is permitted from September 1 to February 28 in Colorado. The daily bag limit is 5 and the possession limit is 10.

In Arizona, hunting is permitted from August 19 to September 15 and from October 7 to November 13. The bag limit is 5 per day. The reported harvest of Abert's squirrels in Arizona is combined with the harvest of other tree squirrels. Thus, we multiplied Arizona Game and Fish Department harvest statistics for tree squirrels by the proportion (0.74) of the harvest represented by Abert's squirrels (Ron Engel-Wilson, Arizona Game and Fish

Department, 1994, personal communication), to estimate an average of 57,900 and 77,600 Abert's squirrels harvested annually in Arizona during the last 5 and 10 years, respectively (Fig. 2).

Ramey (1973) estimated Abert's squirrel densities of 12/km² and 30/km² (depending on time of year) in the Black Forest of Colorado and Ferentinos (1972b) reported 33 and 56 Abert's squirrels/km² (depending on time of year) in an area immediately west of Boulder, Colorado. Trowbridge and Lawson (1942, cited by Nash and Seaman 1977) and Keith (1965) reported densities of 30 and 2.5-5 Abert's squirrels/km², respectively, in the same region of Arizona, and Patton (1975b) estimated a density of 247 squirrels/km² (1/acre) in another part of Arizona. However, no statistically valid statewide population estimates are available for Abert's squirrels in Colorado, Arizona, or elsewhere.

We contacted biologists (J. O. Keith, D. J. Nash, D. R. Patton, C. A. Ramey, personal communication) that had previously conducted estimates of Abert's squirrel densities in Colorado and Arizona and one biologist (M. A. Snyder, personal communication) that recently had studied Abert's squirrels in Colorado and asked them to estimate statewide Abert's squirrel densities in ponderosa pine habitat in Colorado and Arizona. Abert's squirrel distributions coincide with the distribution of ponderosa pine in Colorado (Fig. 3) and in Arizona (Hoffmeister 1986, Conner et al. 1990). Two biologists (J. O. Keith and C. J. Ramey) felt that the densities reported for the Black Forest of Colorado (Ramey 1973) and near Boulder, Colorado (Ferentinos 1972b) were higher than the average densities in ponderosa pine habitat in Colorado. Three biologists (J. O. Keith, D. R. Nash, and M. A. Snyder) felt that Abert's squirrel densities were higher in Arizona than in

Colorado. J. O. Keith and D. R. Nash felt that Abert's squirrel densities may be around $2/\text{km}^2$ ($5/\text{mi}^2$) and $5-15/\text{km}^2$, respectively, in Colorado. D. J. Nash and D. R. Patton felt that squirrel densities may be slightly higher than $5-15/\text{km}^2$ and about $12-16/\text{km}^2$ (1/15-20 acres), respectively, in Arizona.

Colorado contains about $11,200 \text{ km}^2$ of ponderosa pine (Benson and Green 1987) and Arizona contains about $13,600 \text{ km}^2$ of ponderosa pine (Conner et al. 1990). We multiplied the area of ponderosa pine in Colorado by J. O. Keith's and D. J. Nash's estimates of Abert's squirrel densities ($2-15 \text{ squirrels}/\text{km}^2$) to estimate a population of 22,400-168,000 squirrels in Colorado. We also multiplied the area of ponderosa pine in Arizona by D. J. Nash's and D. R. Patton's estimates of Abert's squirrel densities ($>5-16 \text{ squirrels}/\text{km}^2$) to estimate a population of $>68,000-217,600$ squirrels in Arizona. Based upon these estimates and reported harvest, we estimate that 2-14% of the Abert's squirrel population may have been harvested annually in Colorado during the past 5 years, whereas these computations suggest $<27-85\%$ of the Arizona population was harvested annually. We recognize that Abert's squirrels cannot sustain an 85% harvest rate and thus believe that the lower density estimate provided for Arizona may be in error. The above harvest reports suggest that Arizona harvests 20-30 times as many Abert's squirrels as Colorado harvests while our calculations indicate that Arizona may have 2-3 times as many squirrels. These data suggest that Colorado's harvest of Abert's squirrels is not excessive compared to Arizona.

