

The Abert's Squirrel (*Sciurus aberti*): A Technical Conservation Assessment



**Prepared for the USDA Forest Service,
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AUTHOR'S BIOGRAPHY

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COVER PHOTO CREDIT

The Abert's Squirrel (*Sciurus aberti*)
Photograph by William Ervin, used with his permission.

INTRODUCTION REMARKS

“This truly elegant squirrel I procured in the San Francisco mountain, during the month of October, where I found it quite abundant, and after leaving which place I did not see it again. I have been informed by Major Backus, U.S. Army, that they are quite numerous near Fort Defiance, in the Navajo country. I have called it Sciurus Abertii, in honor of Col. J. J. Abert, Chief of the Corps of Topographical Engineers, to whose exertions science is so much indebted.”

S. W. Woodhouse, 1853.

“The most characteristic, as well as most abundant species of Squirrel, is the Tuft-eared - [Abert squirrel] discovered by Dr. Woodhouse in the San Francisco Mountains. It is one of the largest, and certainly the very handsomest of all our North American species. Besides very beautiful and harmonious colors, it rejoices in the possession of long pointed ear-tufts, extending an inch or more from the edge of the conch of the ear, which give it a peculiarly sprightly and truly elegant appearance.

The pine-clad mountains of northern and central Arizona are the chosen home of this Squirrel, and it rarely, if ever, quits these woods for other situations. It is there a resident species, breeding in abundance, and braving the rigors of winter. Its food is chiefly pine and other seeds.”

Elliott Coues, 1867.

“We came to a glorious forest of lofty pines, through which we have travelled ten miles. The country was beautifully undulating, and although we usually associate the idea of barrenness with the pine regions, it was not so in the instance; every foot being covered with the finest grass, and beautiful broad grassy vales extending in every direction. The forest was perfectly open and unencumbered with brush wood, so that the traveling was excellent.”

E.F. Beale, 1859. (From Cooper, 1960)

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE ABERT'S SQUIRREL

Status

Colorado is the only state in Region 2 in which significant populations of Abert's squirrels (*Sciurus aberti*) exist. Populations of the squirrel have fluctuated widely over the past 100 years, but the species' viability does not appear to be threatened, nor is the species in danger of extinction at a landscape or forest level anywhere in Colorado. It is normal for the abundance of Abert's squirrels to vary greatly and frequently due to weather conditions and food supplies. Numbers change over longer periods with forest management practices that alter squirrel habitat condition. Large wildfires have eliminated squirrels and squirrel habitat over vast areas, but such losses do not threaten the species' viability in Colorado. The species currently seems quite secure in Region 2.

Primary Threats

The primary threat, or limiting factor, to Abert's squirrel populations in Colorado at the present time appears to be the condition of their habitat. By 1900, original forests had been severely degraded by logging, grazing, and wildfires. Replacement forests provided less valuable habitats for squirrels, and forest management stressed timber production rather than creation of habitat for wildlife. Current forest conditions are not sustainable. Forest management is now focused on thinning and fuels reduction to protect watersheds and human dwellings. Habitat requirements of squirrels could be accommodated but are seldom considered. The future condition of squirrel habitat in Colorado will depend on management decisions, and it easily could decrease in value. Global climate change is increasingly becoming a threat to the squirrels and to their habitat. Recent droughts have restricted reproductive success, and heavy and persistent winter snowfalls have caused increased mortality.

Primary Conservation Elements, Management Implications and Considerations

Abert's squirrels rely on ponderosa pine (*Pinus ponderosa*) for most of their life requirements. The needs of the squirrel that are met by the pine have been defined sufficiently to enable management of pine forests to support squirrel populations. Forest managers must decide on forest management goals. Squirrel abundance can be maintained and even increased by using available knowledge of squirrel habitat requirements. Good squirrel habitat contains open, uneven-aged stands, with clusters of even-aged groups connected by canopy corridors to provide secure travel routes. Such forest structure will provide the foods required by squirrels, as well as the canopy cover necessary for fungi production, nesting, and escape. Squirrels reduce cone crops and perhaps growth in ponderosa pine. However, they contribute to the well-being of the pine by dispersing spores of hypogeous fungi that facilitate water and nutrient uptake by the trees and thereby enhance seedling survival, forest regeneration, and growth.

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INTRODUCTION

This assessment is one of many being prepared to support the Species Conservation Project for the Rocky Mountain Region, U.S. Forest Service (USFS). The Abert's squirrel is the focus of an assessment because it is a Management Indicator Species (MIS) on multiple national forests in Region 2, and as such, it serves as a barometer for species viability at the forest level. MIS have a dual functionality: 1) to estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a) (1)) and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a) (6)). This assessment addresses the biology of the Abert's squirrel throughout its range in Region 2. The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal of Assessment

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussions of the broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations but provides the ecological background upon which management must be based. However, it does focus on the consequences of changes in the environment that result from management (i.e. management implications). Furthermore, it cites management recommendations proposed elsewhere and, when management recommendations have been implemented, the assessment examines the success of the implementation.

Scope of Assessment

The Abert's squirrel assessment examines the biology, ecology, conservation status, and management of this species with specific reference to geographic and ecological characteristics present in the Rocky Mountain Region. Although much of the literature on the species originates from field investigations in Arizona and Utah, this document places that literature in the ecological context of the southern

Rockies. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of Abert's squirrels in the context of the current environment, which changed radically beginning about 150 years ago. The evolutionary environment of the species is considered in conducting the synthesis but placed in a current context.

The following sources were reviewed in preparing this assessment: refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on Abert's squirrels are referenced in the assessment, nor was all published and unpublished material considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were regarded with greater skepticism and used only when information was unavailable elsewhere.

Treatment of Uncertainty

Science attempts to attain a systematic approach to obtaining knowledge. Competing ideas are measured against observations. Because descriptions are always incomplete and observations limited, science includes approaches for dealing with uncertainty. Sorting among alternatives may be accomplished using a variety of scientific tools. It is difficult to conduct critical experiments in the ecological sciences and often observations, inference, good thinking, and models must be relied on to guide the understanding of ecological relations.

In this assessment, the strength of evidence for particular ideas is noted and alternative explanations are described when appropriate. While well-executed experiments represent the strongest approach to developing knowledge, alternative methods (observations and inference) were accepted as sound approaches to understanding features of biology.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as a book or report. More important, it facilitates revision of the assessments, which will be accomplished based on guidelines published by Region 2.

Peer Review

Assessments developed for the Species Conservation Process have been peer reviewed prior to release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology which chose two recognized experts to provide critical input on the manuscript. Peer review was designed to improve the quality of communication and increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The Abert's squirrel has a Natural Heritage Program ranking of G5; it is demonstrably secure globally, though it may be quite rare in parts of its range, especially at the periphery (Natural Heritage Program, public communication). The Abert's squirrel has no federal legal protection and is not considered rare or threatened. The USFS considers the squirrel to be a "management indicator species", and it is a "demand species" in Colorado, Arizona, and New Mexico, where it is hunted. The State of Utah has designated the squirrel as a sensitive species, based on its limited range in the state.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The Abert's squirrel is a game species in Colorado and is protected against "take", except as prescribed by Colorado's Small Game Hunting Regulations. None of the states in Region 2 are known to have developed management plans or conservation strategies for the squirrel. The National Forest Management Act directs the USFS to provide for biodiversity as part of meeting multiple-use objectives. The MIS concept is used by the agency to provide an indication of species viability at the forest level. Population responses are used to show the effects of management activities. MIS must be identified in a forest plan and their populations monitored to determine their relations to habitat changes. MIS currently are being identified in forest plans along with conservation strategies (e.g. Grand Mesa, Uncompahgre and Gunnison National Forest MIS Assessment).

The life requirements of the Abert's squirrel have been identified and should be considered in management of ponderosa pine forests. Several studies

have suggested specific approaches to create and enhance squirrel habitat during timber harvest or forest restoration activities and to monitor squirrel populations (Patton 1984, Dodd et al. 1998, Elson 1999). Another source of reference is the publication on managing forest lands for wildlife by Hoover and Wills (1984), which is the basis for the HABCAP computer model used by some forests to estimate habitat capability for the Abert's squirrel. Existing state and federal laws, if properly enforced, appear adequate to protect the Abert's squirrel from overexploitation. However, no information is available to determine the level of illegal take of the squirrel.

Biology and Ecology

Systematics

The Abert's squirrel is classified under the Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Genus *Sciurus*, and Subgenus *Otosciurus* (Nash and Seaman 1977). The taxonomy of the Abert's squirrel at the specific level has become confused over the years and new evidence (Seaman 1975, Wettstein et al. 1995, Wettstein et al. 1996, Lamb et al. 1997) continues to develop a basis for further revisions. Hall and Kelson (1959) and Nash and Seaman (1977) considered the Abert's squirrel and the Kaibab squirrel (*Sciurus kaibabensis*) to be separate species. In contrast, Cockram (1960) and Findley et al. (1975) regarded the Kaibab squirrel as one of nine subspecies of the Abert's squirrel, while Hoffmeister and Diersing (1978) placed the entire group into six subspecies of the Abert's squirrel. The group collectively is known as the tassel-eared squirrels, and the habits of all squirrels in the group appear to be basically the same (Goldman 1928). To illustrate the widest proposed separation of the species, the nine subspecies defined by Cockram (1960) and Finley (1999) and their general distribution are listed in **Table 1**.

General species description

The Abert's squirrel is a large tree squirrel with a long, full tail. It has long ear tufts during most of the year, but tufts are usually lacking on adults during July, August, and September when animals are in summer pelage (Keith 1965). The pelage of the squirrel is unique and perhaps the most beautiful of any North American squirrel. The body of most subspecies is a grizzled-gray dorsally with a variable rusty band down the middle of the back. The length and width of this rusty band varies among individuals and is greater in summer pelage than in winter pelage (Keith 1965, Armstrong 1972). A thin

Table 1. Distribution of nine subspecies of Abert's squirrel, as defined by Cockram (1960) and Findley et al. (1975).

Subspecies	Distribution
<i>Sciurus aberti aberti</i>	Mountains of central Arizona and southwestern New Mexico
<i>Sciurus aberti barberi</i>	Sierra Madre Occidental of west-central Chihuahua
<i>Sciurus aberti chuscensis</i>	Chuska Mountains of northwestern New Mexico and northeastern Arizona
<i>Sciurus aberti durangi</i>	Sierra Madre Occidental of southwestern Durango
<i>Sciurus aberti ferreus</i>	Eastern slope of the Rocky Mountains in Colorado and extreme northern New Mexico
<i>Sciurus aberti kaibabensis</i>	Kaibab Plateau of northern Arizona
<i>Sciurus aberti mimus</i>	San Juan Mountains of Colorado and mountains of north-central New Mexico
<i>Sciurus aberti navajo</i>	Abajo Mountains of southeastern Utah
<i>Sciurus aberti phaeurus</i>	Sierra Madre Occidental of southwestern Chihuahua and northwestern Durango

black line is present laterally, separating the dorsal fur from the white ventral fur. The tail is grizzled above and white beneath. The Kaibab squirrel is equally striking, with a black belly and a pure white tail. White-bellied individuals can be found in Kaibab populations (Hall JG 1981) and black-bellied squirrels are common in New Mexico (Findley et al. 1975) and occur in Arizona (Hoffmeister 1971, Allred 1995).

In north-central Colorado, Ramey and Nash (1976b) reported pelage polymorphism occurring in *S. a. ferreus*, with melanism being present in 68 percent of the animals. Both the agouti (gray) and non-agouti (black) phases showed varying phenotypes ranging from light brown to black (1973). Most brown squirrels have been reported from central Colorado in Elbert, El Paso, and Jefferson Counties (Ramey and Nash 1971). The predominant color along the Front Range is black. All three color phases can occur in a single litter. In southwestern Colorado, almost all squirrels (*S. a. mimus*) are salt-and-pepper gray.

Fitzgerald et al. (1994) reported body weights of Abert's squirrels between 550 and 750 g, and this range encompasses those given by Keith (1965), Patton et al. (1976b), and Pederson et al. (1987). The ranges for measurements given by Fitzgerald et al. (1994) (total

length 450 to 580 mm, tail 200 to 300 mm, hind foot 65 to 75 mm) include the ranges given by Hall and Kelson (1959) and Keith (1965).

Distribution

Abert's squirrels occur in the cool, dry forests of interior ponderosa pine (*Pinus ponderosa* var. *scopulorum*) in the Southwest. They do not inhabit the moister coastal and northern stands of ponderosa pine, where winters are longer and snows are deeper. In Colorado, Arizona, and New Mexico, the squirrels are usually found within the montane forests of ponderosa pine and mixed ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*). They were described as being dependent on these forests for their life requirements of food and shelter (McKee 1941, Keith 1965, Dodd et al. 1998). They make only minor incursions into pinyon pine (*Pinus edulis*) at lower elevations (Reynolds 1966, Reynolds et al. 1970) and spruce-fir forests at higher elevations (Ferner 1974). In contrast, Hoffmeister (1986) found that of collection records in Arizona, 20 percent are in pinyon-juniper woodlands. Likewise, Hutton et al. (2003) reported sightings of 498 Abert's squirrels during a 12-year period in the two types of spruce-fir forests on Mt. Graham in southern Arizona.

The range of the Abert's squirrel includes the southern Rocky Mountains and the Colorado Plateau in the United States and the Sierra Madre Occidentals in Mexico (**Figure 1**). They occur naturally in some isolated mountain ranges, such as the Chuskas on the northern part of the border between New Mexico and Arizona and the Abajos in southwestern Utah. In addition, they were successfully introduced into several isolated ranges in Arizona and in the Sandia and Manzano mountains of New Mexico (Davis and Brown 1988).

Throughout the species' range from Mexico, through New Mexico and Arizona, and into Utah,

Colorado, and Wyoming, the squirrel naturally occurs in disjunct patches of ponderosa pine, many of which are separated by miles of inhospitable habitat. Some authors believed that the isolated segments of habitat, many with a compliment of squirrels and associated fauna and flora, were relics of a continuous forest that existed during the late Pleistocene (McKee 1941, Keith 1965).

Davis and Brown (1989) reviewed the historical distribution of ponderosa pine and Abert's squirrels and concluded that the squirrel did not occur north of 36° N latitude in the late Pleistocene, primarily because at that time the pine did not grow north of that latitude (Lomolino et al. 1989). They proposed the current

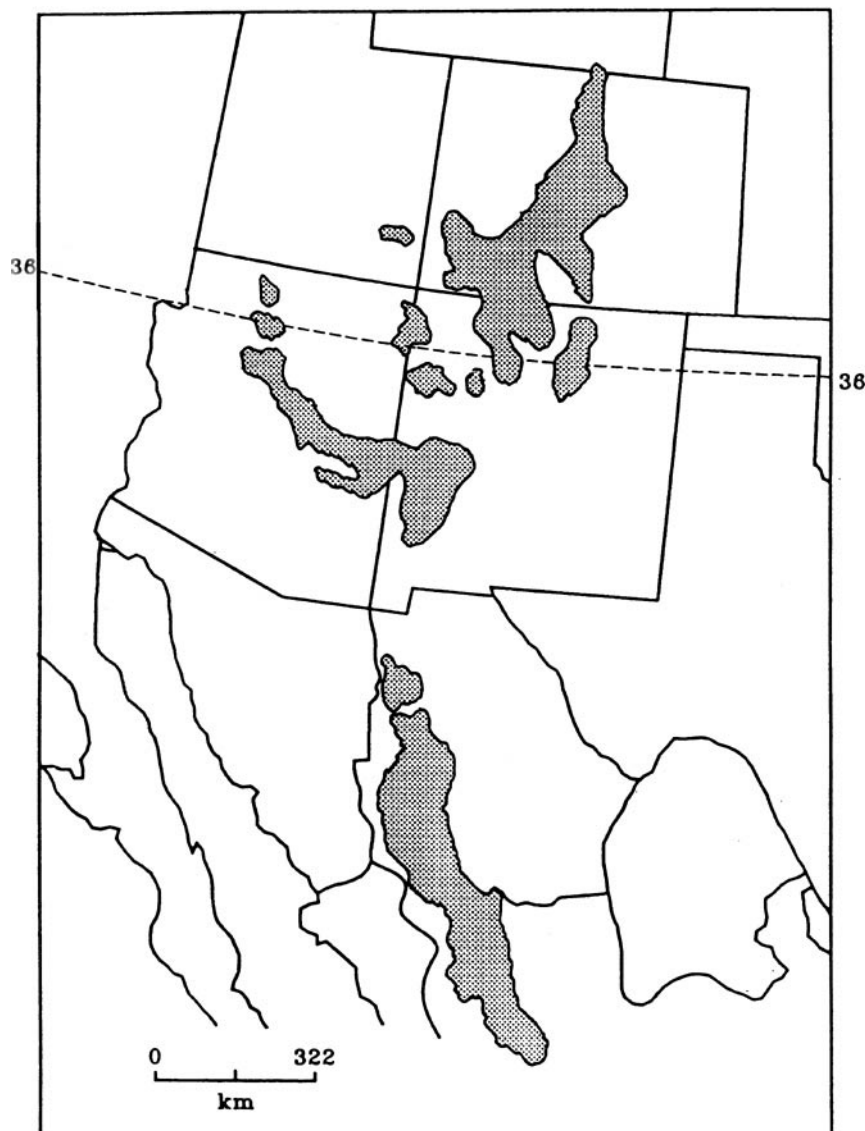


Figure 1. Range of the Abert's squirrel in the Southwestern United States. (Source: Davis and Brown 1989)

distribution of the squirrel north of 36° N latitude is the result of a relatively recent immigration that is apparently continuing.

