Pine Squirrel (*Tamiasciurus hudsonicus*)
A Technical Conservation Assessment

Prepared for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project

July 20, 2005

John L. Koprowski, Ph.D.
Wildlife Conservation and Management
School of Natural Resources
University of Arizona
Tucson, Arizona 85721

Peer Review Administered by
[Society for Conservation Biology]

Koprowski, J.L. (2005, July 20). Pine Squirrel (*Tamiasciurus hudsonicus*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/pinesquirrel.pdf [date of access].

ACKNOWLEDGMENTS

I thank Wendy McCoy for assistance in gathering data and literature. The comments of two anonymous reviewers and Bret Pasch markedly improved the manuscript. Respondents from various museums and state agencies were always helpful above and beyond the call of duty. A most sincere thanks to Dr. Greg Hayward for his assistance, editorial comments, and understanding throughout the completion of this assessment.

AUTHOR'S BIOGRAPHY

John L. Koprowski is an Associate Professor in the Wildlife and Fisheries Resources Program of the School of Natural Resources at The University of Arizona in Tucson. Originally born in Cleveland, Ohio, he holds degrees in Zoology from Ohio State University (BS) and Southern Illinois University (MA) and Biology from the University of Kansas (PhD). John serves as the Director of the Mt. Graham Red Squirrel Monitoring Project and the Desert Southwest Cooperative Ecosystems Studies Unit. His research program focuses on the ecology and conservation of small mammals with a particular emphasis on tree and ground squirrels. He has worked on each of the 10 species of tree squirrel found in North America over his nearly 20 years of research. He has authored numerous articles on the ecology of tree squirrels to include the text North American Tree Squirrels (co-authored with Michael Steele) published in 2001 by the Smithsonian Institution Press.

COVER PHOTO CREDIT

Pine Squirrel (*Tamiasciurus hudsonicus*). Photograph by Red Squirrel Monitoring Program, University of Arizona. Used with permission.

Summary of Key Components for Conservation of the Pine Squirrel

The pine squirrel (*Tamiasciurus hudsonicus*) is found in three states within USDA Forest Service Region 2: Colorado, South Dakota, and Wyoming. The species is under consideration as a potential Management Indicator Species (MIS) by the USDA Forest Service within Region 2 on the Bighorn National Forest. Pine squirrels are restricted to mature pine, Douglas-fir, fir, spruce, and mixedwood riparian forests in Colorado, Wyoming, and South Dakota within Region 2. Individuals live solitarily and vigorously defend territories around larderhoards of tree seed. Their heavy reliance on tree seeds for food and cover restricts the species to mature forests. Although widespread in suitable forests, local populations of pine squirrels can be threatened by increased fragmentation, catastrophic wildfire, timber practices that remove excessive areas of mature timber, and insect infestations that kill all seed producing conifers. Conservation requires retention of and management for continuous mature uneven aged forests that contain snags for nesting. Forestry practices that promote such conditions will favor pine squirrel populations. Pine squirrels are found in most conifer and mixedwoods forests with significant stem densities and canopy closure irrespective of anthropogenic or natural disturbances. Pine squirrels have a high biotic potential and are capable of moving at least several kilometers. Such characteristics likely enable pine squirrels to exist in the mosaic structure of natural forests that results from the multiple disturbances of fire, windblow, and insect outbreaks as well as the fragmented environments, anthropogenic mosaics, and monocultures that characterize many current forests.

TABLE OF CONTENTS

EDITOR: Greg Hayward, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Tables:

Figures:

INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the USDA Forest Service (USFS) Rocky Mountain Region (Region 2). The pine squirrel is the focus of an assessment because it is a proposed Management Indicator Species (MIS) on at least one national forest in Region 2. MIS serve as barometers for species status at the forest level and have two functions: 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 pine squirrel throughout its range in Region 2. Due to a dearth of studies in the Region, information was gathered from the literature on pine squirrels in other regions as well as from the appropriate state and federal agencies. I attempted to use data from similar ecosystems and adjacent states and provinces wherever possible.

Goal

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. Assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. This assessment does not seek to develop specific management recommendations. Rather it provides the ecological background upon which management may be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). This assessment also cites management recommendations proposed elsewhere and examines the success of those that have been implemented.