We are not certain what impact a possible harvest of 2-14% might have on Abert's squirrels in Colorado. However, we recognize that animal populations normally produce a surplus of animals which can be harvested without producing detrimental effects on their populations. For example, Smith et al. (1981)

and Clark (1987) reported that muskrats (Ondatra zibethicus) could sustain a harvest of up to 75% and 64%, respectively, of the fall populations. Clark (1987) reported that density-dependent increases in nonharvest survival compensated for increases in harvest mortality of muskrats. Mosby (1969) reported that an average harvest of 37.4% of the estimated fall population of gray squirrels in Virginia produced no significant difference in the average annual mortality rate compared with the rate of an adjacent unharvested area. Shorten (1959) reported that intensive hunting and trapping had no noticeable effect on squirrel densities in Great Britain, and Carson (1957) believed that heavy hunting had no effect on gray squirrel population levels in West Virginia.

Because no studies have been conducted in Colorado or elsewhere to assess the effect of various levels of harvest on density and population dynamics of Abert's squirrels, we identified and surveyed 35 individuals interested in Abert's squirrels in Colorado (Tables 1, 2) to determine possible changes in Abert's squirrel populations in Colorado and factors causing these changes. The majority of respondents to our telephone survey indicated that population levels of Abert's squirrels in their local vicinity were similar in 1994 compared to 5, 10, and 20 years ago (Table 1). Most respondents believed that squirrel numbers were the same or higher in all of Colorado during 1994 compared to 5, 10, and 20 years ago.

Most respondents (5 of 12) that believed Abert's squirrel densities increased in their vicinity or in Colorado attributed those increases to changes in habitat resulting from factors such as fire suppression (Table 2). Two of the 12 respondents reported that higher squirrel densities were related to hunting (presumably that hunting increased the densities of squirrels or

that squirrels increased with less hunting which is contrary to Division of Wildlife statistics indicating that hunting increased in recent years).

~~Loss of habitat from human development was the factor most frequently~~ attributed to decreases in Abert's squirrel densities by respondents that believed that Abert's squirrel densities decreased in their vicinity or in Colorado (Table 2). Several respondents that believed that Abert's squirrel densities decreased also attributed those decreases to changes in habitat, collisions with automobiles, and predation by domestic animals (Table 2). Only one of 9 respondents that believed that squirrel populations were lower in 1994 attributed the decrease to hunting.

MANAGEMENT RECOMMENDATIONS

- 1) Because of limited budgets, the need to conduct research on Abert's squirrels should be prioritized relative to other species. If Abert's squirrels rank high in the prioritization process, research should be conducted to determine causes of mortality and affects of human development on Abert's squirrel populations in ponderosa pine habitat along the Front Range.
- 2) If human development and associated loss of habitat is found to have negative effects on Abert's squirrel populations, consideration should be given to developing a long-term plan to limit and/or direct development so that it will have minimal affects on Abert's squirrels and other wildlife.
- 3) Where human development is occurring, consideration should be given to

leaving or providing the appropriate number, size, and age classes of ponderosa pines on residential acreages to provide optimal habitat for Abert's squirrels. Planting ponderosa pines instead of exotic species likely will maximize benefits for squirrels. Increasing housing density in return for leaving large consolidated open spaces and movement corridors may be less disruptive to Abert's squirrels than current development.

- 4) If predation by domestic pets is found to cause unacceptable mortality, dogs and cats should be kept indoors, on a leash, or at least within private yards.
- 5) If development is found to have a negative effect on Abert's squirrels, an educational program should be directed at county planners, developers, and citizens to inform them how to minimize disruptions to Abert's squirrels.
- 6) Biologists and foresters should work together to insure that future harvest and management of ponderosa pine stands is compatible with Abert's squirrels, following recommendations in this manuscript and elsewhere.

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APPENDIX 1

PONDEROSA PINE HABITAT

Ponderosa pine is the most widely distributed pine in North America Patton (1975_a). It occupies about 44,500 km² mostly in Arizona, Colorado, and New Mexico. In Colorado, ponderosa pine occurs primarily along the Front Range from the Wyoming border southward to New Mexico, westward to Mesa Verde, and northward in the west to the Colorado river at elevations ranging from 1,829 to 2,896 meters (Buttery and Gillam 1984). This ecosystem occupies approximately 11,222.3 km² on warm, dry sites, and on a variety of geologic formations in Colorado (Buttery and Gillam 1984).