Davis and Brown (1989) described the natural range expansion of three Abert's squirrel populations in Arizona that required movements of up to 57 km through habitats lacking ponderosa pine. Abert's squirrels evidently can subsist and move across plant communities outside of ponderosa pine forests to establish new populations. Their movements and migrations have been documented through spruce-fir forests (Hutton et al. 2003) and above timberline (Cooper 1987).

Davis and Bissell (1989) evaluated the distribution of the Abert's squirrel in Colorado based on museum collections and published and unpublished reports. They started with the range map of Armstrong (1972) and added recent records (Figure 2). They proposed that the squirrel's distribution either was underestimated before 1971 or that its range has

expanded since that time. For instance, Armstrong (1972) stated that there were no records from western Colorado north of the San Juan Mountains, and they should not be expected there as ponderosa pine occurs only in small disjunct stands. By 1989, squirrels were reported in 11 additional counties north of the San Juan Mountains, and by 2001, they occupied small areas east and west of Montrose, Colorado (Figure 3). Davis and Bissell (1989) argued that the new records were due to range expansion and believed the process was one that had been occurring as the squirrels moved northward following the post-Pleistocene expansion of ponderosa pine into Colorado.

Bissell (1978) and Meaney (1990) presented the same general distribution for the squirrel in Colorado based on reports of their presence in one-degree blocks of latitude and longitude within the state. Fitzgerald et al. (1994) gave an even more generalized range for the squirrel in Colorado, but it appeared to conform to the distribution shown by Davis and Bissell (1989). The only report of Abert's squirrels in Region 2 outside of

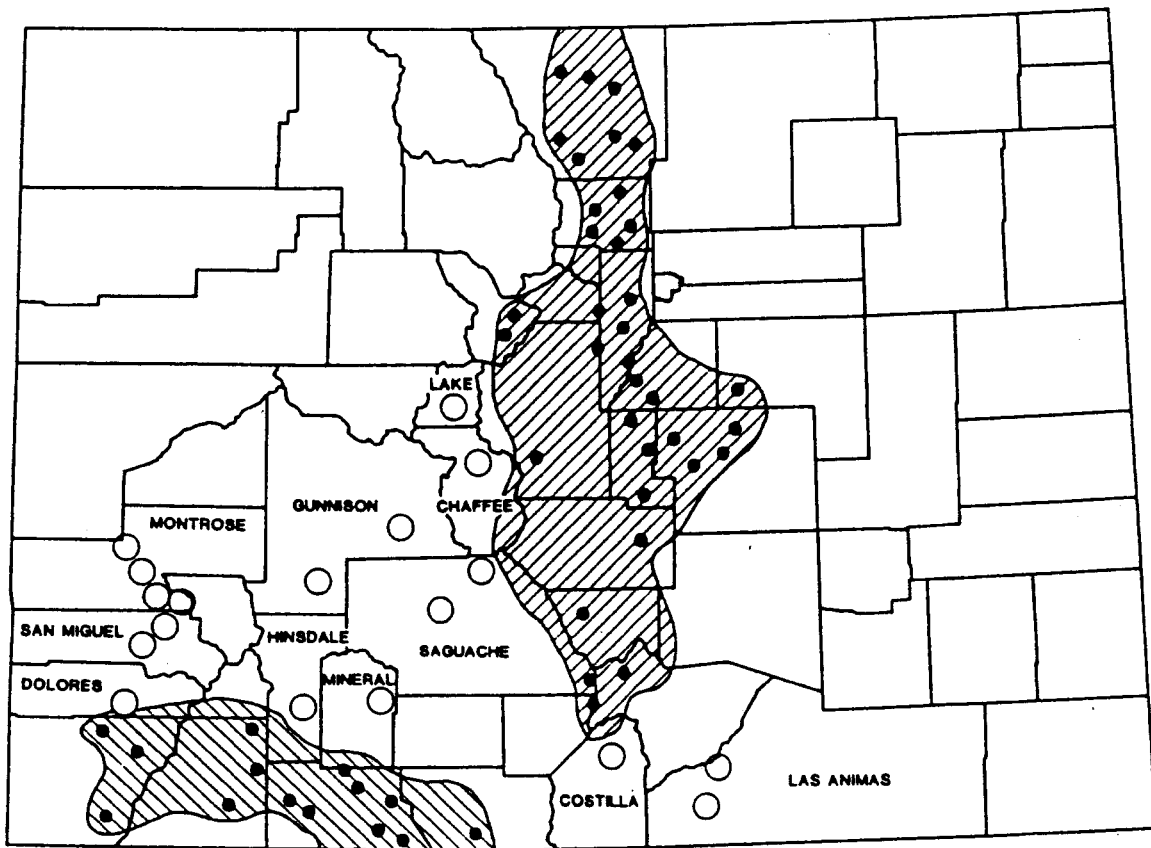


Figure 2. Range of the Abert's squirrel in Colorado. (Source: Davis and Bissell 1989)

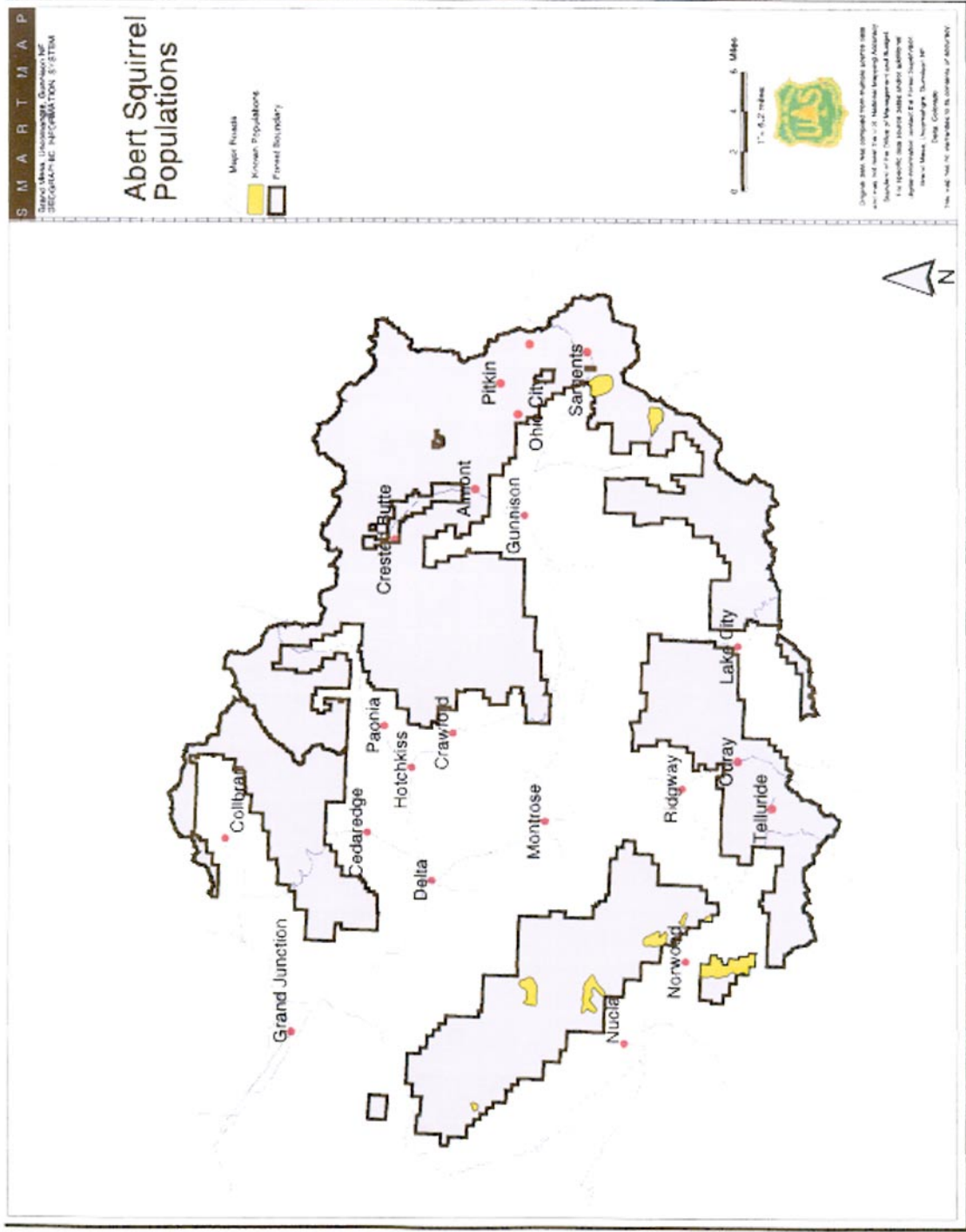


Figure 3. Abert's squirrel distribution on the Grand Mesa, Uncompahgre, Gunnison National Forest. (Source: Grand Mesa, Uncompahgre, Gunnison National Forest)

Colorado is from extreme southern Wyoming. Brown (1969) collected squirrels near Harriman, Wyoming only several hundred meters north of the Colorado border. No Abert's squirrels were reported elsewhere in Wyoming, at least until 1978 (Harju 1978).

Abundance

Historically, Merriam (1890) and Mearns (1907) found squirrels abundant in Arizona. Cary (1911) believed the squirrels were scarce in Colorado, and Rockwell (1916) commented that Abert's squirrels formerly were much more abundant in Colorado. Goldman (1928) reported both the Abert's and the Kaibab squirrel were decreasing in Arizona. Pearson (1950) reported a steady increase at Fort Valley near Flagstaff between 1930 and 1940. Other observers frequently have commented on the variations in Abert's squirrel numbers that are apparent over time and from area to area (Keith 1965, Nash and Ramey 1970, Hoffmeister 1971, Armstrong 1972, Hall ER 1981). Wilson and Ruff (1999) stated that populations of Abert's squirrels fluctuate markedly, with densities varying from 2 to 82 individuals per km². Densities reported in other studies were 2.5 to 5 (Keith 1965), 8 to 16 (Brown 1984), 7 to 33 (Dodd et al. 1998), 1 to 30 (Ramey 1973), 31 to 56 (Farentinos 1972a), 12 to 124 (Lawson 1941), 30 to 124 (Trowbridge and Lawson 1942), and 247 (Patton 1975b).

J.G. Hall (1981) reported that fluctuations in numbers of Kaibab squirrels had concerned National Park Service and Forest Service staffs for many decades. They had seen a considerable reduction in squirrel numbers during the winter of 1918-1919, which was during a strong El Niño event. The squirrels were abundant in 1931 and were believed to be more numerous than in the previous four years. A serious decline in 1962 resulted in low populations in 1963 and 1964. Squirrel populations also declined in 1967 and in 1972. All of the above were subjective appraisals. The Kaibab Plateau is over 9000 ft in elevation at the rim of the Grand Canyon. Annual snowfall is greater than elsewhere in the range of the Abert's squirrel, and snow remains on the ground later in the spring.

At the Fort Valley Experiment Station in Arizona, Trowbridge and Lawson (1942) required 11 trap-days for every squirrel they caught. It took 18, 24, and 22 trap-days to catch each squirrel in 1943, 1944, and 1945, respectively, at Fort Valley (Brown 1984). In 1954, Keith (1956) needed 73 trap-days to catch each squirrel at Fort Valley. By trapping, Trowbridge and Lawson (1942), Keith (1965), and Pederson et

al. (1987) found squirrels to be three to five times as abundant in virgin stands as in logged stands. Seasonal variations are due to increases from reproduction and losses due to mortality (Farentinos 1972a), while variations between areas reflect differences in habitat quality (Pederson et al. 1976) or patterns of habitat use (Hall JG 1981, Dodd et al. 1998). J.G. Hall (1981) observed a shifting of areas of use over years on the Kaibab Plateau. Keith (1965) saw a pattern of change in abundance over months and among areas in central Arizona. Dodd et al. (1998) studied eight areas near Flagstaff, representing a diversity of habitat qualities for the Abert's squirrel. Their results presented some possible reasons for variations in squirrel numbers over time and space. Trapping on their study plots documented that squirrel densities, recruitment, and survival differed among areas, but squirrels used all areas and the resources that each contained. Some sites with rich habitats were production, or source, areas. Other sites with marginal habitats produced few young but were attractive to young squirrels because of the production of cones or fungi. In these latter areas, also called sinks, it was difficult for squirrels to survive after pine seeds dispersed and fungi were depleted.

In seven study areas on the Kaibab Plateau in Grand Canyon National Park, J.G. Hall (1981) measured variations among areas and seasons and found abundance varied by two- to three-fold or more among 13 years. He was able to relate decreases in abundance with the severity of the previous winter. J.G. Hall (1981) reported that after a heavy snowfall (200 percent of normal) during the winter of 1972-1973 the Kaibab squirrel population dropped to near zero throughout the Kaibab Plateau. Brown (1984) confirmed the impact of heavy snow that winter. His indices to squirrel numbers for both the Mogollon Rim and the Kaibab Plateau decreased by more than 90 percent in 1973, an El Niño year. The index increased in 1974 and again in 1975 on the Mogollon Rim with light snow cover but remained low on the Kaibab Plateau where snowfall was again heavy. Snow cover was a persuasive factor in reducing squirrel abundance.

Brown (1984) reported that during the hard winter of 1942-1943, with long periods of snow cover, squirrels were in poor condition. Trapping between January and May 1943 produced high mortality. Many squirrels had mange and about 15 percent of the captured squirrels died, apparently from shock. Keith (1965), trapping under similar conditions of heavy snowfall and prolonged snow cover in 1953 and 1954, found squirrels suffered from mange and died after exhibiting symptoms of hypoglycemia when handled.

Shock disease, as described by Green et al. (1939) and Allen (1943), results from low levels of blood sugar. Restricted consumption of foods high in sugars and carbohydrates during cold, snowy periods of high-energy demands could lead to shock disease.

Snow cover probably restricts squirrel movements from nest trees to search for other trees preferred for feeding on inner bark, and thereby limits the quality of their diet. Snow also covers food in the litter on the forest floor, such as fungi and seeds of pine and other plants. However, Golightly and Ohmart (1978) reported squirrels digging up acorns from under 10 to 15 cm of snow. In their nine-year study, Stephenson and Brown (1980) found that annual mortality in winter was correlated with the number of days with snow cover of 10 cm or more. The greatest annual mortality (66 percent) came after 85 days of snow cover. Snow cover explained more than 70 percent of the variation in annual mortality. Squirrel numbers in spring were a function of population levels the previous fall and snow-induced mortality during winter. Snow forced squirrels to rely for food on the inner bark, or phloem, of trees, which is low in protein. On a steady diet of phloem, squirrels lose weight, become stressed, and die at an increased rate. Pederson and Welch (1985) believed protein deficiency was the main cause of winter mortality, especially in winters of deep, continuous snow cover.

Population trend

Long-term trends in Abert's squirrel populations have not been measured or monitored, but they can be deduced from what has happened to their habitat. All available information indicates that logging degrades the quality of Abert's squirrel habitat and reduces squirrel abundance (Trowbridge and Lawson 1942, Keith 1965, Brown 1984, Pederson et al. 1987, Dodd et al. 1998). Squirrel densities in stands of open old growth can be over 100 individuals per km², while in cut-over forests numbers often range only from 5 to 30 individuals per km². Their numbers and recruitment rates in an area decline after the large trees are harvested (Pederson et al. 1976). Studies showed that squirrels fed less in logged plots than in control plots. Squirrels moved from logged stands to unharvested stands. Basal area and canopy closure of trees in a stand have consistently been significantly related to squirrel density (Ratcliff et al. 1975, Patton et al. 1985, Pederson et al. 1987, Dodd et al. 1998). A habitat capability model for Abert's squirrels predicted a 20 percent decline in their numbers from proposed timber sales on 40 areas in one national forest in Arizona (Dodd and Adams 1989). Brown (1984:37) stated, "Conservative logging,

including even such long-accepted practices as selective cutting on a 120-year rotation may be detrimental to a squirrel and tree that coevolved as climax species." These studies imply that squirrels must be less abundant throughout their range today than they were before European settlement.

Early settlers devastated the ponderosa pine forests inhabited by the Abert's squirrel throughout the Southwest. Jack (1900) described conditions after 20 years of logging on over one million acres in the Pikes Peak, Plum Creek, and South Platte Forest Reserves near Denver. Loggers had removed all trees over 30 cm diameter at breast height (dbh) and smaller trees were cut for ties, posts, charcoal, and pulp. Only a few thousand hectares of merchantable timber remained on the reserves at the turn of the century. In addition, fires had burned over 75 percent of the total area of the reserves between settlement and 1900. Crown fires created even-aged stands containing a greater percentage of Douglas-fir trees. Without a doubt, Abert's squirrel habitat was in much better condition in 1850 than in 2000. Squirrel populations in Colorado were undoubtedly more abundant 150 years ago, before ponderosa pine forests were subjected to logging, grazing, and fire suppression. In Colorado, the catastrophic fires during the last half of the 19th century had as great an impact as logging on montane forests of ponderosa pine and Douglas-fir (Veblen and Lorenz 1991). Forest structure (age, sizes, and spatial arrangement) was completely altered. Humans caused repeated and frequent disturbances and changes in forest stands after 1859. Conditions generally were at their worst in 1900 (Cooper 1960). The USFS was established in 1905, and slowly greater control was attained over use of resources within the reserves.

The Medicine Bow Reserve was also established in 1905 and consisted of the northern two-thirds of the Front Range (Gilpin, Boulder, and Larimer Counties). Boulder County forests were heavily logged during the mining boom of the 1860's. In some areas, most of the timber was removed (Veblen and Lorenz 1991). A large percentage of Rocky Mountain National Park was logged before the Park was established in 1915. In 1900, a single fire burned 29,000 ha at Eldora. Some fires were set by miners for no other reason than to expose parent material for examination for minerals. Thereafter, there was little logging in the Front Range of Colorado, and since the 1960's timber harvest has practically ceased except for fuels reduction, firewood, and insect control (Veblen and Lorenz 1991).