Scope

This assessment examines the biology, ecology, conservation status, and management of the pine squirrel with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although much of the literature on pine squirrels originates from field investigations outside the region, this document places that literature in the ecological and social context of the central Rocky Mountains, which represent only a small portion of pine squirrels extremely large range. Similarly, this assessment is concerned with behavior, survival, reproduction, population dynamics, interspecific interactions, and other characteristics of pine squirrels in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but placed in a current context. As a result, the long association of pine squirrels with coniferous habitats is addressed concurrently with historical trends in forest management in an attempt to understand the current status, distribution, conservation, and management of the species.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and data (particularly on sport harvest, range, timber harvest, and insect damage) accumulated by resource management agencies. Not all publications on pine squirrels are referenced in this assessment, nor are all published materials considered equally reliable. This assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were regarded with greater skepticism. Unpublished data (e.g. Natural Heritage Program records) were important in estimating the geographic distribution. These data required special attention because of the diversity of persons and methods used in their collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches of critical experiments to develop strong inference (Platt 1964). However, strong inference, as described by Platt, suggests that experiments will produce clean results (Hillborn and Mangel 1997), as may be observed in certain physical sciences. The geologist, T.C. Chamberlain (1897) suggested an alternative approach to science where multiple competing hypotheses are confronted with observation and data. Sorting among alternatives may be accomplished using a variety of scientific tools (e.g., experiments, modeling, logical inference). Ecological science is, in some ways, more similar to geology than physics because of the difficulty in conducting critical experiments and the reliance on observation, inference, good thinking, and models to guide understanding of the world (Hillborn and Mangel 1997).

Confronting uncertainty, then, is not prescriptive. In this assessment, the strength of evidence for particular ideals is noted, and alternative explanations are described when appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding.

Publication of Assessment on the World Wide Web

To facilitate their use, species assessments 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 reports. More importantly, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. This report was reviewed through a process administered by the Society of Conservation Biology, employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The pine squirrel is not federally protected throughout most of its range, including Region 2. Only the endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), a montane isolate in southeastern Arizona, is protected under the Endangered Species Act administered by the U.S. Fish and Wildlife Service. The species is not on any state or federal agency list of species of special concern in Region 2. It is considered a small game species in Colorado, South Dakota, and Wyoming. Wyoming lists the species as S5 (secure, no danger of extirpation) in its Natural Heritage Program Database. Pine squirrels are not found, and thus are not regulated, in Nebraska or Kansas.

Data on pine squirrel harvest are not available for either Wyoming or South Dakota. In Colorado, the 2002 hunting season for pine squirrels extended from 1 October until 28 February with a daily bag limit of five and a possession limit of 10 pine squirrels. During 2001, 599 hunters were reported to take 2,786 pine squirrels, with Jackson, Larimer, and Gunnison counties accounting for the majority of the squirrels harvested (n=583, 518, 486, respectively) (Colorado Division of Wildlife, www.wildlife.state.co.us). In neighboring North Dakota, 22.3 percent of the 2000 season take of 10,963 squirrels by 2,502 individuals was reported by hunters to be pine squirrels; annual harvest of pine squirrels varied from 41.5 percent of the squirrels taken in 1996 (the first year for which data were available) to 15.3 percent in 1999 (North Dakota State Game and Fish Department 2001).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Management plans for the species do not exist in most states. In South Dakota the species is restricted to the Black Hills region and is not monitored (John Forney, South Dakota Game Fish and Parks, personal communication, 19 March 02). Populations in Wyoming are not monitored either. Colorado does monitor take at voluntary game stations in some counties, but the statewide population of pine squirrels is not monitored.

Current laws, regulations, and management are likely adequate to conserve pine squirrels given the low reported hunting pressure throughout Region 2 and the local nature of other threats. However, little data are available on the status of populations in some isolated mountain ranges in both Wyoming (Bighorn Mountains and Black Hills) and South Dakota (Black Hills), and the species' range within eastern South Dakota and neighboring North Dakota has not been well documented. Thus, overharvest or certain timber harvest practices in these isolated populations could have more impact than in larger, more continuous populations such as in Colorado.