Ponderosa pine is primarily a climax forest with a complex spatial distribution of trees. Characteristically, ponderosa pine grows in irregular uneven-aged stands, with even-aged groups within the stands.

Throughout much of Colorado, ponderosa pine ecosystems are denser now than they were 50 to 150 years ago (Mutel and Emerick 1984). The change in density is largely the result of logging, fire suppression, and cessation of intensive livestock grazing. These measures, in addition to a wet climatic cycle in the first third of the century, resulted in the successful establishment of an abundance of ponderosa seedlings that matured to form today's dense forests. Under completely natural conditions, the young stands of ponderosa would have been thinned by ground fire. They would have matured to form open parkland. Wide spacing is beneficial to ponderosa trees because they require abundant sunshine and compete for limited moisture.

Lightning frequently starts ground fires which are a natural component of ponderosa ecosystems. While still young, ponderosa pines begin to develop a thick, corky bark that insulates older trees and protects them from all but severe fires. Ground fires kill seedlings and keep stands open, decreasing

the probability of hot crown fires in later years that could kill mature trees. Fires also release nutrients tied up in litter, remove thick litter that suppresses herb growth, and prepare a good ponderosa seed bed. During the last several decades, people have suppressed fires, allowing forests to become more dense and susceptible to severe crown fires which convert the forest to shrubland or meadow.

Ponderosa in dense stands unthinned by fire, such as those found throughout the region today, do not receive the nutrients, sun, or water necessary for vigorous growth. The weakened trees are more susceptible to diseases such as infestation by the mountain pine beetle. Beetle epidemics have occurred throughout recorded history and have been responsible for the loss of thousands of hectares of ponderosa in Colorado. The beetles are always present in low numbers and increase when there is an abundance of unhealthy trees. Weakened trees cannot resist invasion of the woodboring beetles by forcing them out with pitch.

Intensive, long-term grazing can form a meadow out of the forest. This occurs because cattle trample and damage seedlings and saplings, preventing the replacement of older dying ponderosa by young trees. Cessation of intensive grazing can result in the opposite extreme. Overgrazed herbs offer little competition to the large number of ponderosa seedlings that invade when cattle are removed. The seedlings survive and create a dense, unhealthy forest susceptible to disease. The forest may slowly return to a parkland or meadow ecosystem as older trees die and as herbs become re-established, competing with ponderosa seedlings for moisture and nutrients.

Today ponderosa forests are used heavily for recreation, hunting, woodcutting, and as sites for mountain residences. Livestock grazing and timber production are still important.

McCambridge et al. (1982) analyzed the effects of mountain pine beetles in Colorado, and found that mortality increased with tree diameter, but not indefinitely. ~~Trees of 20 or 23 cm dbh were almost as likely to be killed as~~ larger trees. McCambridge et al. (1982) suggested a program of stand thinning to limit tree losses. Larsson et al. (1983) found that ponderosa pines are more susceptible to mountain pine beetles attacks when the trees show reduced vigor.

Ponderosa pine is adapted to periodic wildfire and should benefit from periodic burning programs (Ffolliott et al. 1977). Prescribed fire can reduce wildfire hazard, thin the overstory, provide favorable conditions for seedling establishment, and increase forage production (Ffolliott et al. 1977). In recent years, fire protection and suppression have been reasonably successful in eliminating large periodic fires (Campbell et al. 1977, Dieterich 1980). This protection has resulted in very dense stands, and a reduction of native grasses (Dieterich 1980).

Approximately 26 months is required in Colorado for ponderosa pine seed to mature (Roeser 1941). Primary tissue of both pistillate and staminate cones begin to develop in late summer, and by next spring flowers of both sexes are completely developed. Pollination occurs in June but fertilization does not take place until 13 months later, and cones mature by the middle of September the same year (Roeser 1941).

Table 1. Number of biologists^a and other respondents^a indicating that the abundance of Abert's squirrels is higher, lower, or the same in parts and all of Colorado during 1994 compared to 5, 10, and 20 years ago.