In Arizona, logging began in the late 1850's in the isolated southern mountain ranges (Matheny 1975).

After 1882, large areas of ponderosa pine were clear cut-near Flagstaff (Coconino National Forest), and fires caused by careless logging and embers from locomotive fire boxes were common in the 1880's. With control of forest reserves by the federal government, harvests became more restricted, and in some cases limited to trees < 40 cm dbh. The Arizona timber industry found only limited markets in Arizona, while in California their lumber could not compete in quality or price with lumber from the Pacific Northwest. Logging intensity increased greatly during the 1980's (Brown 1984, Dodd and Adams 1989), and many ancient stands of ponderosa pine were removed at that time.

A vegetation structure change analysis by Covington and Moore (1994) in Arizona found that after logging in the late 1800's, conditions changed and a grass-forb community developed with few trees (none of a size to be classified as timber). This community was replaced in most areas over time by a pine seedling-dominated landscape, which was followed in due course by mature timber and finally old growth over dense saplings by the 1960's. Habitat conditions for wildlife changed from one favoring foraging ungulates to one favoring animals that prefer higher tree density, including Abert's squirrels. Activities and influences of European settlers were not uniform over the range of the squirrel. Even logging intensity varied over large areas of forest, within ranger districts and across national forests. These different intensities of land use over the range of ponderosa pine created a mosaic of habitat conditions for Abert's squirrels. As a result, squirrel abundance and habitat capability varied spatially, depending on local forest conditions. Their populations probably decreased sharply after European settlement, remained low as forests re-established themselves, and gradually increased to their present levels as older trees became established.

Activity

Abert's squirrels are strictly diurnal; they seldom are active before sunrise and usually return to their nests before sunset (Keith 1965). Halloran (1993) recorded squirrels leaving nests 92 times in the morning; the mean departure time was 0.8 h after sunrise. She measured entrance into nests in the afternoon 93 times and found the mean time was 3.0 h before sunset. Abert's squirrels are active every day and during all seasons, even in inclement weather. Halloran (1993) found the squirrels were out of their nests an average of 10.65 h in summer and 6.3 h in winter. There appear

to be two major periods of activity: one in the early part of the day and another in the late afternoon (J.G. Hall 1981). Their movements are reduced after snowstorms (Keith 1965, Golightly and Ohmart 1978). Squirrels spend most of each day foraging for food, often feeding on the ground. They rest primarily in trees. During two days that J.G. Hall (1981) tracked a female Kaibab squirrel, she spent about 50 percent of her time on the ground and 50 percent in trees. The individual rested about 60 percent of her time in the trees, but only during 10 percent of the time she spent on the ground.

The squirrels return to nests during the day, especially during rainstorms and high winds (Golightly and Ohmart 1978, Hall JG 1981). Using radio-collared animals for study, Patton (1975b) found three squirrels used 2, 5, and 6 nests over a period of one month. In another radio-telemetry study, Lema et al. (1999) documented multiple occupancy of nests. Of 28 squirrels, 53 percent shared nests at least once between November and the following May. Likewise, 59 percent were found in trees where other squirrels were present. This contrasts with the observations of Farentinos (1974). He referred to the squirrel's behavior as semi-solitary and usually found individuals more than 30 m apart, a distance greater than that across the crown of most ponderosa pines. These observations are not necessarily contradictory, as the closeness of squirrels to each other may vary with their population density and with their abundance in an area. For example, several authors have commented on unusual concentrations of squirrels in areas of good cone crops. Farentinos (1974) described a variety of olfactory, tactile, auditory, and visual cues used by the squirrels in communication.

Halloran (1993) documented that male and female activity patterns were very similar, both in type and frequency (**Table 2**). Her observations were based on hours squirrels spent on diurnal activities between May 1989 and October 1991.

In fall, the squirrels rested less and traveled more than during the rest of the year (Halloran 1993). In spring, they exhibited more social interactions than in other seasons, and behavior that centered at the nest was much higher in summer than during the rest of the year. Time spent on other activities varied with the types of foods eaten. For instance, they spent more time in activities near the nest when eating cones than when eating inner bark, probably because of the difference in the time necessary to feed to satiation on the two foods.

Table 2. Activity patterns of male and female Abert's squirrels.

<u>Hours spent in activity</u>		
<u>Activity</u>	<u>Females</u>	<u>Males</u>
Feeding	12.5	18.3
Resting	10.8	13.2
Traveling	12.1	16.1
Grooming	2.8	3.6
Nest/Social	5.7	5.4

Movements

Resident Abert's squirrels do not move long distances. Maximum movements recorded for juvenile squirrels during fall dispersal were 840, 870, 1290, and 1440 m (Farentinos 1972b). Movements reported for males during the breeding season ranged up to 1.5 km as they moved to locate females in estrus. These movements were reflected in larger home ranges for males in the breeding season (20.8 ha) than at other times (7.5 ha) (Farentinos 1979). Halloran (1993) also found male home ranges were larger in the breeding season, but Lema (2001) did not. Several workers have implied that there is a temporal and spatial "shuffling" of the squirrel population as individuals emigrate or temporarily move to take advantage of nearby food resources (Keith 1965, Hall JG 1981, Dodd et al. 1998).

Most workers using radio-telemetry or systematic observations of marked animals calculated similar home ranges for males (4 to 21 ha) and females (4 to 17 ha). Home ranges varied much more among studies than between sexes (Patton 1975b, Farentinos 1979, Halloran 1993, Lema 2001).

Home ranges varied among studies, and workers tested effects of seasons, diets, habitats, and logging. Farentinos (1979) found home ranges were larger in winter, while Lema (2001) found them to be smaller in winter, and Halloran (1993) found no differences with seasons and diets. J.G. Hall (1981) noted relatively small home ranges (4.4 ha for males and 2.5 ha for females) in the more pristine stands of ponderosa pine on the Kaibab Plateau. Patton (1985) measured an increase in home range size from 27.2 ha to 49.8 ha following logging on his study area. Likewise, Lema (2001) found squirrel home ranges to be larger in poorer habitat. Most workers found that home ranges of individual squirrels overlapped. Halloran (1993) observed this to occur in 98 percent of the individuals. Keith (1965) found that home ranges of individuals shifted, or "floated", over

larger areas with time (months). These observations may reflect movements noted by other workers as squirrels sought to take advantage of temporarily available food resources, such as cone crops (Dodd et al. 1998).

Habitat

Abert's squirrels live in forests of ponderosa pine that often are rather pure stands with minimal understory. Ponderosa pine forests occur over more than 11 million acres in Arizona, New Mexico, Utah, and Colorado (Schubert 1974). The pine extends throughout Region 2, but Abert's squirrels occur in Region 2 only in Colorado and extreme southern Wyoming. In Colorado, some forests are a mixture of Douglas-fir and ponderosa pine. Both the Abert's squirrel and the pine squirrel (*Tamiasciurus hudsonicus*) occur in these mixed stands. However, Abert's squirrels most often occur at lower elevations, where ponderosa pine is dominant. Pine squirrels, on the other hand, frequent higher elevations where Douglas-fir is mixed with spruce-fir forests (Ferner 1974). At lower elevations, and especially in Arizona, stands of ponderosa pine can be mixed with scattered Gambel oaks (*Quercus gambelii*). The squirrels eat acorns of Gambel oak and will nest in the oak. Stephenson (1975) felt Gambel oaks were important to the squirrel, but unreliable as a source of food because they do not produce acorn crops every year. On the Kaibab Plateau, squirrels ate both the inner bark and the seeds of pinyon pine and occasionally used the inner bark of Douglas-fir for food (Ratcliff et al. 1975).

Some authors (McKee 1941, Keith 1965, Dodd et al. 1998) have stressed the dependence of the Abert's squirrel on ponderosa pine, and in a general sense that is true. In New Mexico, however, the squirrels are often found in mixed forests (Finley et al. 1975), and in Mexico they live in forests composed of ponderosa pine, Apache pine (*Pinus englemannii*), and Chihuahua pine (*Pinus leiophylla*). Hutton et al. (2003) reported 498 sightings of Abert's squirrels over eight years in

spruce-fir associations on Mt. Graham in southern Arizona. The squirrels were observed feeding, basking, chasing, and playing. They built nests in the area, and mating chases and lactating females were seen. Many squirrels appeared to be residents. These records are exceptional and probably represent a unique situation. Abert's squirrels were introduced on Mt. Graham in the 1940's. They may have filled the limited ponderosa pine habitat after their introduction and then adapted to use spruce-fir forests at higher elevations.

The quality of original ponderosa pine forests varied over the range of the species (Schubert 1974). Features of ponderosa pine forests change with elevation, slope exposure, and soil conditions. Pines are more vigorous where soils are well-developed and temperature and precipitation are the highest. On drier, south-facing slopes, pines are the dominant species, and trees are more widely spaced. On north-facing slopes, forests are often denser mixed stands of Douglas-fir and ponderosa pine. Ponderosa pines usually grow at elevations between 6000 ft and 8500 ft, but elevation of stands varies with latitude. They grow best at elevations of 7000 ft to 7800 ft (Schubert 1974), where the best balance between high moisture and high temperature is found. Stands are less vigorous at higher (colder) and lower (drier) elevations.

Over 1 million ha of ponderosa pine occur in Colorado (Schubert 1974, Benson and Green 1987). After European settlement, intense logging, grazing, and fire suppression greatly changed the original conditions of ponderosa pine forests. The first commercial logging in Colorado was in 1860 (Schubert 1974). Tens of thousands of hectares were clear-cut for lumber, mine props, smelter fuels, and firewood, and many sites still are either poorly stocked or dominated by "doghair" stands of overly dense, even-aged trees.

Natural differences in stands of ponderosa pine created variations in the quality of original habitats for Abert's squirrels. In addition, some features of ponderosa pine physiology and ecology currently are being influenced by climate change (Joyce et al. 1990, Waring and Law 2001). Human activities have increased differences in pine stands and the relative quality of squirrel habitat conditions. Most often human activities degraded conditions for squirrels. We now know what the ponderosa pine forests were like originally (Cooper 1960, Allen 1998, Kaufmann et al. 2001), how they changed with human use (Jack 1900, Veblen and Lorenz 1991, Covington and Moore 1994, Huffman et al. 2001), how they can be restored (Sackett et al. 1994, Mast et al. 1999, Covington 2000,

Kaufmann et al. 2001), and what features in the stands are most beneficial to Abert's squirrels (Patton 1977, Patton 1984, Pederson et al. 1987, States et al. 1988, Elson 1999).

High quality habitat for Abert's squirrels consists of an open forest with 150 to 250 trees per acre of various sizes, but mostly >30 cm dbh. Stands with trees clustered in small, even-aged groups best provide for the life requirements of squirrels (Patton 1984, Pederson et al. 1987). The denser "blackjack" stands (younger trees with dark bark) provide greatest production of truffles (States 1985) and effective cover for protection of squirrels from aerial predators along travel routes. Stands should contain nest trees of about 40 cm dbh within several clusters on each acre (Patton 1975a). Stands must have an abundance of vigorous trees from 25 cm to 75 cm dbh to provide a nutritious source of inner bark for squirrels in winter (Allred and Gaud 1994a). In addition, scattered larger trees of 60 cm to 90 cm dbh should be present, as they produce the most cones and seeds (Larson and Schubert 1970).

Large pine trees are used to a greater extent than would be expected by their availability, suggesting clusters of larger pines provide greatest benefits to squirrels (Lema 2001). Squirrels will use most trees in a heterogeneous stand for one or more of their life requirements (States et al. 1988). Corridors with interlocking canopies must be maintained between clusters to facilitate movement, enable safe access to all resources, and prevent overuse of local trees near nests. Differences in home ranges found among studies may primarily reflect quality of squirrel habitats in the study areas. Larger home ranges for individuals may reflect the need of squirrels to travel greater distances to fulfill requirements for their seasonal food habits.

Food habits

Numerous assessments of Abert's squirrel food habits have been conducted. Some confusion has resulted from the conflicting findings of these studies. What soon becomes apparent, however, is that the studies are not contradictory but that the results reflect differences in habitats and food availability in study areas. The availability of different foods varies among seasons, years, and habitats. Abert's squirrels do not store or cache food for future use (Bailey 1932, Keith 1965, Halloran 1993). Instead, they select from what is available each day.

Preferred foods are pine seeds and false truffles (hypogeous fungi), which are relatively high in calories

and protein (Pederson et al. 1987). Squirrels feed on apical buds and inner bark of pine twigs when other foods are unavailable (Keith 1965); these foods are lower in quality and are not favorite foods. Squirrels supplement their diet with staminate cones, mushrooms, and miscellaneous items from the forest floor. Specifics of feeding behavior have been reported (Keith 1965, Stephenson 1975, Hall JG 1981, Pederson et al. 1987, States et al. 1988, Austin 1990). Most squirrels live in ponderosa pine habitats and depend on ponderosa pine for their foods. One important exception is the acorns of Gambel oaks, a high quality food that are eaten whenever available (Reynolds 1966). Studies clearly show that the relative consumption of different foods varies considerably among years and habitats.

Keith (1965) observed the squirrels' feeding activities and estimated that more than 50 percent of their diet was pine seeds from June to October, and 50 percent was inner bark from December to May. They ate mushrooms in August, but seldom were seen digging for truffles. In contrast, Stephenson (1975) examined the stomach contents of 135 Abert's squirrels over a 14 - month period. Fungi was the dominant food eaten (52 to 92 percent) each month between July and October. From December to April, squirrels ate inner bark (41 to 52 percent) and terminal buds (44 to 72 percent). Pine seed averaged only 1.9 percent of diet, with a high of 21.9 percent in August.

Pederson et al. (1987) used feeding evidence (pine twigs, cone scales, and fungi digs) to study food habits in several months over two years. Inner bark was taken at all seasons of the year, rather than only during winter as found in some studies. Use of inner bark was lowest (21 to 76 percent) in 1977, when with a very large cone crop, 40 percent of the squirrels' diet was pine seed. In 1978, 100 percent of the squirrels' diet was inner bark throughout the year, except in April and July when some fungi and pine seeds were eaten.

Halloran (1993) identified the dominant food items of radio-collared squirrels between 1989 and 1991 in Colorado (**Table 3**). Dominant food items were pine cones (both male and female cones), inner bark, other tree foods, and items on the ground (fallen seeds, mushrooms, and hypogeous fungi). Her results provide a good illustration of the changes in diet that occur with changing availability of food.

States et al. (1988) collected data on the food habits of squirrels from signs of feeding activities and focal animal sampling in Arizona (**Table 4**). The availability of squirrel foods varied annually over a five-year period. Feeding activities were recorded from June 1986 to January 1988 (**Table 5**). The proportion of different foods eaten varied considerably among seasons.

Table 3. Food items of radio-collared Abert's squirrels between 1989 and 1991 in Colorado (Source: Halloran 1993).

Food Item	1989									1990									1991									
	M	J	J	A	S	O	N	D		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Cones	O		O	O	O									O													O	O
Inner Bark																				O	O	O	O	O	O			
Other Tree Foods																O		O	O									
Ground Items		O				O	O			O	O	O		O		O											O	

Table 4. Estimated food availability for Abert's squirrels (Source: States et al. 1988).

Year	Truffles (kg/ha)	Cones / Tree	Acorns / Tree	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	20	Very high
1987	0.65	10	10	Moderate

Table 5. Diet of Abert's squirrels by seasons (Source: States et al. 1988).

Food	Summer	Fall	Winter	Spring
Pine Seed	66	62	3	0
Truffles	9	24	1	2
Inner bark	10	11	83	24
Apical buds	14	1	12	63
Staminate cones	0	0	0	9
Other	1	2	1	2

Most sources of food (phloem, mistletoe, truffles, apical buds, and staminate cones) have similar caloric contents of about 5 kilocalories per gram (Austin 1990), but pine seeds offer more energy (over 6 kilocalories per gram) and fungi somewhat less (< 4.5 kilocalories per gram). Most foods are low in protein (< 10 percent), but pine seed and mushrooms and truffles contain higher amounts of protein (50 and 20 percent, respectively). However, Cork and Kenagy (1989) stressed that most of the protein in truffles may be indigestible. Austin (1990) corroborated that squirrels increased their use of fungi in years when seed crops were low or absent. He also documented that females took more high-energy foods in summer than males, but neither sex chose foods based only on their energy and protein content. For instance, Austin (1990) believed that squirrels often continued to eat phloem in the summer and fall because it contained more calcium than any other food and helped them meet their required calcium:phosphorus ratios.

When eating seeds of ponderosa pine, squirrels drop cone bracts and the cores of the cones to the ground. To get phloem, squirrels clip terminal needle bundles and cut off short lengths (7 to 10 cm) of twigs. They remove the outer bark from the twig and then scrape off the thin, moist layer of inner bark. The needle bundles and the peeled twigs (whitish sticks) are dropped to the ground. Squirrels may clip 10 to 1000 or more twigs from a tree, but there seldom are more than 1000 squirrel clippings under a single ponderosa pine

tree. Counts of more than 1200 were reported under each of two trees by Keith (1965). If that number was a record, it did not stand long. Dale Jones (personal communication) related that his family counted 1911 clippings under a tree in the Sandia Mountains of New Mexico in March 1971.

Ffolliott and Patton (1978) collected clippings, when they were present, under 1,390 trees >18 cm dbh for four years. Squirrels used 65 percent of these trees. Of the trees used, 56 percent were clipped in only one year, 29 percent were used in two years. Only 13 trees were used for three years, and just two trees were used in all four years. For trees with more than 10 twigs removed, a pattern of rotation of use was evident. Squirrels did not usually return to a tree the next year, but returned after two to three years. Gaud et al. (1993) collected twigs every six months for 3.5 years under 2,765 trees in Arizona. During that time, squirrels removed >40 twigs from only 393 of the trees. Seventy-six percent of those 393 trees had >40 clippings removed during only one of the seven 6-month periods, and only 5 percent of those trees were clipped during four periods. Findings of these two studies indicate that squirrels selected certain trees for feeding on inner bark, but they found most trees desirable only in one year. Choice is probably made on the basis of taste, as many trees have just several (two to ten) twigs removed, suggesting that their palatability was tested and found to be unacceptable.