Biology and Ecology

General description and taxonomy

The pine squirrel is also commonly referred to as the red squirrel, chickaree, or boomer (**Figure 1**). This small-bodied tree squirrel is generally red to tawny to gray on the dorsum with a white venter; its tail is frosted with buff or white. In the winter, its pelage is often more tawny in color, and short ear tufts are present. Twenty-seven subspecies are reported for *Tamiasciurus hudsonicus* with four reported in Region 2 (from Steele 1998). No other members of the same genus are found

Figure 1. The pine squirrel (*Tamiasciurus hudsonicus*). Photograph by Red Squirrel Monitoring Program, University of Arizona. Courtesy of J.L. Koprowski.

in Region 2. *Tamiasciurus h. fremonti* is the only subspecies found in Colorado (Fitzgerald et al. 1994), and its range extends into extreme southern Wyoming (Long 1965). *Tamiasciurus h. dakotensis* is found in the Black Hills of South Dakota and Wyoming (Long 1965, Turner 1974, Clark and Stromberg 1987). *Tamiasciurus h. baileyi* is found in the Bighorn Mountains and associated mountains of central Wyoming while *T. h. ventorum* is found throughout northwestern Wyoming (Long 1965, Clark and Stromberg 1987). *Tamiasciurus h. minnesota* is found in North Dakota and is likely the subspecies reported from northeastern South Dakota (Over and Churchill 1941).

No genetic assessment has been conducted on the pine squirrels of Region 2, and subspecific assignments have been based primarily on morphology and geographic isolation. A thorough, systematic study to include genetic assessment is sorely needed throughout the range of the species. Arbogast et al. (2001) focused on populations of western North America, and using data from mtDNA and allozymic assessments, they found squirrels in Region 2 to be a closely related clade. Vocalizations of pine squirrels in Wyoming and Colorado also suggest that subspecific differentiation occurs (Yamamoto et al. 2001).

Distribution and abundance

The pine squirrel is extraordinarily widespread for a small mammal (**Figure 2**). Its range extends from southern Arizona, southern New Mexico, and possibly western Texas (Bailey 1931) throughout most of the Rocky Mountains northward to Alaska (Steele 1998). In the north, the range of the pine squirrel extends across the forested regions of the central provinces of Canada into all eastern provinces. Pine squirrels occur throughout the Appalachian Mountains and the Great Lakes states (Steele 1998). The species is not of conservation concern in any region within its extensive range except for the isolated population of the endangered Mt. Graham red squirrel in southeastern Arizona (U.S. Fish and Wildlife Service 1993).

In Region 2, the species is not found in Kansas or Nebraska (Jones et al.1983). In South Dakota, pine squirrels are often considered to be restricted to the Black Hills (Jones et al. 1983), but undocumented sightings of the species are reported from Roberts and Grant counties in the northeastern part of the state (Higgins et al. 2000). Over and Churchill (1941) report observations in 'the timbered area along the west side of Big Stone Lake [Grant County]', and Bailey (1926)

Figure 2. The expansive range of the pine squirrel in North America (after Hall 1981).

mentions sightings in extreme southeastern North Dakota adjacent to these areas, lending credence to the existence of pine squirrels in this area of South Dakota.

Distribution is poorly known in neighboring North Dakota, however, squirrels have been reported from the Red River valley and major tributaries of the eastern border, along the Sheyenne River up into the vicinity of Stump Lake in Nelson Co., along the Goose River at least through Portland, and entering from Canada in the Turtle Mountains and Pembina Hills of the extreme northcentral portion of the state as far south and west as the banks of the Souris River at Towner in McHenry County (Bailey 1926). The status of the northcentral populations and the interior Sheyenne River populations are not well known (Lowell A. Tripp, personal communication, 27 March 2002).

In Colorado, pine squirrels are found or suspected to occur in all counties with conifer habitat above 1800 m in the western half of the state (Warren 1942, Armstrong 1972, Fitzgerald et al. 1994). A similar distribution is found throughout the western and central mountains of Wyoming as well as the Black Hills (Long 1965, Turner 1974, Clark and Stromberg 1987).