Organization	No.	In respondent's vicinity						In entire Colorado									
		5 yrs		10 yrs		20 yrs		5 yrs		10 yrs		20 yrs					
		h ^b	l ^c	s ^d	h	l	s	h	l	s	h	l	s	h	l	s	
Forest Service	5	2	0	3	2	0	3	1	0	1	0	0	0	0	0	0	0
Div. of Wildl.	10	1	3	5	1	1	5	1	0	3	1	0	1	0	1	0	1
University	8	1	1.5 ^e	3.5	1	2.5	2.5	0	2	1	1	1	2	2	1	1	2
Other Govt. Org.	6	3	1	2	2	1	0	0	0	1	1	0	1	1	0	0	0
Non Govt. Org.	4	0	3	1	1	1	0	0	0	0	0	0	1	0	0	0	0
Private citizens	2	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Total	35	7	9.5	15.5	8	6.5	10.5	2	2	6	3	2	4	4	1	2	3

^aChuck Dennis, Colorado State Forest Service, Golden, Colorado
 Dave Leatherman, Colorado State Forest Service, Fort Collins, Colorado
 John Bustos, United States Forest Service, Fort Collins, Colorado
 Jim Cruse (retired), United States Forest Service, Fort Collins, Colorado
 Dr. Richard Reynolds, United States Forest Service, Fort Collins, Colorado
 Dr. Steve Bissel, Colorado Division of Wildlife, Denver, Colorado
 Jerry Brinker, Colorado Division of Wildlife, Evergreen, Colorado
 Harvey Donoho, Colorado Division of Wildlife, Montrose, Colorado
 John Ellenberger, Colorado Division of Wildlife, Grand Junction, Colorado
 Dave Lovell, Colorado Division of Wildlife, Colorado Springs, Colorado
 Jim Oltzman, Colorado Division of Wildlife, Montrose, Colorado
 Steve Porter, Colorado Division of Wildlife, Walden, Colorado

Table 1. Continued.

Organization	In respondent's vicinity									In Colorado										
	5 yrs			10 yrs			20 yrs			5 yrs			10 yrs			20 yrs				
	ents	^b h	^c l	^d s	h	l	s	h	l	s	h	l	s	h	l	s	h	l	s	
Francie Pusaterie, Colorado Division of Wildlife, Fort Collins, Colorado																				
Robert Tully (retired), Colorado Division of Wildlife, Denver, Colorado																				
Susan Werner, Colorado Division of Wildlife, Conifer, Colorado																				
Dr. Donald Nash, Colorado State University, Fort Collins, Colorado																				
Dr. Ronald Ryder, Colorado State University, Fort Collins, Colorado																				
Dr. Bruce Wunder, Colorado State University, Fort Collins, Colorado																				
Dr. Dave Armstrong, University of Colorado, Boulder, Colorado																				
Dr. Margaret (Peg) Halloran, University of Colorado, Boulder, Colorado																				
Dr. Yan Linhart, University of Colorado, Boulder, Colorado																				
Dr. Marc Snyder, University of Colorado, Boulder, Colorado																				
Dr. James Fitzgerald, University of Northern Colorado, Greeley, Colorado																				
Dr. Mike Bogan, National Biological Survey, Albuquerque, New Mexico																				
Mike Figgs, Boulder County Nature Association, Boulder, Colorado																				
James Keith, Denver Wildlife Research Center, Bailey, Colorado																				
Chris Pague, Colorado Natural Heritage Foundation, Fort Collins, Colorado																				
Mike Threlkeld, Colorado Department of Agriculture, Lakewood, Colorado																				
Ann Wichmann, Boulder County Mountain Parks, Boulder, Colorado																				
Bob Angell, Colorado Sierra Club, Denver, Colorado																				
Shirley Casey, Wildlife Rehabilitator, Evergreen, Colorado																				
Brian Peck, National Audubon Society, Boulder, Colorado																				
Mike Smith, Colorado Environmental Coalition, Boulder, Colorado																				
Louise Bennett, Private Landowner, Bellvue, Colorado																				
Kevin Cook, Outdoor Writer, Fort Collin's Coloradoan, Fort Collins, Colorado																				

^bH = Higher.

^cL = Lower.

^dS = Same.

^eThe .5 values resulted from 1 respondent indicating that Abert's squirrel populations were lower in some areas and the same in other areas during 1994 compared to 5 and 10 years ago.

Table 2. Number of biologists and other respondents reporting why they believed that Abert's squirrel populations have increased (maximum n = 12) or decreased (maximum n = 12) in Colorado.