Such patterns of inner bark use, coupled with variations in use of preferred trees, suggest that palatability of phloem may vary among trees and within an individual tree over time. The time frame involved in the repeated use of individual trees suggests palatability could be related to the production of cone crops by the trees. Ponderosa pines usually produce a few cones every year, but large crops are produced only every three to five years (Schubert 1974). If squirrels prefer inner bark from a tree in one year, but do not heavily use the tree for several years thereafter, it may be due to variations in the taste or quality of the phloem. As trees store nutrients in their inner bark, sugar content of phloem may increase during years when cones are not produced, but after cones are produced, sugar levels in phloem may fall (Keith 1965).

Several studies have examined the quality of phloem in attempts to identify why squirrels select some trees and not others for obtaining inner bark. The definition of selected trees, or “feed trees” has varied among studies, as have the characteristics found to be used by squirrels to select trees. Allred and Gaud (1994) examined 668 feed trees and did not find any visual characteristics by which they could be identified except size; the trees used were larger and averaged about 31 cm dbh. Capretta and Farentinos (1979) showed that feed trees contained relatively high concentrations of glucose, fructose, and especially sucrose. Farentinos et al. (1981) found that squirrels selected for low amounts of monoterpenes, especially α -pinene, in twig tissue. Pederson and Welch (1985) failed to find any relationship between monoterpenoid levels and selection of trees for feeding.

Zhang and States (1991) sampled trees with a four-year record of squirrel use and analyzed inner bark from 14 pairs of feed and non-feed tree for 14 terpenes, soluble sugars, and moisture content. They found higher levels of three terpenes in non-feed trees, but not higher levels of α -pinene, as found by Farentinos et al. (1981). Soluble sugar levels in trees were quite variable (4 to 11 percent), but mean levels for feed and non-feed trees were similar. Snyder (1992) monitored squirrel use of trees for five years and analyzed phloem from target and non-target trees on two study areas. Analyses showed significantly lower oleoresin flow rates and levels of β -pinene and β -phellandrene in the xylem of target trees, along with more nonstructural carbohydrates and sodium and less iron and mercury in the phloem of the favored trees. Higher levels of nonstructural carbohydrates were of interest as they are an index to available energy. Studies of Thomas (1979) suggest that sugars might be involved in tree selection in concert

with other factors affecting taste and nutrition. She found feed trees had higher ratios of sugars to non-sugar substances; concentrations did not vary, only ratios.

Recent studies of foraging preferences of black bears by Kimball et al. (1998) showed that bears maximize intake of carbohydrates and minimize intake of terpenes in selecting Douglas-fir trees for feeding when eating inner bark. Free-ranging bears, offered choices of artificial diets, selected a low-terpene diet rather than a high-terpene diet when each had the same carbohydrate content. Likewise, bears preferred a high-carbohydrate diet to a low-carbohydrate diet with identical terpene content. It was thought these choices were the result of post-ingestive feedback mechanisms. Kimball et al. (1998) showed that there was a cost to digesting terpenes and benefits from eating sugars, and bears maximized sugar consumption while minimizing terpene consumption. In Douglas-firs, the sugar content of the inner bark was found to vary with silvicultural practices. For instance, thinning of stands increased sugar content in trees.

The use of individual feed trees by squirrels varies among years (Ffolliott and Patton 1978, Gaud et al. 1993) and is most logically related to variations in either sugar or terpene content (or their ratio) in inner bark, as proposed by J.G. Hall (1981). Studies have shown that the terpene content of xylem and phloem in individual trees is genetically fixed (see reviews in Snyder 1992 and 1993). Variations in the sugar content of inner bark over time have not been studied, but may be related to the production of pine seeds.

Ponderosa pine cone crops vary annually, but every three to five years a good crop is produced (Pearson 1950, Larson and Schubert 1970, Snyder 1993). Large cone crops were recorded on the Coconino and Kaibab National Forests in Arizona in 1908, 1913, 1918, 1927, 1931, 1936, 1942, 1945, 1956, 1960, 1965, 1968, and 1971 (Larson and Schubert 1970, Schubert 1974). In Colorado, Roeser (1941) counted cones produced in a 0.2 ha stand between 1926 and 1934. By years, cone production was 1280, 25, 514, 0, 2998, 41, 2, 733, and 13. Thus, cone production varies annually in a stand, and even over a forest. These ups and downs in cone production within areas require a synchrony of causation and responses in individual trees. Variations among years suggest that a common factor may control cone production in stands and over larger areas. Maguire (1956) gathered data over 21 years in California and was able to show that high spring temperatures resulted in an abundance of spring flowers in pines one year later and an excellent potential for a good cone crop in the

third year. Since such a long period is required for a cone crop to develop, other factors could intervene and alter ultimate cone production. Finally, for reasons not known, cone production varies among individual trees (Schubert 1974).

Truffle production appears to be positively correlated with increased density of canopy cover (States 1985, States and Gaud 1997). Biomass of the fungi is greatest under stands of intermediate-aged pines that have the greatest canopy cover (blackjack stands). Production is positively related to rainfall and is dependent on warm temperatures during the growing season (States and Gaud 1997).

Breeding biology

It is not known at what age Abert's squirrels breed nor what proportion of their population breeds each year. Flyger and Gates (1982a) believed they probably bred first at 10 to 12 months and that is reasonable, as other species of squirrels first breed at that age.

Abert's squirrels were reported to mate in May (Keith 1965), in April and May (Farentinos 1972b), and between mid-February and early June (Halloran 1993). Breeding was reported by others to occur between April and June and to peak in May (Mearns 1907, Stephenson 1972). Testes can reach maximum size in January, but males may need high-quality foods for full development of accessory organs (Stephenson 1975). Austin (1990) found females became energy deficient in winter and required foods of higher quality than inner bark before breeding. Brown (1984) noted that breeding coincided with the opening of staminate flowers. However, their opening is controlled by temperature and is not reported to occur until late May and early June (Schubert 1974). Stephenson (1975) believed that the initiation of reproduction was correlated with snowmelt, but in Arizona he reported litters in August, indicating that breeding was well after snowmelt. There clearly are variations among years and locations in the initiation of breeding, but peak mating activity is usually in May (Mearns 1907, Keith 1965, Stephenson 1975).

Female Abert's squirrels remain in estrus for < 18 h (Brown 1984). Females are followed by troops of males while they are receptive and may mate with several males (Rice 1957, Keith, 1965, Farentinos 1972b, Brown 1984). Farentinos (1972) gave a thorough description of the social interactions during mating chases. Gestation was reported as 40 days (Keith 1965) to 46 days (Farentinos 1972b, Stephenson 1975) and litter size from 2.9 to 3.4. Young remained in nests

for seven to nine weeks and emerged in August (Keith 1965). For 12 litters, Halloran (1993) found the average time between mating and the emergence of young from the nest was 15 weeks. At emergence, litter size ranged between one and five young, with an average of 2.9, and females that breed later in the season tend to have larger litters. Females may move young from one nest to another while they are small (Keith 1965, Hall JG 1981, Halloran 1993), and the female and young remain as a family unit into November (Keith 1965).

Hall and Kelson (1959) reported that Abert's squirrels might have more than one litter each year in the southern part of their range. Stephenson (1978) found litters in August in Arizona and suggested that some females did not breed every year. Apparently environmental factors can influence if and when Abert's squirrels breed. Dodd (*in litt*) documented that in central Arizona, during the drought year of 2000, most female squirrels (153 out of 160) on his study areas completely failed to breed. Pogany and Allred (1995) and Pogany et al. (1998) discovered that Abert's squirrels are capable of two reproductive periods in one year. They found three females with embryos in March and a lactating female in March. Other females had embryos in June and July, and one female was lactating in August. Males are capable of spermatogenesis most of the year, as they maintain a residual meiotic activity that permits spermatogenesis at any time females enter estrus (Rose 1997, Pogany et al. 1998).

Guzman (1997) examined female squirrels and found follicular development peaked in February and again between July and September. She believed that this dual peak indicated separate periods of gestation for females, but the different times of follicular development could represent females of different ages (yearlings and adults). A dual peak in estrus could explain the rare observations of multiple litters in one year. Cahalane (1947) reported three to four young were born in May, with some litters found between May and October. Hall and Kelson (1959) claimed that three to four young were usually born in April or May, with there often being more than one litter.

Abert's squirrels build, maintain, and use nests throughout the year. Halloran (1993) observed only females building nests. In pine forests, the nests are constructed of pine twigs, usually 2 to 10 cm in length. They are large, 30 to 100 cm in diameter (Keith 1965, Pederson et al. 1976), and the insides are lined with shredded grasses and bark when young are present (Keith 1965, Hall JG 1981). The most common location reported for nests is against the bole (Patton 1975b),

30 to 50 ft above the ground (Patton 1975b), and on the south (Keith 1965, Farentinos 1972), southeast (Halloran 1993), or south to east side (Snyder and Linhart 1994) of the nest tree. Patton (1975b), Hall JG (1981), and Halloran (1993) presented detailed descriptions of the nest trees. Snyder and Linhart (1994) also described nest tree characteristics, including the chemical composition of phloem.

Demography

Reliable values for many of the factors that influence the population dynamics of the Abert's squirrel have not been definitively established. However, even with variation among studies, sufficient information exists to consider the balance between natality and mortality and the principal factors affecting abundance.

There do not appear to be any concerns about genetic factors that might negatively influence the squirrel. Squirrel populations are fragmented, and some groups are small. However, the squirrel has demonstrated an ability to thrive in sparse populations and to emigrate considerable distances to successfully establish new stable populations (Davis and Brown 1989).

Sex ratios reported for the Abert's squirrel are not consistent. Brown (1984) tallied sex-ratio data of Keith (1965), Farentinos (1972), and Pederson (1976) for 853 animals and found 56.7 percent were males. In contrast, Mearns (1907), Stephenson (1975), and Dodd et al. (1998) examined a total of 614 squirrels and found that 54 percent were females. Combining these data gives a male to female ratio of 52:48. A higher winter mortality of females has been suggested for Abert's squirrels, especially in winters of heavy snowfall (Lema 2001).

Social interactions among Abert's squirrels are not known to influence their breeding success and survival. The squirrels are not territorial and do not defend feeding or breeding areas. Females will defend nests with young, however. An overlap among home ranges is common, especially when squirrel density is high (Halloran 1993, Lema 2001). Halloran (1993) found that 98 percent of the space used by a squirrel overlapped areas used by other squirrels. The home range of males is largest during the breeding season (Farentinos 1972b, Halloran 1993). Home range size also varies with habitat quality, snow cover, and food supplies (Keith 1965). Halloran (1993) reported that the size of home ranges of both sexes changed with seasons and increased when cone crops were poor.

Recruitment has usually been measured in Abert's squirrel populations as the percent of young of the year in the fall population. Farentinos (1972b) found that 50 to 63 percent of the squirrel population in the fall consisted of young on his study area in Colorado. Stephenson and Brown (1980) reported that recruitment in Arizona averaged 45 percent (37 to 56 percent) between 1969 and 1978 (1.6 young per female, assuming an adult sex ratio of 1:1). Brown (1969) had determined a similar value (49 percent) for average recruitment between 1962 and 1968 in the same area of Arizona. Both studies compared numbers of young and adults (based on closure of the epiphyseal cartilage in a foreleg, Carson 1961) in hunters' bags in October and November.

Of 35 young produced in one spring in Colorado, only five survived to the following breeding season (Halloran 1993). In May 1971, Farentinos (1972b) recaptured seven adults first marked in December 1969, when they were at least 1.5 years old. Therefore, in 1971 the squirrels were at least three years old.

Survival rates calculated from trapping during four periods over 16 months on seven study plots in Arizona varied between 0.68 and 0.86, with an average of 0.78, and did not suggest any difference due to habitat quality (Dodd et al. 1998). Survivorship was significantly lower between January and April (0.63) than during other periods (0.81, 0.81, 0.91) and was highest in April through August (0.91). Lema (2001) followed the survival of 50 squirrels fitted with radio transmitters for 19 months on two of the same study areas used by Dodd et al (1998), Fort Tuthill (poor habitat) and Marshall Mesa (good habitat). She, too, could not show a significant difference in survival due to habitat quality (0.51 and 0.61, respectively). Likewise, even though calculated survival (Kaplan-Meier survivorship estimator) was 0.81 for adult males vs. 0.52 for adult females, and 0.74 for adults vs. 0.48 for young, differences between sexes and ages were not statistically significant.

Mortality is largely due to the following five factors, listed in their order of importance: 1) a decrease in the availability of high quality foods due to logging (Keith 1965, Patton et al. 1985, Pederson et al. 1987); 2) persistent winter snow cover (Stephenson and Brown 1980, Brown 1984), responsible for reducing food availability (Hall JG 1981, States et al. 1988) and resulting in a lower nutritional state (Patton 1974, Brown 1984, Austin 1990), that can cause shock disease (Keith 1965, Brown 1980), and/or death; 3) predation (Lema 2001, Sieg 2002), especially by northern goshawks

(Reynolds 1963, Reynolds et al. 1992); 4) hunting harvest, estimated in Colorado to be $1,312 \pm 44$ squirrels during the 2000-2001 season (Lyn Stevens, Colorado Division of Wildlife) and in Arizona to be 82,370 animals in 2001 (Harvest has varied annually in Arizona from 25,231 in 1962 to 106,875 in 1978. These numbers include all squirrels, the majority of which were Abert's squirrels) (Norris Dodd, personal communication); and 5) highway mortality (Brown 1984).

The lack of a relationship between annual recruitment (an almost constant value) and changes in population levels (which vary widely) lead Stephenson and Brown (1980) to conclude that population fluctuations were primarily caused by differences in annual mortality, and especially that related to persistent snow cover. Two winters, those of 1918-1919 and 1972-1973, were widely reported as ones with heavy snowfall and high squirrel mortality. The heavy snows may have resulted from El Niño events that occurred during both of these periods (Schreiber and Burger 2001:197). Rasmussen (1941:257) cited a report by the supervisor of the Kaibab National Forest: "Squirrels seem to have suffered considerable loss last winter (1918-19)---" J.G. Hall (1981) referred to 1973 as the most disastrous year for squirrels during his 15-year study on the plateau. By summer, the Kaibab population of squirrels was near zero. During the winter of 1972-1973, over 500 cm of snow fell at the Jacob Lake weather station on the Kaibab Plateau. Ratcliff et al. (1975) conducted a trapping study in a 2400 ha stand of virgin ponderosa pine in 1973 on the Kaibab National Forest and found it took an average of 224 trap-days to catch each squirrel (33 squirrels caught in 7,380 trap-days). In other studies, it required only 11 to 73 trap-days to catch each squirrel, and these studies were conducted in all kinds of forest and weather conditions, even in heavily logged stands and during periods of heavy snowfall. Squirrel populations on the North Kaibab Plateau in 1973 evidently were extremely low, the lowest of any reported in the literature.

Stephenson and Brown (1980) calculated Abert's squirrel mortality rates in central Arizona from 1970 to 1978. Mortality for that period averaged 0.41 percent and varied annually from 0.22 to 66.00 percent. Annual mortality rates were significantly correlated with the number of days with snow cover of 10 cm or more during the previous winter, and snow cover accounted for more than 70 percent of the variance in annual mortality. The highest mortality rate for squirrels was 66 percent in 1973. The previous winter (1972-1973), during an El Niño event, >10 cm of snow covered the

ground in central Arizona for 85 days compared to 14 to 49 days for other winters between 1970 and 1978.

Kufeld (1966) reported fall recruitment of young and an index to population abundance in central Arizona between 1962 and 1965. Young constituted between 48 to 55 percent of the fall population during the four years, but population indices varied seven-fold (41, 20, 33, 6) during the same four years. He concluded that factors other than breeding success were influencing fall populations. He did not know that the lowest index to squirrel numbers that he obtained was during an El Niño event (1965).

In central Arizona, reproductive performance and mortality were calculated from the proportion of young animals shot by hunters on the Mogollon Rim in October and November during 18 years. Apparently squirrels reproduced successfully each year as the fall population consistently contained about 45 percent young each year. In 1981, the last year of this study, the percentage of young decreased to 21 percent, and Brown (1984) questioned why this occurred after 18 years of recruitment between 38 percent and 56 percent. Recent findings by Dodd et al. (1998) suggest that low recruitment in 1981 might have been caused by low precipitation that year.

Dodd et al. (1998) used capture-recapture trapping (in January, April, and August) to determine squirrel densities, survival rates, recruitment, and fitness on eight study areas (55 to 72 ha) in central Arizona over two years (1996 and 1997). Study areas were selected to provide a range in forest structural conditions. They found variations in squirrel densities among study areas in each of the six trapping periods (3 to 64 squirrels per plot) and seasonally within each study area (lowest in January and highest in August), but the average annual density of squirrels on each area remained constant between years. Squirrel survival rates were calculated for most plots during four periods over two years, and they varied from 0.42 to 0.97. In the winter of 1997-1998, increased mortality apparently reduced survivorship on some plots. Squirrel losses may have been related to heavy snows and persistent snow cover on the ground, as snowfall that winter (338.3 cm) was the 13th highest ever recorded in central Arizona. Heavy snows fell during nine storms, and depths of >10 cm persisted for 61 to 74 days.