Few data are available on historic abundance or trends in pine squirrels. Range may have decreased in North Dakota when current distribution is compared to that found in the late 1890's by Bailey (1926); however, present distribution of the species remains poorly known in this state. Densities of pine squirrels typically range from 0.2 to 2.0 squirrels/ha (Gurnell 1987, Steele 1998). Pine squirrels are present in most coniferous forest types from high elevation spruce-fir

(*Picea-Abies*) and lodgepole pine (*Pinus contorta*) forests to low elevation ponderosa pine (*P. ponderosa*), jack pine (*P. banksiana*), and pinyon pines (*P. edulis*) as well as mixed riparian forests with significant proportions of deciduous species including aspens (*Populus tremuloides*) and cottonwoods (*Populus* spp.) in Region 2 (Bailey 1926, Long 1965, Jones et al. 1983, Clark and Stromberg 1987, Fitzgerald et al. 1994, Higgins et al. 2000). Whitebark (*Pinus albicaulis*; Mattson and Reinhart 1996) and lodgepole (Sullivan and Moses 1986, Sullivan and Klenner 1993) pine forests often possess high densities of squirrels. Ponderosa pine forests are used except in areas where Abert's squirrels (*Sciurus aberti*) are present and appear to competitively exclude pine squirrels (Ferner 1974). Plantations of red pine (*P. resinosa*) and Norway spruce (*Picea abies*) in Colorado appear to be used less frequently (Gurnell 1984).

Few data are available on historic abundance of pine squirrels. Densities of pine squirrels typically range from 0.2 to 2.0 squirrels per ha (Gurnell 1987, Steele 1998).

Population trends

Little quantitative data are available on pine squirrel population trends. Historic distributions in some states of the upper Midwest have declined (Bowles 1975, Hoffmeister 1989) while in other areas distributions have expanded (Mumford and Whitaker 1982, Goheen et al. 2003). Introductions to Newfoundland were successful, and populations rapidly increased to cover the entire island (Hall 1981). In Region 2, long-term data are lacking for individual or regionwide populations.

Activity pattern

Pine squirrels are diurnal throughout their range (Gurnell 1987). Inactive periods are spent in nests or subnivean tunnels (Zirul and Fuller 1970). During winter, a unimodal activity period is centered on midday while a bimodal diel activity pattern is evidenced in summer (Pruitt and Lucier 1958, Deutch 1978, Pauls 1978, Gurnell 1987). Activity patterns likely vary with seasonal changes in day length associated with latitude and attitude. Pine squirrels do not hibernate; they remain active throughout the winter although activity is reduced and short periods of torpor are known to occur (Pauls 1979).

Pine squirrels are territorial and relatively sedentary; home ranges of about 1 ha are most commonly centered around a conspicuous midden of stored cones and cone scales (**Figure 3**; C.C. Smith 1968, Finley 1969, Lair 1987, Munroe et al. in press). Vocalizations are often used in response to territorial incursions (Smith 1978, Gurnell 1987). No seasonal or annual migrations have been reported for pine squirrels, but males do expand their range during the breeding season (C.C. Smith 1968, Arbetan 1993). Most juveniles disperse from natal territories during their first year of life, and there is no sex bias in dispersal (Klenner 1991, Larsen and Boutin 1994, Sun 1997). Prior to natal dispersal, juveniles range up to 1 km from their natal area on forays (Larson and Boutin 1994, Sun 1997). Breeding dispersal is also known to occur; however, adult females are particularly reluctant to move even when prompted by supplemental food (Klenner 1991, Larsen and Boutin 1995, Larsen et al. 1997).

Populations of pine squirrels in western North America are often isolated in forested mountains surrounded by less suitable areas/vegetation types (Arbogast et al. 2001, Young 2001). Not surprisingly, this isolation appears to result in divergence at the subspecific level. The only subspecies that is federally endangered is the montane endemic Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) in southeastern Arizona (USFWS 1993). The four subspecies of pine squirrel found in Wyoming are clearly delineated by isolated mountain ranges (Long 1965). Populations in North Dakota and eastern South Dakota appear to rely on connectivity through riparian forests. These habitats are also preferred for urban and agricultural development; however, the effect of development on movement rates is unknown. Development may create edge and thus inhibit successful movement of squirrels through riparian forests. The Turtle Mountain population in north central North Dakota may be dependent on its linkages with other pine squirrel populations to the north in the prairie provinces of Canada.