Reason	<u>Caused increase</u>			<u>Caused decrease</u>		
	Yes	No	Uncertain	Yes	No	Uncertain
Loss of habitat from development	0	0	0	9	3	0
Habitat change (fire suppression)	5	5	2	5	5	2
Disease and/or parasites	0	1	11	1	3	8
Competition with fox squirrels	1	7	3	4	6	2
Collisions with automobiles	0	9	3	5	4	3
Predation by wildlife	2	4	6	0	8	4
Predation by domestic animals	0	7	5	4	2	6
Hunting by humans	2	5	4	1	8	3
Pine seed production	2	4	6	3	7	2
Snow cover	2	5	5	1	10	1
Other	7	5	0	5	6	1

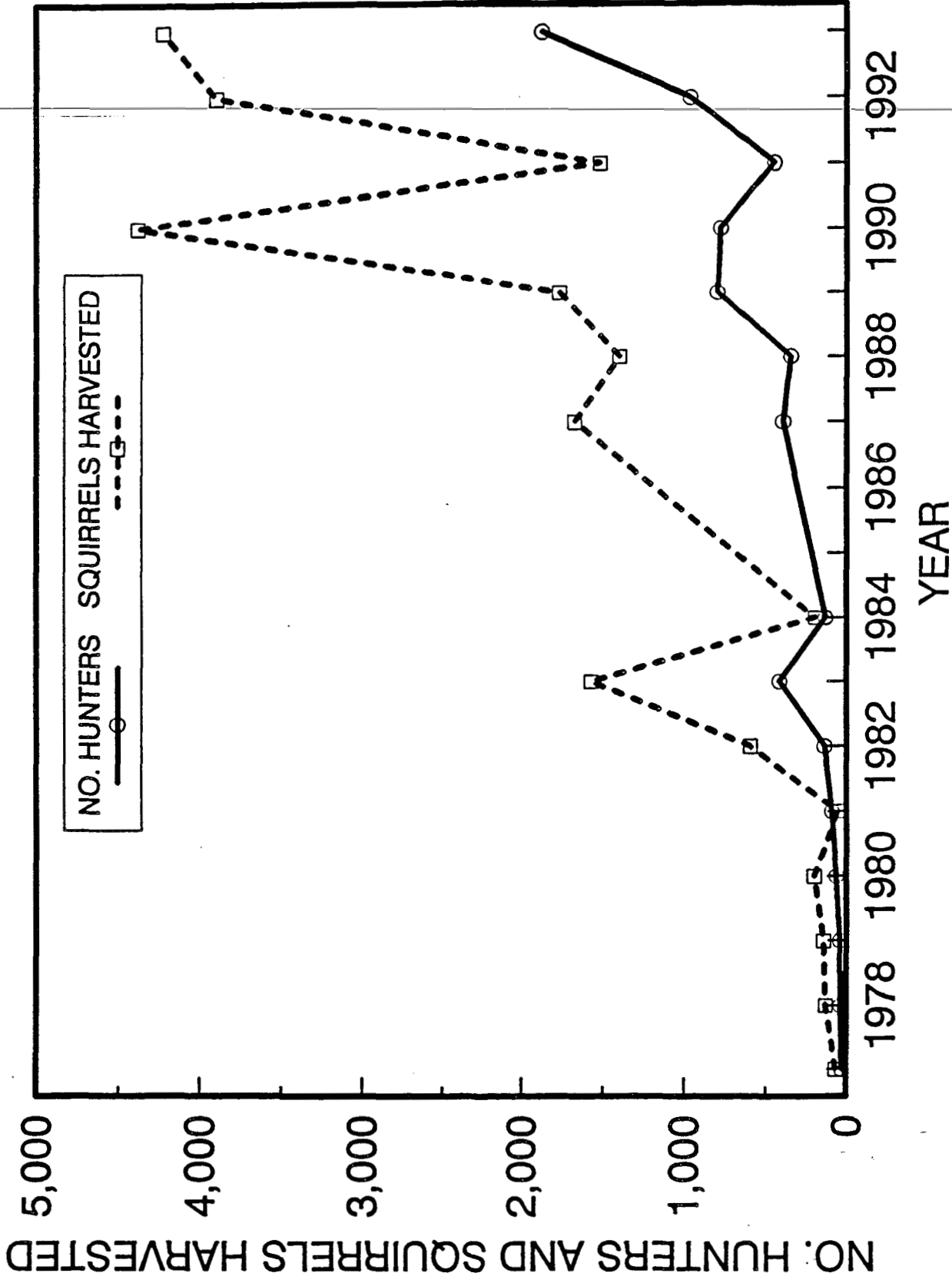


Figure 1. Number of hunters and number of Abert's squirrels harvested in Colorado from 1977 to 1993 (from Colorado Division of Wildlife, unpublished data).