Average recruitment rates for all study areas (0.02 to 0.33 juveniles per adult female) and for both years (0.15 and 0.13 juveniles per adult female) appeared very

low, perhaps reflecting the fact that they were based on the percentage of young squirrels in the January population rather than in the fall population. Fitness values were also low for the study plots (Dodd et al. 1998). It is possible that recruitment rates and fitness values calculated in this study were actually valid and were low because reproductive success in squirrels was minimal in 1996 and 1997. Those were drought years and had the 4th and 7th lowest precipitation, respectively, on record at Bellemont, Arizona, a station in the area of study plots (Dodd et al. 1998).

A later study was conducted by Dodd et al. (2003) on nine larger plots (each ~500 ha) in the same area of Arizona between 1999 and 2001. In 2000, during the driest winter and spring ever recorded for Arizona (42 percent of normal precipitation), they found that only seven out of 160 adult females even tried to reproduce (mean recruitment was 0.04 juveniles per adult female on the nine areas). Conversely, with 75 percent of normal precipitation in 1999 and 90 percent in 2001, recruitment was 0.83 and 1.79, respectively. Clearly, features of the weather, including both heavy winter snowfall and winter and spring drought, can radically alter reproductive success in Abert's squirrels.

Goldman (1928) reported that there were known cases of hawks killing Kaibab squirrels. Reynolds (1963) first reported a northern goshawk (*Accipiter gentilis atricapillus*) taking an Abert's squirrel near Beaverhead, Arizona. Keith (1965) in a one-year study on the Fort Valley Experimental Forest near Flagstaff found remains of four squirrels killed by hawks; in addition he observed an attack by a goshawk on a breeding group. Based on remains under goshawk nests, Bailey and Niedrach (1965) concluded that Abert's squirrels provided most of the food eaten by young northern goshawks, while Reynolds et al. (1992) reported that tassel-eared squirrels made up more than 10 percent of the biomass in their diet. J.G. Hall (1981), who studied Kaibab squirrels during summers from 1960 to 1974, observed a number of attacks on squirrels by predators, including hawks, a coyote, and a bobcat, but none were successful. During a 21-month study in Colorado, Farentinos (1972a) found skulls of Abert's squirrels in castings of great horned owls (*Bubo virginianus*), observed five unsuccessful attacks by goshawks on squirrels, and twice saw goshawks eating squirrels.

Reynolds et al. (1992) considered Abert's squirrels to be a key prey species for northern goshawks in the Southwest. Dodd et al. (1988) felt Abert's squirrels were especially important to goshawks in winter when most other prey species either migrate or hibernate.

Several workers concluded Abert's squirrels were more susceptible to predation in open habitat (Austin 1990, Lema 2001), but Beier and Drennan (1997) found goshawks preferred to hunt in mature forests with high canopy cover.

Two studies used radio telemetry to follow squirrels and were able to assess the causes of mortality. Lema (2001) compared survival over 19 months of adults and young squirrels on two sites; one site represented poor squirrel habitat (22 radios) and the other represented good squirrel habitat (28 radios). Five squirrels were killed on each site, all presumably by predators. Only one other radio-collared squirrel died in the study, and the cause of death was unknown. Evidence suggested raptors killed the squirrels and northern goshawks were suspected as causing most deaths. Most predation occurred in dense stands of trees that were present on or near both plots. No differences in mortality were apparent due to age or sex of squirrels or the habitat quality. In contrast, Sieg (2002) found differences in raptor predation on squirrels due to the quality of habitat. He radio-tracked 73 squirrels on six plots of varying habitat quality. Raptors killed 24 squirrels, and predation increased on plots as habitat quality increased.

Historically, large variations in the abundance of tassel-eared squirrels were consistently reported over time (Goldman 1928, Lawson 1941, Pearson 1950, Keith 1965, Hoffmeister 1971, Armstrong 1972, Farentinos 1972, Hall JG 1981, and Hall ER 1981). Abert's squirrel abundance and density have been found to vary with forest management (Keith 1965, Pederson et al. 1987), with habitat quality (Patton 1984, Dodd et al. 1998, Dodd et al. 2003), and with climate and season (Dodd *in litt*). States et al. (1988) felt that a 'boom or bust' fluctuation was a characteristic of short-term, Abert's squirrel populations.

Fluctuations in Abert's squirrel populations appear to result from: 1) variations in the abundance and quality of their foods (Patton 1974, Brown 1984, Pederson et al. 1987, States et al. 1988), 2) serious mortality after deep, persistent snows in winter (Stephenson and Brown 1980, Brown 1984), 3) poor recruitment during droughts (Dodd et al. 2003), and 4) differential predation (in the case of goshawks) among habitats with different densities of trees (Lema 2001, Sieg 2002).

Using the above figures on demography, David McDonald developed the life cycle diagram and matrix analysis for the Abert's squirrel shown in [Appendix A](#).

Community ecology

Abert's squirrels interact primarily with the ponderosa pine on which they depend and with which they have several symbiotic relationships. The squirrels increase nutrient transfer to the pine by their contribution to litterfall (Skinner and Klemmedson 1978). The squirrels use the fruiting bodies of hypogeous mycorrhizal fungi for food. Underground the hypogeous fungi form a mutualistic association with conifer roots, especially in stands of blackjack pine with high canopy density (States 1985, States and Wettstein 1998). The fungi facilitate nutrient and water exchange in ponderosa pine and enhance seedling survival and forest regeneration. Being underground, hypogeous fungi can not disperse their spores into the air as epigeous fungi (mushrooms) do. Abert's squirrels disperse spores of hypogeous fungi by eating the fruiting bodies and defecating the live spores in their pellets elsewhere (Kotter and Farentinos 1984, States and Wettstein 1998).

Abert's squirrels and pine squirrels can aggressively interact at higher elevations where ponderosa forests adjoin stands of Douglas-fir, lodgepole pine (*Pinus contorta*), and spruce-fir (Ferner 1974). Pine squirrels seldom frequent ponderosa pine forests when Abert's squirrels are present, but outside of the range of Abert's squirrels, pine squirrels can be common in ponderosa pine. Also, in some circumstances, Abert's squirrels will use and live in spruce-fir habitats occupied by pine squirrels (Hutton et al. 2003).

Abert's squirrels remove terminal bundles of needles from ponderosa pine while feeding on the phloem of twigs during winter. These bundles often contain developing cones and squirrels may reduce cone production by 20 percent in the process of removing the bundles (Allred et al. 1994). Squirrels also eat seeds from cones after they begin to develop in spring. By cutting developing cones to obtain seeds, squirrels may further reduce cone crops by an average of 20 to 35 percent (Larson and Schubert 1970, Allred et al. 1994). J.G. Hall (1981) found that trees used by squirrels while obtaining phloem from twigs showed less vigor and had lower growth rates. However, neither J.G. Hall (1981) nor Ffolliott and Patton (1978) believed that twig clipping seriously decreased overall forest productivity or increased tree mortality. Allred and Gaud (1993) found that heavy snow load on pine branches could cause greater twig loss than squirrels.

By selectively feeding on certain trees while eating phloem, squirrels may alter the genetic variation

and select for biodiversity in ponderosa pine (Linhart et al. 1989). They may act to select against certain genetically determined traits in ponderosa pine such as high sugar or terpene content of phloem. Fitness in "feed trees" can be reduced by squirrels (Snyder 1993), and squirrels feasibly could select against the ultimate survival of their favorite trees. Still, it would not seem that selective herbivory by squirrels would be a dominant factor in the survival of pine forests, as the trees and the squirrels have existed together for centuries. Snyder (1998) has recently shown that chemical characteristics of trees appear to determine their selection for feeding by Abert's squirrels, porcupines (*Erethizon dorsatum*), mountain pine beetles (*Dendroctonus ponderosae*), and parasitic dwarf-mistletoe (*Arceuthobium vaginatum*). These organisms are believed to select for different chemical characteristics in ponderosa pine, which could negate each other's effects on pine survival.

Snyder (1998), Snyder and Linhart (1998) and States and Wettstein (1998) reported that the ranges of subspecies of Abert's squirrels are similar to broad geographical regions in which pine xylem resins differ. It was implied that selective squirrel herbivory by different squirrel subspecies created unique arrays of pine xylem resins in the trees of the area. The ultimate question is whether or not selective herbivory by squirrels actually occurs.

Zhang and States (1991), Snyder (1992), and others (see discussion under Food habits) have presented evidence for selective herbivory, but Linhart et al. (1989) stated "--- the biochemical bases of target tree selection have not been clearly demonstrated." Identification of the factors influencing squirrel selection of trees for bark feeding is not yet compelling. The criteria for selecting trees for sampling, the inconsistencies in the kind of chemicals measured, and differences in results obtained leave many questions unanswered.

CONSERVATION

Threats

Threats to squirrels and their habitat

The activities that most severely influenced the habitat quality of the Abert's squirrel were logging, grazing, and wildfires that occurred in the late 1800's. Logging of virgin ponderosa pine continued in Arizona during the 1980's and early 1990's. In the aggregate these factors scarified ponderosa pine forests and seriously degraded or eliminated squirrel habitats. In many cases, large, open parks later developed within

areas that were formerly forests. As the squirrel is so highly dependent upon ponderosa pine forests for its life requirements, it is surprising that the species survived in these altered forests. Subsequent fire suppression and continued logging and grazing reduced the incident of slow-burning ground fires and encouraged the development of thick stands of even-aged pine regeneration. Replacement forests that developed in the last century are often homogenous in structure and are not high quality squirrel habitat. As has now been recognized throughout the Southwest, these stands are overstocked, have great accumulations of fuels, are not defensible against fire, and are not sustainable.

Forests in the Front Range of Colorado were largely devastated before 1900 by the removal of most trees for lumber, mine props, railroad ties, pulp, and charcoal. Replacement stands developed during the 20th century, but due to the impacts of grazing and fire suppression, these stands are relatively uniform, even-aged, and overly dense. During the last several decades, management of ponderosa pine forests in Colorado has stressed stand improvement and fuel reduction over rather small areas. For instance, over the last 23 years, the Grand Mesa, Uncompahgre and Gunnison National Forest (GMUG) has rehabilitated only about 80,000 acres using a variety of harvest methods: clearcuts (patch, strip, and overstory removal), even-aged shelterwood cuts, selection cuts of various ages and group sizes, improvement cuts (thinning and mistletoe), and salvage cuts. In addition, 68,000 acres were improved by precommercial thinning and release treatments and by prescribed burns. Another 10,000 acres were disturbed by wildfires, windthrow events, and insect outbreaks. In Colorado, wildfires destroyed relatively small areas (4,000 ha or less per year) of ponderosa pine forests from 1988 to 1995. The incidence and size of fires has increased since then, with acreages burned ranging from 12,000 to over 40,000 ha per year. Drought, perhaps aggravated by climate change, was largely responsible for recent dry conditions and the large sizes of fires.

Forest management practices have negatively influenced the abundance of Abert's squirrels, primarily by altering the squirrel's habitat structure. Patton et al. (1985) found higher squirrel densities on unlogged than on logged forests in Arizona. Squirrel abundance was positively correlated with the number of trees per acre and quadratic mean diameter of stands. Squirrel numbers were greatest where larger trees (30 to 74 cm dbh) were most abundant, probably because large trees produce more cones and cover than small trees.

Pederson et al. (1987) found that squirrels spent 62 percent more time feeding in unlogged stands, and more often fed on hypogeous fungi there than in logged areas. Less fungi was produced on logged plots, probably due to a more open canopy, reduced amounts of litter and available moisture, and greater soil compaction.

Restoration of ponderosa pine forests is being undertaken in both Arizona and Colorado, and, at least in Arizona, restoration of Abert's squirrel habitat has become an ancillary objective (Elson 1999). Restoration based on reconstruction of pre-settlement forest density and structure could reduce the density of large trees as much as 98 percent, leaving only 150 large trees or less per hectare (Mast et al. 1999). Such restoration could exacerbate the effects of past even-aged management of ponderosa pine and further reduce stand, patch, and landscape diversity (discussed in Dodd et al. 2003). With prescriptions that greatly reduce the diversity in forest structure, basal area of trees, canopy cover, and the frequency of interlocking canopies, squirrel productivity and densities would be expected to decrease.

The objective of many current management activities is not to create original forest conditions or to improve the quality of Abert's squirrel habitat. The increased susceptibility of ponderosa pine/Douglas-fir forests to large fires due to the thick, uniform characteristics of stands and excessive fuels, lead to planning to reduce this threat in the South Platte Watershed of the Pike National Forest in Colorado. The South Platte Watershed produces 80 percent of the water used in Denver and contains some of the reservoirs serving the city. Forests on the watershed were historically open, patchy, and comprised of uneven-aged stands with an open canopy. Now the forests are homogenous (dense, even-aged) and have a high canopy cover and few ground openings (Kaufmann et al. 2001). Mechanical treatment (logging, thinning, and chipping of trees on site) is planned to reduce canopy density to 25 percent or less and to create scattered openings of 2.5 to 100 ha in size. Prescribed fire will also be used to remove excessive fuels and to open up forest structure. The objective is to restore watershed function to the 645,000-acre drainage through commercial and non-commercial thinning, fuels reduction with use of prescribed fires, reforestation, and sediment control (Culver et al. 2001). Plans did not include consideration of habitat needs of Abert's squirrels. As knowledge is now available of forest structure that is beneficial to squirrels, planners should integrate habitat requirements of squirrels into their objectives and activities.

Current management of ponderosa pine forests in Colorado seldom considers the specific habitat requirements of Abert's squirrels. Management for squirrels is possible, but only at the cost of reducing manpower and funds available to attain other objectives. In planning for multiple-resource management, forest managers decide on the relative emphasis that they wish to give different objectives. Their decisions will never eliminate the squirrels, but squirrel numbers will rise or fall depending on the extent that forest management provides for the needs of the animals.

Between 1995 and 2002, wildfires consumed hundreds of thousands of hectares of forests in Colorado. These fires undoubtedly killed many squirrels and seriously degraded or destroyed the potential of the habitats to support squirrels. If such an incidence of wildfires continues, fire could become a serious mortality factor, both directly and through habitat destruction. Drought was largely responsible for creating the conditions that enabled these fires to burn over such large areas of forests.

Other possible relationships between weather and Abert's squirrel population dynamics have been documented recently in Arizona. Deep and persistent winter snow cover has been found to be correlated with increased squirrel mortality. Heavy snows may be the result of El Niño events in the Pacific, as the storms occur during the same winter and El Niño events are known to bring increased precipitation to the western United States. Serious drought conditions dominated the weather in Arizona between 1996 and 2002. Reproductive success of Abert's squirrels in central Arizona varied with precipitation during that period. Precipitation was 42 percent and 90 percent of normal in 2000 and 2001, respectively, while squirrel recruitment (juveniles per adult female) in those two years averaged 0.04 and 1.79 (Dodd *in litt*). The impacts of El Niños and of droughts are aggravated by global warming, and it is possible that climate change related to global warming could be influencing mortality and reproduction in Abert's squirrels.

Threats from exotic species

The Eastern fox squirrel is the only invasive mammal that might threaten the Abert's squirrel. Although not strictly an exotic species, the fox squirrel has expanded its range into the mountains of Colorado and now resides in ponderosa pine forests up to 9000 ft or above. Its populations remain sparse in the forests, however, and it does not appear to be a threat to the

Abert's squirrel, as the two species do not directly compete for life requirements.

Threats of overutilization

Commercial, scientific, and educational pursuits do not threaten the Abert's squirrel. Sport hunting of Abert's squirrels is undertaken in Colorado, Arizona, and New Mexico. The annual harvest is minimal in Colorado (estimated at 1,312 animals in 2000-2001), and should be sustainable at that level. Over 100,000 squirrels per year have been shot in Arizona for many years without decreasing the population of squirrels.

Conservation Status of Abert's Squirrel in Region 2

The best available evidence indicates that the overall, average abundance and the range of the Abert's squirrel are not decreasing in Region 2. In fact, the squirrel has expanded its range in Colorado and crossed the border into extreme southern Wyoming during the last half of the 1900's. In Colorado, new populations were reported in 11 additional counties, including sites west of the continental divide in central Colorado and north of the San Juan Mountains and the Dolores Plateau in western Colorado (Davis and Bissell 1989). The Abert's squirrel is a habitat specialist; it obtains most of its life requirements from ponderosa pine. The squirrel co-evolved with ponderosa pine in the virgin pine forests of the southwestern United States and is dependent on many features of pristine forests to provide for its foods, nesting sites, and travel and escape cover. In the Front Range of Colorado, its habitat is currently in a degraded state due to alteration of the density, age, spacing, and overall structure of forest stands from logging and fire suppression. Recent forest management practices have not been directed at reestablishing conditions that would increase habitat quality for the squirrel.

Ponderosa pine habitats offer a variety of foods to Abert's squirrels during the course of a year. However, the abundance of these foods can vary over time, and the carrying capacity of habitats can fluctuate with changes in food abundance. In the absence of cone crops, squirrels feed more on hypogeous fungi. If neither cones nor fungi are available, squirrels will feed on the inner bark of pine during summer and will largely subsist on inner bark during winter. As inner bark is a low quality food, squirrel body condition can decrease and mortality can occur when they are forced to subsist on inner bark for extended periods. Management cannot

control these variations other than to ensure that forest structure enhances the availability of young vigorous trees for inner bark feeding, large cone-producing trees, blackjack clusters with high canopy to enhance fungi production and protection for travel. Since 1850, forest management, through selection and even-aged cutting, has been counterproductive to squirrels and has continued to decrease the carrying capacity of ponderosa pine forests for Abert's squirrels.

The habitat of the Abert's squirrel is the ponderosa pine forest. The age, density, and structure of forests preferred by squirrels have been described (see Management Considerations). Timber harvest has caused the greatest disturbance and deterioration to the quality of squirrel habitat. The squirrel has proven to be a survivor and should not be considered vulnerable to elimination as a species from demographic or environmental stochasticity.