Habitat

Pine squirrel dependence on trees for food and nests restricts them to forests with a mature tree component capable of producing quality tree seeds. Highest quality forests are typically described as mature boreal coniferous forests because these forests provide food resources through seed production by mature trees and shaded environments through high canopy closure that facilitate foraging, maintain appropriate microclimates for middens, and provide cover from predators (Rusch and Reeder 1978, Flyger and Gates 1982, Vahle and Patton 1983, Mahan and Yahner 1992,

Figure 3. A pine squirrels midden composed primarily of cone scale debris. Photograph by the Red Squirrel Monitoring Program, University of Arizona. Courtesy of J.L. Koprowski.

Steele 1998). Forest types that are more open are used, and pine squirrels appear to use second growth forests as frequently as old growth forests (Ransome and Sullivan 1997). Densities of pine squirrels typically range up to 2.0 squirrels per ha (Gurnell 1987). Pine squirrels are present in most coniferous forest types throughout Region 2, especially in whitebark and lodgepole pine forests (Sullivan and Moses 1986, Sullivan and Klenner 1993). Mixed coniferous-deciduous forests that include aspen, fence rows, old orchards, beech-maple-hemlock, mixed hardwoods, and developed suburban and urban parklands serve as habitat in many eastern forests (Layne 1954, Yahner 1980, 1986, 1987, Mahan and Yahner 1992). Seasonal use of habitats has not been reported; however, during prolonged periods of snow cover pine squirrels can spend the vast majority of their active periods in the subnivean environment (Pruitt and Lucier 1958, Zirul and Fuller 1970).

Nest and midden habitat and associated territories

Nest site selection is important for thermoregulation, cone and fungal storage, and predator avoidance (Hatt 1929, Layne 1954, C.C. Smith 1968, Rothwell 1979, Fancy 1980). Cavities in snags or decadent logs are commonly used and may be preferred to other nest types for they are commonly used by pine squirrels in the eastern portion of their range (Hamilton 1939, Layne 1954). In coniferous and mixed forests, cavities may be limiting, and nests constructed of leaves (also termed dreys) (Rothwell 1979, Fancy 1980, Young et al. 2002) and underground burrows (Hatt 1929, Yahner 1980) are most often used. Nest sites are typically in stands of trees with large diameter and significant canopy closure and interdigitation with adjacent trees (Rothwell 1979, Fancy 1980, Vahle and Patton 1983, Young et al. 2002).

Midden sites require cool temperatures and moist environs for optimal storage of cones (Shaw 1936, C.C. Smith 1968, Finley 1969). In spruce-fir and mixed forests of Arizona, pine squirrel midden sites exhibit high canopy closure, high foliage volume, numerous decadent logs, many standing snags, and high stem density relative to random sites (Vahle and Patton 1983, Smith and Mannan 1994). Territories are usually centered around middens likely because they contain one to two years of cone resources (C.C. Smith 1968, Gurnell 1984) and are critical to pine squirrel survival (M.C. Smith 1968). Territory size appears to be determined in large part by the energetics of cone acquisition (C.C. Smith 1968, 1981). Territory sizes across a wide variety of forest types typically are less than 1 ha (Gurnell 1987, Munroe et al. in press). Territory size increases markedly during years of food shortage (M.C. Smith 1968) or in suspected marginal habitat (Kreighbaum and Van Pelt 1996, Munroe et al. in press). Gurnell (1987) provides a thorough review of territory size (mean ± SD) relative to forest type; territories are smallest in white spruce (0.24 ± 0.07 ha, Rusch and Reeder 1978), Wyoming mixed conifer (0.28 ± 0.09 ha, Rothwell 1977), mixed spruce (0.35 ± 0.07 ha, Rusch and Reeder 1978), western hemlock (0.51 ± 0.18 ha, C.C. Smith 1968), lodgepole pine (0.48 ± 0.16 ha, Rothwell 1977; 0.60 ± 0.13 ha, Gurnell 1984; 0.91 ± 0.20 ha, C.C. Smith 1968), and jack pine (0.66 ± 0.45 ha, Rusch and Reeder 1978).