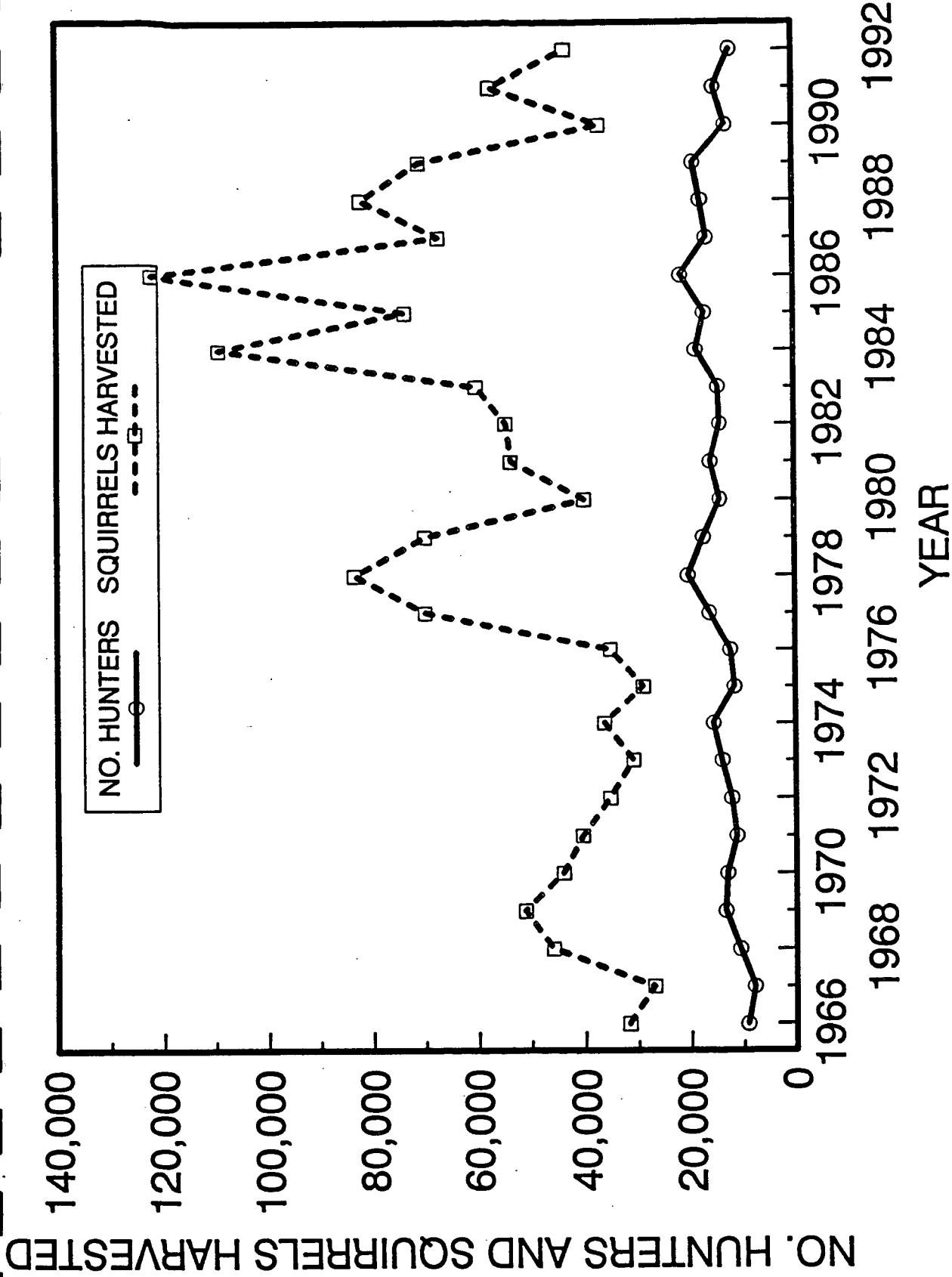
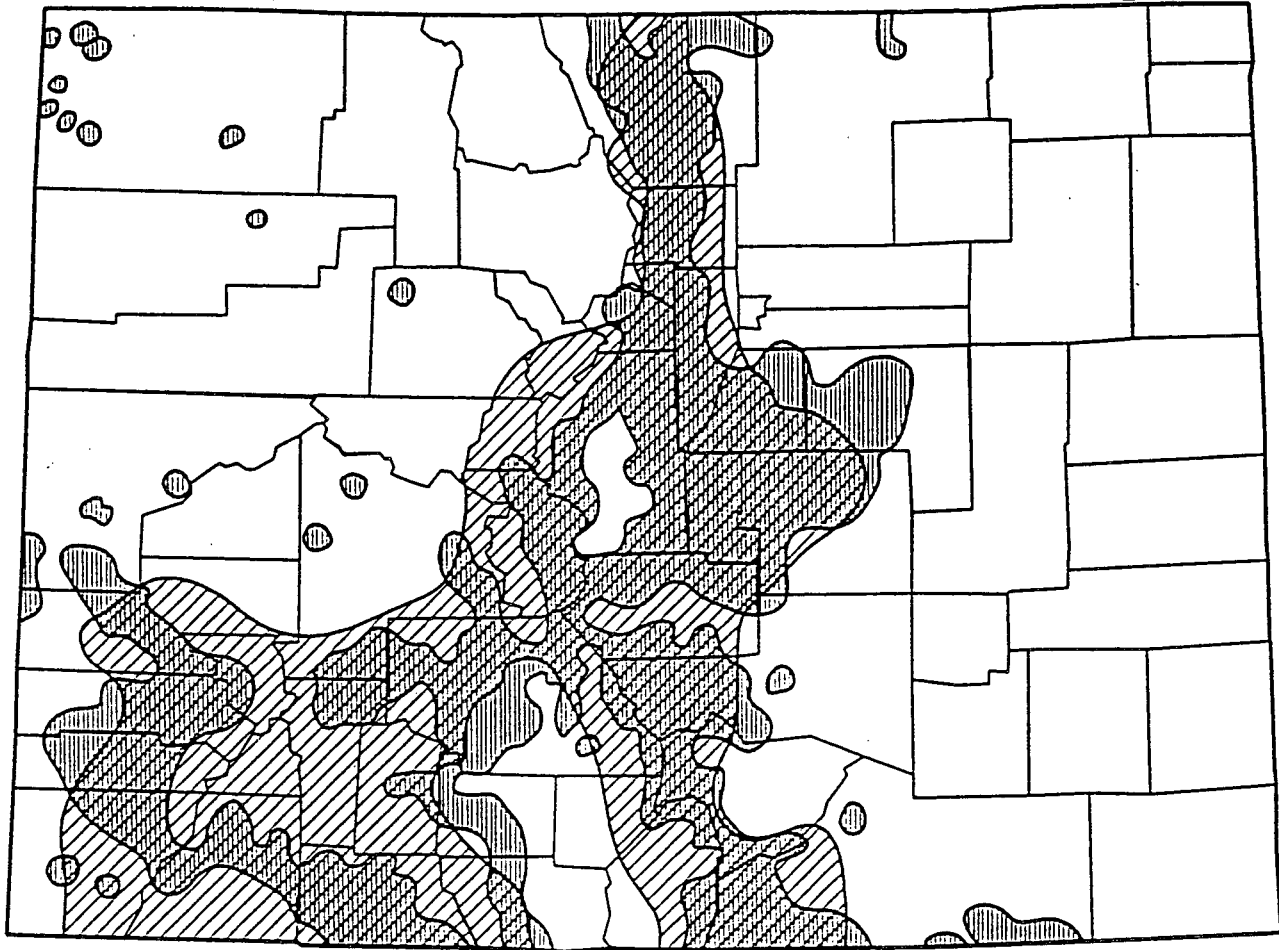


Figure 2. Number of hunters and number of Abert's squirrels harvested in Arizona from 1966 to 1992 (from Arizona Game and Fish Department, unpublished data; Ron Engel-Wilson, Arizona Game and Fish Department, 1994, personal communication).



 Abert's Squirrels  Ponderosa Pine

Figure 3. Distribution of Abert's squirrels and ponderosa pine in Colorado (from Little 1971, Fitzgerald et al. In press).