The Abert's squirrel is a survivor and will persist as a species, although perhaps in reduced numbers, even as its habitats are degraded by human activities. By 1900 on the Pike Forest Reserve (Jack 1900), squirrel habitat had been devastated by logging, grazing, and fire, and it probably was in as poor a condition as ever occurred there. Food sources were depleted, as few trees were present of an age to produce good cone crops, few trees were present of an age preferred by squirrels for feeding on inner bark, the shaded moist habitat required by hypogeous fungi undoubtedly was scarce, and even the simple requirement of the squirrel for nesting and escape cover probably was not met. Yet, the Abert's squirrel survived. Misuse of ponderosa pine forests may degrade their value to the squirrel and reduce squirrel numbers, but squirrels will persist if some resources remain. Currently, there is no known risk of the species disappearing from any areas in Region 2, except those completely devastated by wildfire.

Management Considerations

Patton (1984) reported that squirrel densities were related to habitat quality, with 0.05 squirrels/ha in poor habitats, 0.35 squirrels/ha in good habitats, and 2.45 squirrels/ha in optimum habitats, which are rare. Abert's squirrels require food sources, nesting cover, and escape cover. Many foods and types of cover are provided by ponderosa pine trees, but different ages and size classes of trees are needed to provide for specific life requirements. Pine seeds are an important, but unreliable, source of nutrition and energy. Larson and Schubert (1970) found that squirrel use of cones

on a tree was strongly correlated with the number of cones produced by the tree. Large trees (60 to 100 cm) produce the most cones (200 to 450 per tree) and are most heavily used by squirrels. They also found that squirrels preferred particular individual trees for feeding on inner bark, but did not select trees on the basis of tree position, dominance, diameter, or age-vigor class. Allred and Gaud (1994a) examined 668 "feed trees" and also found that squirrels did not select trees on the basis of any physical characteristics, other than size. They found that squirrels did not feed on trees < 11.2 cm dbh, and trees used for bark feeding averaged 31 cm dbh. Other studies have shown that "feed trees" range from 30 to 70 cm dbh in Arizona (Keith 1965), and in Colorado from 15.3 to 50.5 cm (mean 34.5 cm) at Bald Mountain and 30.0 to 52.9 cm (mean 36.9 cm) at Betasso Preserve (Snyder 1992).

Ratcliff et al. (1975) found a significant positive relationship between stand basal area and squirrel abundance, while States and Gaud (1997) found a reduced abundance of hypogeous fungi in stands with the least basal area. Patton et al. (1985) and Pederson et al. (1987) documented lower squirrel density, lower squirrel recruitment, and less hypogeous fungi with reduced basal area, canopy closure, and tree density in logged forest stands. Dodd et al. (1998) studied the characteristics of squirrel habitat and found that squirrel recruitment was positively related to the number of interlocking tree canopies in their habitats, while overall fitness in squirrels was positively related to basal areas of the stands.

States et al. (1988) documented that squirrels, over time, use cones and inner bark from most blackjacks and yellow pines within stands. Hypogeous fungi used by squirrels are usually associated with denser stands of blackjacks (States 1985). Nest trees are usually in the center of a cluster and surrounded by higher trees that provide protective cover from avian predators (Hall JG 1981, Brown 1984). Thus, squirrel habitat requires uneven-aged stands with clusters of even-aged groups connected by corridors to provide secure travel routes. Such forest structure will provide the necessary foods, as well as the canopy cover necessary for fungi production, nesting trees, and protection from avian predators (States et al. 1988, Dodd et al. 1998).

Historic and present forest management has not contributed to development of forest structure that supports the needs of Abert's squirrels. Lower squirrel numbers and recruitment rates were found after logging removed most of the larger trees (Pederson et al 1976).

Trapping required more trap-days to catch each squirrel after logging. Squirrels moved from logged to uncut areas. Logging removed litter cover and reduced the abundance of hypogeous fungi. Brown (1984, p. 37) claimed even conservative logging, including such long-term practices as selective cutting and a 120-year rotation, may be detrimental to the squirrel. He stated, “--- squirrel numbers and distribution will suffer with the elimination of old growth ponderosa pine and poor or sporadic regeneration of new forests.” Patton (1984) believed that optimum squirrel habitat may seldom exist today because of the intensity of past logging.

There was an unprecedented intensity of timber harvest in Arizona from the mid-1980’s into the 1990’s (Brown 1984, Johnson 1994) that severely reduced Abert’s squirrel habitat quality. Dodd and Adams (1989) modeled 40 timber sales in Arizona and showed habitat capability would be expected to decline by 20 percent.

Ponderosa pine forest restoration projects are currently underway in Arizona (Covington 2000, Huffman et al. 2001), New Mexico (Kaufmann et al. 1998), and Colorado (Kaufmann et al. 2000, Kaufmann et al. 2001, Lynch 2001). The objectives of these projects (Covington 2000) are to, “-recreate forest structural and compositional characteristics similar to those of the reference historical or pre-European settlement condition so that ecosystem processes, particularly frequent light underburning, can resume their suitable, self-perpetuating patterns.” Or, similarly, “--- to reestablish pre-settlement structure and functions in the forests, with the goal of restoring original biological diversity and ecological relationships in ponderosa pine forests of the southwest.” (Covington et al. 1997). To accomplish this, each project has developed a “prescription” for restoration, varying somewhat depending on the specific objectives of each project. These prescriptions usually include the following elements: 1) an analysis of past change in the forest unit, 2) identification of living pre-settlement trees, 3) identification of the number and location of pre-settlement trees that have been removed, 4) selection of trees to be maintained, 5) some level of thinning, primarily the smallest trees, 6) one of several uses of fire, and 7) reseedling with native plants.

Covington and Moore (1994) found that vegetative changes since 1867 altered wildlife habitats from those favoring grassland species to habitats favoring forest species. At a landscape scale, forest restoration to a presettlement condition could have a negative impact on Abert’s squirrels. Squirrels need trees, and some restoration prescriptions call for reducing tree density

up to 98 percent (Mast et al. 1999), as well as patch, stand, and landscape diversity and patch homogeneity (Patton 1992). In addition, restoration activities may reduce the amounts of habitats that are of minimal quality overall, but that have features that contribute to the maintenance of squirrel populations (Patton 1884, Dodd et al. 1998). For instance, States (1985) found that truffles, a favorite food of squirrels and necessary for forest health, were most abundant in blackjack stands with high canopy cover. Few thick clusters of blackjacks will remain in restored forests. Prescriptions for thinning and basal area retention should be altered to maintain the structural heterogeneity required by squirrels. Likewise, management practices (e.g. fuel reduction) that rely on intensive, widespread thinning will deteriorate Abert’s squirrel habitat and reduce their abundance (Dodd et al. 1998).

A study by Elson (1999) is in progress at Mt. Trumbull in northern Arizona to evaluate how forest restoration affects Abert’s squirrel populations and habitat. He suggested that the restoration prescription maintain trees with evidence of moderate use by squirrels for feeding on inner bark, as well as existing patches of trees that benefit squirrels by maximizing foraging habitat, nesting habitat, and protective cover. In the Mt. Trumbull area, pre-settlement reference conditions did not indicate that such patches existed in the structure of stands, and they were not deemed to be important. However, these small, even-aged clusters are now recognized as being important to the squirrels. States et al. (1988) found clustered stands necessary to provide the canopy cover needed for truffle production and for cover and nesting sites for squirrels. Elson (1999) also believed that it is important to mark for retention the most important cone producers in restored stands.

Tools and Practices

Distribution surveys and population monitoring

Distribution surveys of Abert’s squirrels in the State of Colorado originally relied on collection locations described on tags attached to museum specimens. Only squirrels that had been collected and could be examined were viewed as valid records. Later, sightings by biologists published in scientific journals became accepted as valid records of distribution. The most recent description on the squirrel’s distribution in Colorado (**Figure 2**) included both museum records and sightings of squirrels by professional field biologists working for the USFS, the National Park Service, and the Colorado Division of Wildlife (Davis and Bissell 1989). Sight records of vertebrate species are now accepted as

valid by zoologists, as a requirement for the collection of specimens could reduce numbers of threatened species and remove individuals involved in range extension. The survey by Davis and Bissell (1989) was accomplished and reported in a professional manner and is totally acceptable. Such statewide surveys probably will continue. National forests are beginning to produce more detailed maps of Abert's squirrel distribution on their lands (**Figure 3**) as part of their Management Indicator Species programs. The survey information on squirrel presence will be useful for following changes in squirrel abundance and distribution over time on national forests. Regrettably, similar data will not be available for lands in other ownership.

A consistent characteristic of parameters affecting Abert's squirrel demography is their variability. Food habits differ depending on the availability of foods. Home range varies with the quality of squirrel habitat and the weather. Frequency of breeding, breeding success, and population mortality are all influenced by the weather, which is the most variable and perhaps influential factor of all. Finally, the temporal or spatial abundance of squirrels is determined by the interaction of natality, mortality, and habitat quality. As a result, squirrel numbers vary considerably both spatially and temporally.

Many methods have been tested to census and monitor Abert's squirrels populations: strip censuses; time-area counts; Peterson indices and related techniques; counts of animals, tracks, and sign; fall age-ratios; and hunting success. Of these methods, only hunting success gave satisfactory indices to squirrel abundance (Brown 1984). J.G. Hall (1981) used twig clippings to index squirrel numbers, and Brown (1982b) further tested the technique. The problem with monitoring the number of twigs cut in an area is that squirrel use of twigs varies with the availability of other foods (Pederson et al. 1976). Dodd et al. (1998) evaluated nest counts, counts of snow tracks, and counts of feeding sign as methods to obtain population indices on plots with known numbers of squirrels. The most reliable results were obtained with counts of combined feeding sign (fungi digs, cone cores, peeled twigs, and terminal bundles) on sampling plots in April. Costs of these counts were lower than costs of other methods. Track station counts were about as reliable as feeding sign counts, but they cost more to conduct. Drennan et al. (1998) also found track station counts to correlate highly with mark-recapture indices and to be less costly than trapping.

Monitoring of squirrel populations on a national forest would be more informative if it included annual

documentation of winter mortality and the percentage of young squirrels in the fall population. The objective of monitoring the squirrel is to use their numbers to illustrate the effects of forest management. Obtaining information on the numbers of squirrels helps meet this objective but does not consider changes in abundance due to other factors, such as winter mortality (due to snow cover) and reproductive failure (due to drought). In Colorado, trapping programs would be required to obtain information on winter mortality and the success of reproduction. Hunters kill too few squirrels in Colorado to obtain reliable fall age-ratios from the harvest.

Habitat inventory and monitoring

More is probably known about the biology and distribution of ponderosa pine than of Abert's squirrels. A great deal of knowledge exists on methods for inventory (Benson and Green 1987) and for silvicultural practices (Schubert 1974). There are about one million ha of ponderosa pine in Colorado. The resource is almost equally divided between public and private ownership, but only about 20,000 ha are protected from commercial use. Most forests of ponderosa pine in Colorado have been logged and/or grazed by cattle. Heavy logging destroyed the original structure of the forest and grazing was one factor in limiting the ground fires that maintained the original forests. Attempts have been made to classify site quality of ponderosa pine (Meyer's, Minor's, and Mogren's curves). Mogren's curves were developed because the other techniques were not applicable to the Front Range of Colorado (Schubert 1974). The pines there were too short to meet even the poorest site class (40 ft at base age of 100 years) used in other methods.

Sites within the pine forests differ in their biological potential and in their history of use. Throughout most areas, forests were harvested at different times and at different intensities. Thus, on a landscape scale, a mosaic of forest conditions (habitat patches) has developed. The value of these forest mosaics to Abert's squirrels would be expected to vary, and the ability to quantify the value of local and landscape habitats to the squirrels must be developed (see ROMPA on page 40).

Patton (1977:266) claimed that, "If man did not interfere, areas of good and poor habitat would change over time because of the dynamic nature of forest succession." To help in surveying squirrel habitats, Patton (1977) developed a scoring method to evaluate squirrel habitat quality. A food rating of 2 to 8 increased in value with the percentage of the stand with pines

>20 cm dbh. A cover rating of 3 to 12 considered basal area and stand dbh. Finally, two diversity ratings were generated: 1) a rating of 2 to 8 based on tree arrangement in the stand and 2) a rating of 1 to 4 depending on the number of canopy stories. Scores were added to estimate the value of the habitat to squirrels. Later, Patton (1984) proposed using diameters of nest trees, feed trees, and stands, as well as stand density (trees/ha) to develop five habitat quality classes for squirrels. Class 1 was considered poor habitat, while Class 5 was considered optimum. Squirrel density was predicted to vary from 0.02 squirrels per acres in Class 1 habitat, to 0.99 squirrels per acres in Class 5 habitat. Patton (1984) believed that optimum habitat was now rare because of disturbance from past logging. His model accommodated requirements for cone producing trees, interlocking crowns as travel corridors, canopy cover over nest trees, and trees of a size selected by squirrels for feeding on inner bark during winter. In the model, additional value is given to stands containing small, connected clusters of trees. Cluster size should range between 0.1 acres and 0.5 ha. Large trees contribute to habitat quality only if they occur in clusters of other trees.

Silvicultural methods to measure and monitor ponderosa pine forests have been developed and are in wide use (Schubert 1974). However, survey methods for determining the health and ecological stability of forests are still needed. For instance, concern over responses of ponderosa pine to climate change, increases in CO₂ and ozone levels, and soil and vegetation changes were recently discussed in a workshop at Oregon State University (Waring and Law 2001). Conclusions were that a multi-disciplinary approach will be needed in monitoring effects of these threats to forests.

The value of ponderosa pine as squirrel habitat has not been surveyed on a landscape scale. Evaluation and monitoring of squirrel habitat quality over districts or forests will become necessary in developing management plans in the future. Patton (1984) developed methods for such surveys, and they have been used by the GMUG. Forest staff found it desirable to monitor the quality of squirrel habitat before and after

logging, controlled burns, or forest restoration projects to evaluate the effects of those activities on squirrels. Rosenstock et al. (1997) and Germaine (1997) evaluated wildlife response to forest restoration programs in Arizona. Additional approaches for measuring effects of forest restoration on squirrels were developed by Elson (1999) on the Kaibab Plateau.

Dodd et al. (1998) analyzed squirrel habitats and measured squirrel population parameters on eight study plots (each of about 70 ac) in central Arizona. At a stand scale, their study plots differed in intensity of logging history, trees per hectare, basal area per hectare, trees per diameter class, stand density index, and canopy closure. Some forest structural variables on plots were correlated with some squirrel population variables. Recruitment (juveniles per adult female) was highly related ($r^2 = 0.970$) to interlocking canopy trees (**Figure 4**). Recruitment averaged 0.20 on four plots with uneven-aged stands but only 0.07 on intensely logged, even-aged stands. Squirrel fitness was highly related ($r^2 = 0.845$) to tree basal area (Dodd et al. 1998). What became evident from this study was that at a specific time squirrel densities were not highly correlated with overall habitat quality. Some plots with marginal habitat supported high squirrel numbers seasonally because they produced large cone crops. Findings lead authors to conclude that high quality “source areas” produced most of the squirrel population. Surplus squirrels then immigrated into “sink areas” of lower habitat quality, but with some temporary resources. Survivorship was low in “sink areas” (**Figure 5**).

Dodd (*in litt*) continued these studies on a landscape basis, with plots >500 ha. This research is evaluating relationships between “source” and “sink” habitats based on their ROMPA (Ratio of Optimal to Marginal Patch Area) (Lidicker 1988, Krohne 1997). Squirrel populations correlate better with ROMPA values than with individual habitat features such as patch area, forest structure, and spatial patterns in stands, which were identified as important in earlier studies (Pederson et al. 1976, Patton 1984, Patton et al. 1985, Pederson et al. 1987).

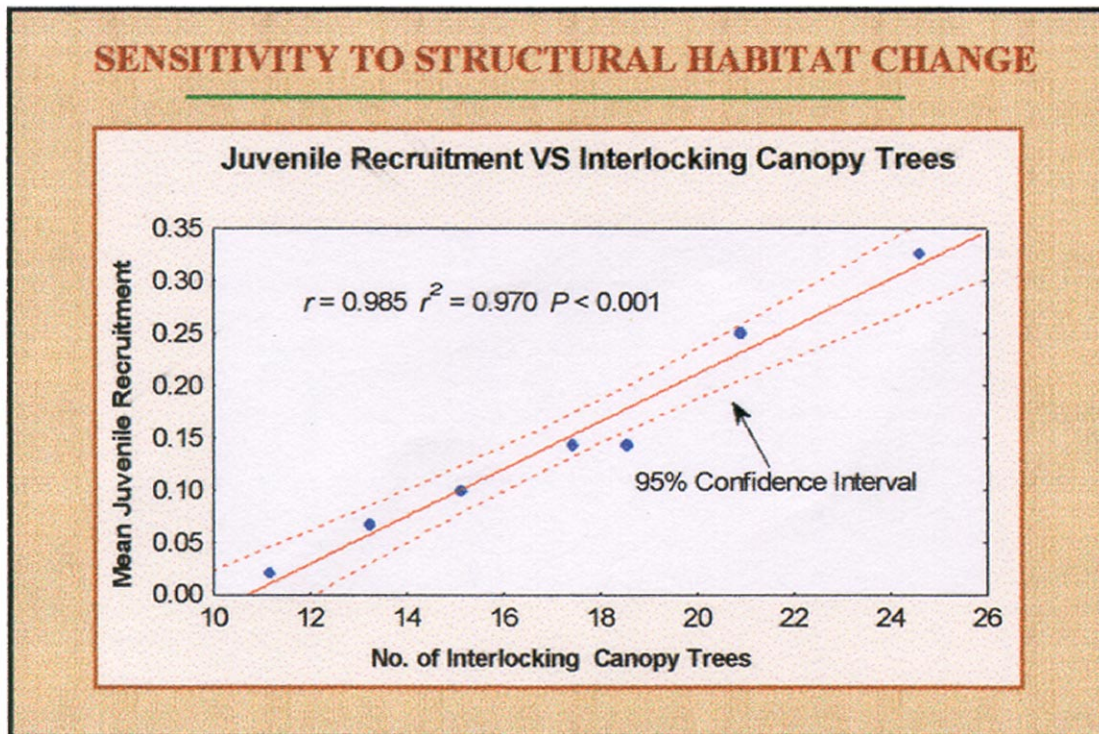


Figure 4. Abert’s squirrel recruitment vs. forest canopy cover. (Source: Norris Dodd, Arizona Game and Fish Department, Pinetop, Arizona)

ROMPA was calculated by determining the area of optimal (multi-layered, uneven-aged) and marginal (open, even-aged) habitat and ignoring “gray” areas in between those clearly definable habitat qualities (**Figure 6**). The percentage of areas in each condition was measured with the FRAGSTAT program using spectral signatures from LANDSAT imagery. Optimal habitats were found to have higher squirrel density and greater recruitment (**Figure 7**). Optimal habitats were “source” habitats as they produced sufficient young to support emigration. Marginal habitats were found to be “sinks”. Those habitats were relatively unsuitable for recruitment, but they attracted immigrants due to desirable, but temporary resources. Above 37 percent ROMPA, squirrel densities averaged 0.41/ha. Densities averaged only 0.18/ha on plots with lesser ROMPA values. Highest densities were at 40 to 50 percent ROMPA, and highest recruitment was at 50 percent ROMPA. Both squirrel density and recruitment dropped sharply at 37 to 42 percent ROMPA. On a landscape scale, it appears important to maintain about 50 percent high quality source habitats, but there are benefits to

squirrels from mosaics (Smith et al. 2003) and edges (Patton 1975c) in habitats.