The ability of pine squirrels to use a diversity of forest types (Layne 1954, Steele 1998) suggests that many forest mosaics may provide habitat. The primary landscape feature that appears to limit pine squirrel use of forest landscapes is fragmentation by any stand replacement agent including harvest, fire, or insect-induced mortality. The resulting isolation of stands appears to be one means by which fragmentation influences pine squirrels. Pine squirrels often range out to 1 km from their territory (Larsen and Boutin 1994) and demonstrate a strong homing instinct (Bovet 1984, 1991); however, edge habitats appear to be avoided (King et al. 1998, Cotterill and Hannon 1999). Thirty-nine percent of translocated animals crossed gaps to return to their home territory if the gap was relatively short compared with alternative routes. This result illustrates the complexities of habitat fragmentation (Bakker and Van Vuren 2004). On a range-wide basis, small fragments of habitat tend to have high densities of pine squirrels (Koprowski 2005). Such findings suggest that forest mosaics that maintain canopy cover over continuous areas provide habitat for pine squirrels (Carey 2001).

Food habits

Pine squirrels are granivores (Steele 1998). No sex or age specific differences in diet or foraging behaviors have been reported. *Tamiasciurus hudsonicus* feed heavily on the seeds of coniferous trees including all pines (*Pinus*), true firs (*Abies*), Douglas-firs (*Psuedotsuga menziesii*), and spruce (*Picea*) (C.C. Smith 1968, Gurnell 1987). Squirrels typically clip cones from trees in late summer and fall; seeds from some cones are immediately consumed by removing individual cone scales to access seeds beneath (C.C. Smith 1968, Finley 1969). The core of the cone is discarded. Cone cores resulting from the feeding of pine squirrels are very neatly clipped with little remaining stubble from cone scales and can be easily distinguished from the relatively stubble-ridden cores of Abert's squirrels (Rasmussen et al. 1975). Cones not immediately eaten are often stored in large larderhoards in traditional middens of debris resulting from scaling of previous year's cones (Finley 1969). Squirrels rely on larderhoarded cones throughout the winter. Some cones are also scatterhoarded as singletons or in small groups (Hurly and Robertson 1986) particularly in forests in eastern North America where pine squirrels do not form middens (Hatt 1929, Layne 1954, Duetch 1978). In these eastern mixed forests and in lower elevation forests of the West, pine squirrels often rely on mast of oaks (*Quercus*), walnut (*Juglans*), beech (*Fagus*), hickory (*Carya*), maple (*Acer*), tulip tree (*Liriodendron*), and sycamore (*Platanus*) (Hatt 1929, Layne 1954, C.C. Smith 1968). A variety of tree tissues and products are secondary foods of pine squirrels including buds, flowers, fruits, sap, cambium, bark, and galls (Klugh 1927, Hosley 1928, Hatt 1929, Hamilton 1939, Kilham 1958, Linzey and Linzey 1979, Salt and Roth 1980, Gurnell 1987, Heinrich 1992). Damage associated with bark stripping to access cambium is apparent particularly during winter as girdling or the clipping of branch tips (Hosley 1928, Pike 1934, Cook 1954, Tackle 1957, McKeever 1964, Rasmussen et al. 1975).

Fungi are also a major component of pine squirrel diets, particularly during summer and autumn (C.C. Smith 1968). Both hypogeous and epigeous fungi are eaten or cached, and squirrels often dry fungi in the canopy or cavities for consumption throughout the winter (C.C. Smith 1968, M.C. Smith 1968, Gurnell 1987). Animal foods are also consumed opportunistically. These include insects (Hamilton 1939, Layne 1954), bones, antlers (Koprowski personal observation), birds (eggs, nestlings, and adults; Layne 1954, Rathcke and Poole 1974, Reistma et al. 1990, Bayne and Hobson 2000), and small mammals to include cottontails (*Sylvilagus floridanus*; Hamilton 1939), eastern gray squirrels (*Sciurus carolinensis*; Hamilton 1939), and chipmunks (*Tamias dorsalis*; Koprowski personal observation).