Management approaches for Abert’s squirrels

There has been little direct management of Abert’s squirrels, other than activities necessary for the conduct of sport hunting. Only recently has forest management considered the life requirements of the Abert’s squirrel. For instance, the GMUG has prepared an MIS Assessment for 12 species, including the squirrel, while the San Juan National Forest revised an MIS Assessment for the squirrel in 2003. The Abert’s squirrel was selected because of its specialized association with ponderosa pine. The assessment for the squirrel includes a review of its biology, its distribution in the forest, the distribution of ponderosa pine, habitat condition and trend, squirrel population and trend, and forest monitoring. Since 1990, forest management in GMUG has emphasized preventive bark beetle

“SOURCE” VS “SINK” HABITATS

SOURCE HABITATS

- High quality
 - ✓ high basal area
 - ✓ high canopy closure
 - ✓ large trees
- Populations stable
- Juvenile recruitment consistent
- Produce squirrels to disperse to adjacent sink habitats
- Analogous to “optimum” habitat

SINK HABITATS

- Lower quality
 - ✓ low basal area
 - ✓ low canopy closure
 - ✓ few large trees
- Populations fluctuate seasonally
- Juvenile recruitment limited
- Dominated by immigrating nonresidents seeking food
- Analogous to “marginal” habitat



“SOURCE” VS “SINK” HABITATS

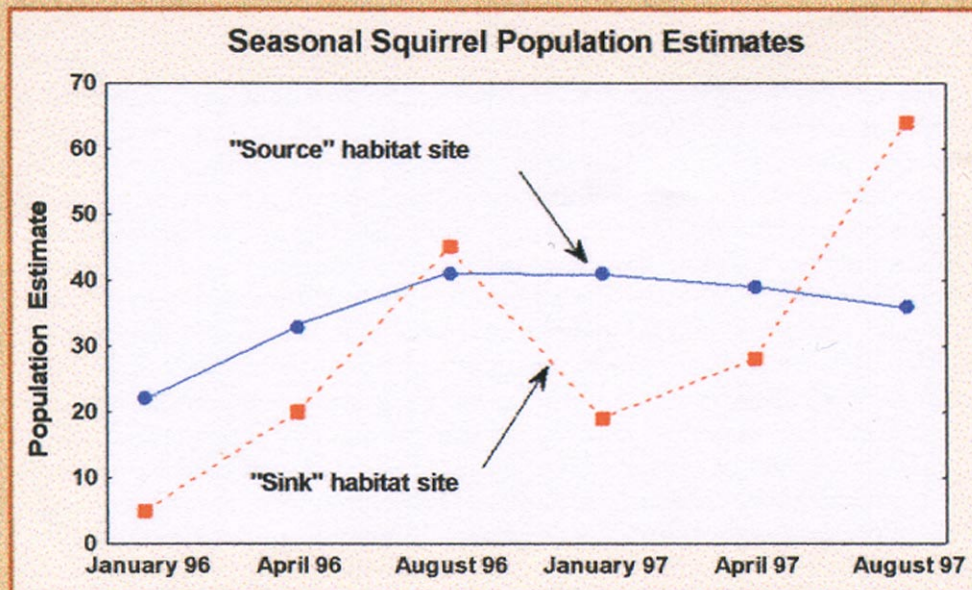


Figure 5. Sinks gain squirrels in August from source habitats, but lose them in winter. (Source: Norris Dodd, Arizona Game and Fish Department, Pinetop, Arizona)

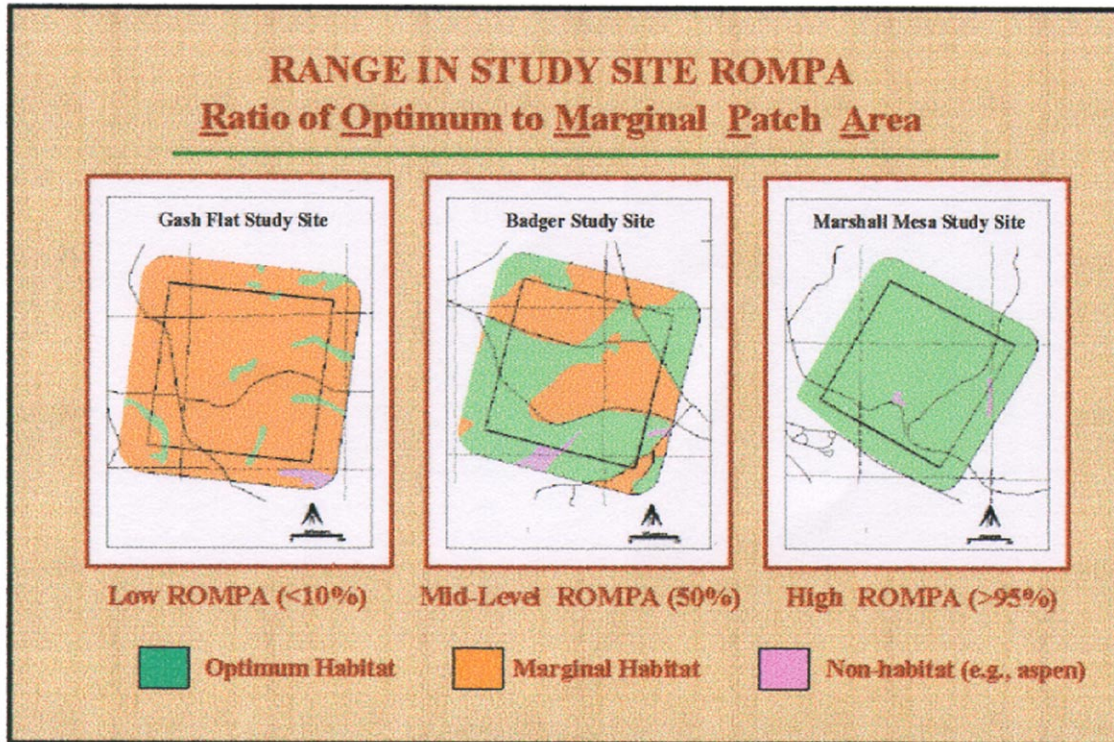


Figure 6. ROMPA calculated from optimum and marginal patch area. (Source: Norris Dodd, Arizona Game and Fish Department, Pinetop, Arizona)

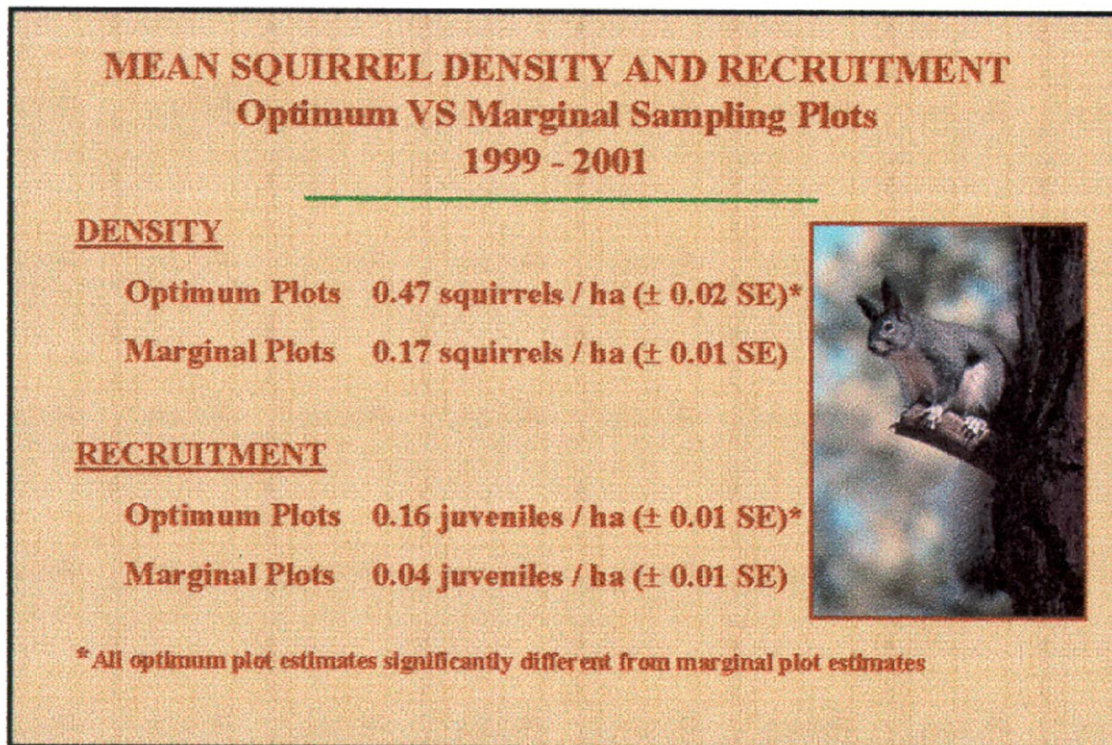


Figure 7. Abert's squirrel density and recruitment in optimum and marginal areas. (Source: Norris Dodd, Arizona Game and Fish Department, Pinetop, Arizona)

management by thinning and underburning to reduce stand densities to a 60 to 80 ft² basal area. This program has resulted in converting many 4c and 4b sites to 4a structural stage condition, which is viewed as inimical to the squirrel. To alleviate impacts on Abert's squirrels from this conversion activity, several clusters containing nest and feed trees were left on every 2 ha within the treatment area. The MIS assessments for the Abert's squirrel on the forests are impressive in their coverage of the biology, habitat, and life requirements of the squirrel. They are weakest in the recommendations that they give for integrating squirrel habitat requirements into forest management planning. Other forests are developing MIS Assessments of Abert's squirrels, if the squirrels and their habitat are sufficiently abundant (**Appendix B**).

The Upper South Platte Watershed Protection and Restoration Project, a cooperative venture among several agencies, proposes to use multiple approaches to restore stands of ponderosa pine within the South Platte watershed to sustainable or pre-settlement conditions. In contrast to the attention given to the squirrel on the GMUG and despite the fact that about 200,000 ha of the project land are located on the Pike National Forest, there were no considerations of Abert's squirrels or their habitat requirements in planning this vast, long-term project. The project was proposed in 1998, and planning for restoration projects began in 2000 (Culver et al. 2001).

Likewise, no consideration of Abert's squirrels was given in the prescription for conducting a restoration project in 183,000 acres of ponderosa pine near Cortez, Colorado in the San Juan National Forest (Lynch 2001).

In Arizona, experiments on ecological restoration of ponderosa pine forests have been underway since 1975 on at least 10 sites using several different methods, including fire and various combinations of thinning (Covington 2000). Several of these projects have included monitoring to determine wildlife effects from restoration of the forests (Germaine 1997, Rosenstock et al. 1997, Elson 1999). For instance, Elson (1999) found that the restoration prescription used at Mt. Trumbull removed one-half of the twig trees used by squirrels for feeding on inner bark. Before thinning, his assessments showed twig trees tended to be clumped, which was suggested as desirable by J.G. Hall (1981), States et al. (1988), and Linhart (1989). Elson (1999) recommended

that in restoration projects clusters containing twig trees be maintained, or at least the most heavily used twig trees be preserved.

Prescriptions for forest restoration can include actions to help develop and maintain forest characteristics of value to the Abert's squirrel (Patton and Green 1970, Patton 1975b, Ratcliff et al. 1975, Patton 1977, Patton 1984, States et al. 1988, and Smith et al. 2003).

Desirable actions and characteristics include:

- 1) Stand densities of 300 to 600 trees per ha, mostly >30 cm dbh.
- 2) Trees clustered into small, even-aged groups (0.1 to 0.5 ha in size) in uneven-aged forest.
- 3) Stringers of canopy cover between tree clusters to give protection for escape and travel.
- 4) Protection of existing nest trees within groups of taller trees (several per hectare).
- 5) Protection of 20 trees per ha used for bark feeding (>20 twigs on ground under tree).
- 6) Retention of areas of dense canopy cover to form habitat on ground for truffle production.
- 7) Protection of groups of cone producing trees, especially those >50 cm dbh.
- 8) High ROMPA values (> 50 percent).

Information needs

Distribution

The gross distribution of the Abert's squirrel in Colorado is known and maps are available to show the species' general location in the state. State and county maps should be updated periodically, as accurate maps will be needed in formulating regional conservation strategies. Local distributions within forests, sections, and townships have not been defined for the state, but they have been determined for some forests (GMUG, for instance, **Figure 3**). Such detailed maps will be necessary when management of the squirrel becomes more intense on individual forests.

Responses to habitat changes

The squirrel's abundance and habits in forest stands with different histories of management have been investigated, as have the squirrel's responses to timber harvest and other management practices. Although some studies are continuing, additional work will be needed to more clearly understand the effects of management on the squirrel. Likewise, the impact of winter snow cover on squirrel survival and the depressing effects of drought on reproduction are poorly understood, and the subjects need better definition and evaluation.

The Abert's squirrel should be studied in conjunction with forest management and forest restoration projects. The squirrel is closely dependent on ponderosa pine forests and can serve as an indicator species of the consequences of management actions. The squirrel is sufficiently numerous throughout Region 2 to permit gaining reliable population data for comparing areas, treatments, and experimental evaluations in different years. Squirrels are particularly sensitive to reductions in tree densities, basal area, and canopy closure, all of which result after forest logging, thinning, and restoration practices.

Movements

Annual, seasonal, and daily movements of squirrels in local areas have been studied and shown to vary. Variations in movements were evident among areas studied by different investigators and between decades on the same study areas. Movements were influenced by differences in weather and between habitats (source vs. sinks), which determine the availability of foods (pine seeds and hypogeous fungi). Evaluation of the changes in source and sinks habitats at landscape scales will be complicated by concurrent influences of weather and food availability on movements. These relationships should receive further evaluation.

Demography

Reliable techniques are available to measure population density, recruitment, survival, and fitness of Abert's squirrels. These methods are time-consuming and costly, and will not be the same at different temporal and spatial scales. Methods for measuring the population dynamics and status of squirrel populations in Colorado must be validated and modified, as necessary, to provide accurate information for management planning and activities.

Population trend

Reliable methods have been developed and tested to monitor population trends. These techniques have used counts of feeding detritus and tracking stations on sample plots to provide an index to changes in Abert's squirrel populations. They do not help in separating among causes of population changes that could include, 1) forest management practices, 2) local weather influences, and 3) climatic events, such as El Niños and global warming. The normal boom or bust fluctuations in squirrel numbers could confound interpretation of MIS monitoring, unless it includes consideration of all factors that make populations go up and down.

Trapping in April has been useful in determining survival of squirrels the previous winter. Age ratios obtained from trapping in October are good indicators of reproductive success the previous spring. Weather records can be used to interpret the influence of snow cover on winter survival and the influence of drought in suppressing productivity. MIS monitoring of Abert's squirrels should include information on the severity of El Niño/La Niña events, as well as evidence of global climate change and its ecological effects. Global warming is expected to considerably reduce the abundance and distribution of ponderosa pine in the southern Rockies. The size of stands will decrease, and ponderosa pine will retreat to higher elevations as the climate warms (Leverenz and Lev 1987, Joyce et al. 1990, and Shugart et al. 2003).

Restoration methods

Criteria for both forest restoration and for enhancement of Abert's squirrel habitat are available, but "recipes" or "prescriptions" have not been specifically developed and tested. Still, considerable information exists on the most desirable elements in habitats for the squirrels. In Arizona, for instance, squirrel-habitat relationships have been studied at multiple scales: tree clumps, stand or habitat patches, and landscape scales. At the clump level, sites used by squirrels, compared to random sites, had 16 percent higher canopy closure, 80 percent more old growth trees (VSS 5 and 6 structure), 35 percent higher tree basal area, and 35 percent higher stand density index (Arizona Game and Fish Department 2001, Lema 2001).