Such dietary flexibility and hoarding strategies enable pine squirrels to effectively cope with the seasonality of available food resources found at temperate latitudes. In addition, fruiting of trees is notoriously variable, with most species only producing large crops of seed in three to six-year intervals known as mast years (Silvertown 1980). The ability to feed on a diversity of species and on numerous plant tissues, fungi, and animals permit pine squirrels to energetically cope with the vagaries of coniferous forest ecosystems. A generalized year of pine squirrel food habits includes feeding on cones and other mast beginning in summer and relying on stores of these items through the winter. Additionally, fungi supplement the summer diet when the fruiting bodies are fresh, and stores are used over winter (Steele 1998). Squirrels quickly incorporate developing buds and insects into their diet as these items become available in spring and early summer while continuing to use any remaining cone or mushroom stores.

Squirrel population dynamics appear to be closely associated with cone crops of coniferous trees; reproduction and density are often related to food availability (Rusch and Reeder 1978, Gurnell 1984, 1987). Mast years, years when trees produce prolific numbers of cones, are usually followed by excellent reproduction and squirrel population growth while cone failures result in poor reproduction and recruitment (M.C. Smith 1968, Erlien and Tester 1984, Gurnell 1984, 1987). The major conifers within Region 2 produce cones at irregular intervals (Fowells 1965, Burns and Honkala 1990). Typically, pine cones (*Pinus*) develop over two or even three years while cones of true firs (*Abies*), Douglas-fir (*Pseudotsuga*) and spruce (*Picea*) develop over the course of a single year. Species described as dependable seed producers in Region 2 include Engelmann spruce (*P. engelmannii*), blue spruce (*P. pungens*), and lodgepole pine (Burns and Honkala 1990).

Breeding biology

Typical of many tree squirrels, male and female pine squirrels are able to breed as yearlings (Gurnell 1987). Ovulation is spontaneous (Millar 1970). Females are in behavioral and physiological estrus for less than one day per breeding season when the vulva enlarges to three to four times its normal size (Smith 1968, Arbetan 1993). Males are capable of breeding over extended periods when their testes descend into the scrotum; testes estrous diminish and are withdrawn into the abdomen when males are not reproductively active. Most males are reproductively active from December until August (Layne 1954). Females in mild climates with extended growing seasons may produce two litters per year (Layne 1954, Wrigley 1969, Millar 1970, Linzey and Linzey 1971); however, a single litter is most common in western North America and at high elevations (Hatt 1929, Smith 1968, Davis 1969, Kemp and Keith 1970, Millar 1970, Ferron and Prescott 1977, Prescott and Ferron 1978, Young 1995, Munroe et al. in press), including Colorado (Dolbeer 1973). Females are known to produce litters in consecutive years (Gurnell 1987) and may do so fairly commonly in some populations (Koprowski personal observation). Most litters in Colorado appear to be conceived from April through June (Dolbeer 1973). In other regions, females may be found in estrus from February through July (Layne 1954, Lair 1985, Arbetan 1993, Munroe et al. in press). Mating occurs during a female's single day of estrus when numerous males congregate around the receptive female and compete vigorously for access to the female; females may mate with more than one 1 male (Smith 1965, Smith 1968, Koford 1982, Arbetan 1993, Munroe et al. in press). Males do not assist with parental care (Smith 1968, Boutin et al. 1993).

Gestation lasts approximately 33 days (range 31-40 days; Hamilton 1939, Ferron and Prescott 1977, Lair 1985). Pregnant females typically demonstrate moderately swollen teats that become hairless and distended while nursing; teats retain a blackened pigmentation for at least a year following lactation (Layne 1954). The proportion of females producing a litter during a given year can range widely from 0 percent to nearly 100 percent (Smith 1968, Kemp and Keith 1970, Dolbeer 1973, Becker 1993, Young 1995) and appears crudely related to seed crop availability (reviewed in Gurnell 1987). Litter size varies from 2.7 to 5.4 (Layne 1954, Wood 1967, Smith 1968, Davis 1969, Kemp and Keith 1970, Millar 1970, Ferron and Prescott 1977, Steele 1998, Munroe et al. in press).