The latest studies are suggesting other factors for consideration in restoration of squirrel habitat. At a habitat patch scale (small study plots), recruitment

tended to increase with the number of interlocking canopy trees and the fungal content of the diet. Winter survival and overall density were higher with increased fungal diversity in diet. Changes in the numbers of squirrels between spring and fall were less pronounced on areas with the highest mean diameter of trees (Dodd et al. 1998).

Research priorities in Region 2

The objective of establishing Management Indicator Species is to use sensitive animals to determine how forest management practices affect the forest ecosystem. A species has utility as an MIS only if methods are available to measure changes in its abundance and distribution in response to forest management activities. Reliable methods must exist to measure these parameters for the species and to separate the influence of forest management from

the influence of other factors that could change their abundance and distribution. Highest research priorities for the Abert's squirrel should include the following: 1) to validate reliable census techniques that can be used to determine and monitor squirrel densities and distribution in Colorado, 2) to monitor weather conditions, and especially the relation of snow cover, drought, and climate change to squirrel demography, 3) to live trap squirrels in April (winter survival) and in September (age ratios) on large plots on a national forest scale to determine annual survival rates and reproductive success, 4) to determine patterns of squirrel habitat conditions across districts and forests and to correlate them with squirrel abundance to validate ROMPA concepts (a high correlation would allow monitoring ROMPA rather than squirrel densities), and 5) to evaluate effects of prescribed burning on Abert's squirrels.

DEFINITIONS

Basal area is the cross section at breast height (4.5 ft above ground level) of a tree or trees expressed as square feet per acre. It is a measure of stand density.

Canopy cover or closure is the percentage of a given area covered by the crowns of plants based on a vertical projection to the ground from the outermost perimeter of the canopy.

Climax species are the plants and animals that occur in a relatively stable plant community.

Clusters are groups of trees that occur within a stand.

Diameter at breast height (dbh) is the diameter of a tree measured at 4.5 ft above the forest floor on the uphill side of the tree.

Density is the number of squirrels per unit area, most often on multiple ha or km².

Dominant / co-dominant trees are the tallest and next to tallest trees in a stand and comprise the main canopy cover of a stand.

Epigeous refers to living at the soil surface.

Estrus refers to both the period of time and the physical condition during which females are receptive for breeding.

Fitness is a value calculated to express the relative probability of a species viability (density x recruitment x survival) on different areas.

Habitat quality refers to the relative ability of an environment to provide a species with its life requirements.

Home range is the area used by an animal for foraging, traveling, resting, nesting, and other essential activities.

Hypogeous refers to living below the soil surface.

Landscape is a level of ecological complexity above the community level containing mosaics of habitat qualities over a large areas.

Logging is the removal of trees from an area by cutting them down and removing them from the site.

Management Indicator Species (MIS) are those species used in land management planning because their population changes indicate the effects of management activities.

Minimal patches consist of habitat with low basal area, low canopy closure, and few trees <40 cm. Squirrel numbers fluctuate seasonally and recruitment is limited. This is “sink” habitat where populations are maintained by immigrants seeking food.

Mosaic refers to variable patterns of habitats ranging from optimum to marginal in value on a local or landscape scale.

Mycorrhizae are symbiotic fungi on plant roots that function to assist the plant absorb water and nutrients from the soil.

Optimal patches consist of habitat with high basal area, high canopy closure, and numerous trees <40cm. Squirrel numbers and recruitment are stable. This is “source” habitat as excess young disperse from these patches.

Patch is a local area of relatively homogeneous habitat.

Prescriptions are recipes of methods to be used in altering a forest stand.

Recruitment refers to the annual production of young in a population. It can be expressed as percentage of young or as the number of young per female (when the sex ratio is not equal) in the fall population.

ROMPA is the Ratio of Optimal to Marginal Patch Area within a habitat mosaic.

Scale refers to the overall area under consideration, as in a study or management activity.

Shelterwood is a forest regeneration method of establishing seedlings under overstory trees. As the young trees grow, portions of the overstory are subsequently harvested.

Silviculture refers to the practices involved in growing trees for timber production.

“Sink” habitat (see minimal patches).

“Source” habitat (see optimal patches).

Species is one of the taxonomic levels used to classify organisms (family, genus, species, subspecies).

Species viability refers to the probability of a species persisting over time.

Stands are areas of trees possessing sufficient uniformity or isolation to be distinguishable from trees on adjacent areas.

Survival compares the number of animals on an area after a period of time (month, season, year) with the number that were originally present.

VSS refers to the Vegetation Structure Stage of a forest. VSS 5 is a mature forest, and VSS 6 is an old forest.

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APPENDIX A

Life Cycle Graph and Model Development for the Abert's Squirrel

We formulated a life cycle graph for the Abert's squirrel that comprised two stages: young of the year and "adults" - yearlings or older. Because of the indication of lower adult female survival rates (0.52 vs. 0.81 for males), we used 68 percent as the "adult" survival rate. This was the lower end of the range of survival rates given by Dodd et al. (1998). We used an average litter size of 2.9 (1.45 female offspring) at emergence as the basis for calculating fertilities (Halloran 1993). We further assumed considerably lower survival in the first year, a value for which we solved by assuming that the population growth rate (λ) was 1.002. This "missing element" method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the species will go extinct or grow unreasonably large. We did not assume any change in fertility with age, though such changes are common in many species. From the resulting life cycle graph (**Figure A1**), we produced a matrix population

analysis with a post-breeding census for a birth-pulse population with a one year census interval (McDonald and Caswell 1993, Caswell 2001). The models had two kinds of input terms: P_{ij} describing survival rates, and m describing number of female offspring per female (**Table A1** and **Figure A2a**). **Figure A2b** shows the numeric values for the matrix corresponding to the life cycle graph of **Figure A1**. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the offspring number used was half the total annual production of offspring, assuming a 1:1 sex ratio. Note also that the fertility terms (F_{ij}) in the top row of the matrix include both a term for offspring production (m_i) and a term for the survival of the mother (P_{ij} from the census (just after the breeding season) to the next birth pulse almost a year later. The population growth rate (λ) was 1.002, based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.

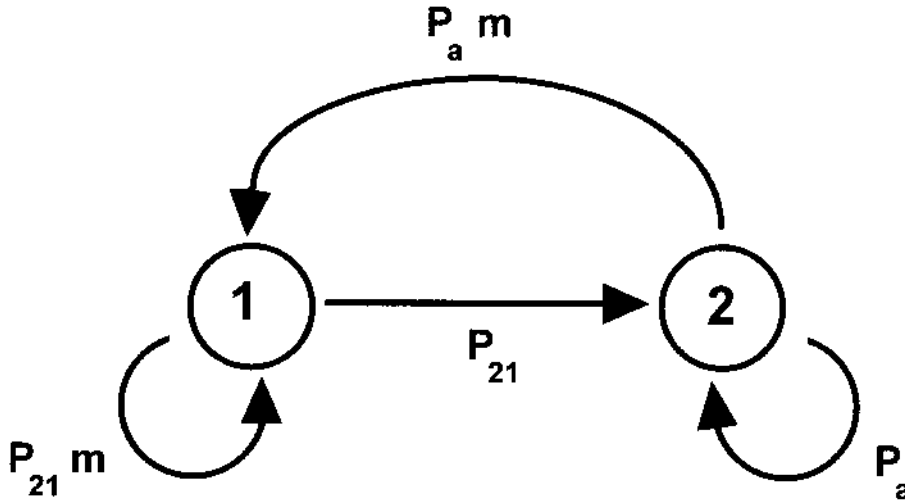


Figure A1. Life cycle graph for the Abert's squirrel. The numbered circles ("nodes") represent the three stages (first-year squirrels, second-year squirrels and "older adults"). The arrows ("arcs") connecting the nodes represent the vital rates — transitions between age-classes such as survival (P_{ij}) or fertility (F_{ij} , the arcs pointing back toward the first node).

Table A1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for Abert’s squirrels.

Parameter	Numeric value	Interpretation
m	1.45	Number of female offspring produced by a first-year female
P_{21}	0.222	First-year survival rate
P_a	0.68	Survival rate of “older adults”

	1	2
1	$P_{21}m$	$P_a m$
2	P_{21}	P_a

Figure A2a. Symbolic values for the projection matrix of vital rates, A (with cells a_{ij}) corresponding to the Abert’s squirrel’s life cycle graph of **Figure A1**. Meanings of the component terms and their numeric values are given in **Table A1**.

	1	2
1	0.322	0.986
2	0.222	0.68

Figure A2b. Numeric values for the matrix.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on population growth rate (λ) of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, A [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to population growth rate, which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of survival (P_{ij}) and fertility (F_{ij}) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of

vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth of endangered species or the “weak links” in the life cycle of a pest. **Figure A3** shows the “possible sensitivities only” matrices for this analysis (one can calculate sensitivities for non-existent transitions, but these are

	1	2
1	0.321	0.222
2	0.984	0.679

Figure A3. Possible sensitivities only matrix, S_p (blank cells correspond to zeros in the original matrix, A). The λ of the Abert's squirrel is most sensitive to changes in first-year survival (Cell $s_{21} = 0.984$) and "adult" survival (Cell $s_{22} = 0.679$).

usually either meaningless or biologically impossible — for example, the biologically impossible sensitivity of λ to the transition from Stage 2 "adult" back to being a Stage 1 first-year bird).

The summed sensitivity of λ to changes in survival (75.4 percent of total sensitivity accounted for by survival transitions) was greater than the summed sensitivity to fertility changes (24.6 percent of total). The single transition to which λ was most sensitive was first-year survival (44.6 percent of total). The second most important transition was "adult" survival (30.8 percent of total). The major conclusion from the sensitivity analysis is that survival rates, with a slight emphasis on first-year survival, are most important to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, an absolute change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 to

40 percent). On the other hand, an absolute change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus partly avoid the problem of differences in units of measurement (for example, we might reasonably equate changes in survival rates or fertilities of 1percent). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_{ij}) and survival (P_{ij}) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for Abert's squirrels are shown in **Figure A4**. λ was most elastic to changes in "adult"

	1	2
1	0.103	0.218
2	0.218	0.461

Figure A4. Elasticity matrix, E (remainder of matrix consists of zeros). The elasticities have the property of summing to 1.0. The λ of the Abert's squirrel is most elastic to changes in "adult" survival ($e_{22} = 0.461$), followed by first-year survival and "adult" fertility ($e_{21} = e_{12} = 0.218$).

survival ($e_{22} = 46.1$ percent of total elasticity). Next most elastic were first-year survival and “adult” reproduction ($e_{21} = e_{12} = 21.8$ percent of total elasticity). First-year reproduction was relatively unimportant ($e_{11} = 10.3$ percent of total elasticity). The sensitivities and elasticities for Abert’s squirrels were generally consistent in emphasizing survival transitions, with the elasticities placing a heavy emphasis on “adult” survival. Thus, survival rates are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The stable stage distribution (SSD, **Table A2**) describes the proportion of each stage or age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For Abert’s squirrels at the time of the post-breeding annual census (just after the end of the breeding season), emergent young of the year represent 59.2 percent of the population, and “adults” represent 40.8 percent of the population. Reproductive values (**Table A3**) can be thought of as describing the value of a stage as a seed for population growth relative to that of the first (newborn or, in this case, offspring at emergence) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of

a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is, by definition, 1.0. An “adult” female individual (Stage 2) is “worth” 3.1 offspring. The cohort generation time for this species was 3.1 years (SD = 2.6 years).

Stochastic model

We conducted a stochastic matrix analysis for Abert’s squirrels. We incorporated stochasticity in several ways (**Table A4**), by varying different combinations of vital rates, and by varying the amount of stochastic fluctuation. We varied the amount of fluctuation by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation we used a standard deviation of one quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Under Case 1 we subjected the fertility arcs (F_{11} and F_{12}) to high levels of stochastic fluctuations (SD one quarter of mean). Under Case 2 we varied the survival arcs (P_{21} and P_{22}) with high levels of stochasticity (SD one quarter of mean). Under Case 3 we varied only “adult” survivals (P_{22}) with high levels of stochastic fluctuation. Case 4 resembled Case 2 in varying both survival transitions, but with only half the level of stochastic fluctuation (SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution of the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The

Table A2. Stable age distribution (right eigenvector). At the census, 59.2 percent of the individuals in the population should be young of the year. An additional 40.8 percent will be “older adult” females with a mean age of 3.1 years.

Stage	Description	Proportion	Mean age (\pm SD)
1	Young of the year (to yearling)	0.592	0 \pm 0
2	“Older adult” females	0.408	3.1 \pm 2.6

Table A3. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, offspring at emergence) stage. The reproductive value of the first age-class or stage is, by definition, 1.0.

Age Class	Description	Reproductive Value
1	First-year females	1.0
2	“Older adult” females	3.1

Table A4. Results of four cases of different stochastic projections for Abert’s squirrels. Stochastic λ fluctuations have the greatest effect when acting on both survival transitions (Case 2).

	Case 1	Case 2	Case 3	Case 4
Input factors:				
Affected cells	All the F_{ij}	All the P_{ij}	P_{22} only	All the P_{ij}
S.D. of random normal distribution	1/4	1/4	1/4	1/8
Output values:				
Deterministic λ	1.002	1.002	1.002	1.002
# extinctions / 100 trials	0	77	65	1
Mean extinction time	N.A.	1,077	1,183	1,919
# declines / # surviving populations	49/100	20/23	31/35	55/99
Mean ending population size	354,835	12,679	27,197	156,465
S.D.	1.6×10^6	42,726	107,470	804,570
Median ending size	10,360	68	212	8,361
Log λ_s	-0.0001	-0.0077	-0.0062	0.0020
λ_2	1.0004	0.9995	0.9989	-0.0002
Percent reduction in λ	0.21	0.97	0.82	0.22

overall simulation consisted of 100 runs (each with 2,000 cycles). We calculated the stochastic growth rate, $\log \lambda_s$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table A4**) produced two major results. First, stochastic fluctuations in survival transitions had appreciably greater detrimental effects than did varying fertility transitions. Even low level stochastic fluctuations in survival (Case 4, SD of one eighth) resulted in more extinctions (1 vs. 0) and more declines (56 vs. 49) than did varying the fertility rates. High levels of stochastic fluctuation in survival (Cases 2 and 3) led to substantial extinction losses (e.g., 77/100 in Case 2). Second, the level of the stochastic fluctuations greatly affected the strength of the detrimental effects (Case 4 vs. Case 2; 77 extinctions vs. 1 extinction). The difference in the effects of which vital rate was most important is predictable largely from the elasticities. λ

was most elastic to changes in the first-year transitions. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model — the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. The extinctions and declines simulated should not be interpreted as estimates of extinction risk — instead they should be viewed as a way to compare the detrimental effects of stochasticity within the bounds of the models. That is, Case 4 (**Table A4**) does not indicate an 80 percent chance of extinction, but does suggest that fluctuations in survival rates will have much stronger effects on population dynamics than will fluctuations in fertility rates. These results indicate

that populations of Abert's squirrels are vulnerable to stochastic fluctuations in survival (due, for example, to variations in snowfall), especially when the magnitude of fluctuations is high. Nevertheless, the importance of "adult" survival to the life cycle of Abert's squirrels ($e_{22} = 0.461$ in **Figure A4**) may, to some extent, help buffer them against environmental stochasticity. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Abert's squirrels may, therefore, have responded evolutionarily by reducing factors that would lead to variability in "adult" survival.

Potential refinements of the models

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase confidence in any demographic analysis. The most important "missing data elements" in the life history for Abert's squirrels is for first-year survival, which emerges as a vital rate to which λ is sensitive as well as elastic. Better data on "adult" survival rates and their variability would also be useful. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on our "uncorrelated" assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation

among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of Major Conclusions from Matrix Projection Models

- ❖ Survival accounts for 75 percent of the total "possible" sensitivity, with first-year survival as the most important (45 percent of total) fairly closely followed by "adult" survival (31 percent of total). Any absolute changes in survival rates will have major impacts on population dynamics.
- ❖ "Adult" survival ($e_{22} = 46.1$ percent) and, to a lesser extent, first-year survival and "adult" reproduction ($e_{21} = e_{12} = 21.8$ percent) account for the great majority of the total elasticity. Proportional changes in survival rates will have a major impact on population dynamics.
- ❖ The reproductive value of "older" females is reasonably high. Thus "adult" females appear to be the key reservoir of population dynamics, and a buffer against environmental stochasticity, under the model formulated here.
- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of survival rates to population dynamics. Abert's squirrels appear fairly vulnerable to environmental stochasticity that would affect "adult" survival.

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APPENDIX B

MIS Species Assessments for Abert's Squirrels on National Forests in Region 2

Information provided by P. M. McDonald, Region 2 and staff on the Forests.

Grand Mesa, Uncompahgre, and Gunnison National Forest

A Forest Plan identified 17 MIS species, including the Abert's squirrel. Abert's Squirrel Species Assessment was prepared in 2001 and posted on the internet at <http://www.fed.us/cgi-bin/texis/searchallsites/search.allsites/xml.txt?query=abert+squirrel&db>.

San Juan National Forest (Mark Ball)

Abert's Squirrel Species Assessment was revised by Bob Frye and issued March, 2003.

Pike National Forest (Nancy Ryke)

MIS Assessment is in draft form.

Arapahoe – Roosevelt National Forest (Dennis Lowry)

The Abert's squirrel was selected as an MIS in the Forest Plan (1983), but no Species Assessment was prepared for the squirrel. The Forest Service HABCAP model and the Fish and Wildlife Service HIS model have been used to evaluate projects.

Rio Grande National Forest (Laurel Kagan-Wiley)

The Abert's squirrel has not been designated as an MIS. GAP analysis indicated there was only sparse habitat on the Forest. There was little baseline information on the squirrel and only weak techniques for monitoring the animal.

Routt National Forest (Jena Hickey)

There are no Abert's squirrels on the Routt Forest.

White River National Forest (Keith Giezentanner)

There are no Abert's squirrels on the White River Forest.

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