Natal nests can be ground, drey, or cavity (Hatt 1929, Hamilton 1939, Layne 1954, Yahner 1980). Young emerge after about seven weeks and are weaned by about eight weeks of age (Layne 1954, Nice et al. 1954). Juveniles often explore areas up to 900 m from the natal nest prior to dispersal (Larsen and Boutin 1994, Sun 1997). The vast majority of young disperse from their natal area (Price et al. 1986, Boutin et al. 1993, Kreighbaum and Van Pelt 1997); however, many settle within 500 m of the natal area (Larsen and Boutin 1994). In a small number of cases, adult females bequeath their midden and associated territory to their offspring through a short distance post-breeding dispersal event (Price et al. 1986, Boutin et al. 1993, Price and Boutin 1993). Breeding biology has the potential to influence estimation and enumeration methods that require assessment of midden activity and detection of individuals. During the breeding season, male home ranges often increase as males search for estrous females. In addition, natal dispersal of juveniles results in an influx of individuals moving within a location, thus changing probability of detection and likely inflating estimates of animal abundance.

Demographics

Genetics

Genetics of pine squirrels are poorly described. Pine squirrels have a 2N=46 chromosome number. Mitochondrial DNA analyses of most recognized subspecies in the western and southwestern United States suggests that differentiation is not as great as might be expected for subspecies (Arbogast et al. 2001). Protein electrophoresis of isolated montane subspecies of the southwestern United States suggested that some of the most isolated populations did possess fixed electromorph differences (Sullivan and Yates 1995). Despite the suggestion of reduced genetic variation in isolated populations (Sullivan and Yates 1995), consequences of low levels of variation are not known. Intergeneric hybridization between pine squirrels and other tree squirrels has not been reported (Gray 1972). Interspecific hybridization is suspected to occur in parapatric populations of pine squirrels and Douglas squirrels (*Tamiasciurus douglasii*) in the Pacific Northwest (Smith 1968, Hatton and Hoffman 1979, but see Lindsay 1982). Douglas squirrels do not occur in Region 2.

Survivorship

Trends in age-specific pine squirrel survivorship demonstrate a classic mammalian Type III survivorship curve (Steele 1998) in which mortality is high (>60 percent) during the first year of life, about half that rate during the second year of life followed by relatively high survivorship and constant mortality through the adult years (Kemp and Keith 1970, Davis and Sealander 1971, Rusch and Reeder 1978, Halvorson and Engeman 1983, Erlien and Tester 1984). Juvenile survival during the first three months is markedly lower than adult survival (Boutin and Larsen 1993, Stuart-Smith and Boutin 1995a), but it then often approaches adult survival by the first winter of life (Stuart-Smith and Boutin 1995a). Sex-specific survivorship is often higher for females than males (Halvorson and Engeman 1983, Erlien and Tester 1984, Boutin and Larsen 1993). Maximum reported longevity in captivity is nine years (Klugh 1927), and in the wild it is reported to be 10 years (Walton 1903). Studies of radio-collared animals suggest that predation accounts for a large proportion of mortality in red squirrels (Kemp and Keith 1970, Rusch and Reeder 1978, Stuart-Smith and Boutin 1995a,b, Kreighbaum and Van Pelt 1996, Wirsing et al. 2002). Availability of alternative prey for predators (Stuart-Smith and Boutin 1995a), availability of food for pine squirrels (Halvorson and Engeman 1983, Wirsing et al. 2002), and inter-individual variation in vigilance and use of open habitats (Stuart-Smith and Boutin 1995a) may predispose animals to higher susceptibility to predation. Food availability may be positively correlated with juvenile survival (M.C. Smith 1968, Halvorson and Engeman 1983); however, food supplementation studies generally do not demonstrate significant increases in survivorship of juveniles or adults (Sullivan 1990, Klenner 1991, Boutin and Larsen 1993).

Some authors have considered predation a minor factor for pine squirrel populations (Layne 1954, Stuart-Smith and Boutin 1995b) while others have suggested that a minimum of 19 percent and perhaps as much as 70 percent of pine squirrel mortality was due to predators (Kemp and Keith 1970, Rusch and Reeder 1978, Wirsing et al. 2002). In Idaho, the annual predation rate was 72 percent of 113 pine squirrels over a two year period (Wirsing et al. 2002). On Mt. Graham in southern Arizona, 40 percent of 10 radio-collared squirrels were killed by avian predators over 6 months, a rate very similar to Idaho (Kreighbaum and Van Pelt 1996).

Two Population Viability Analysis approaches have been used to model the endangered Mt. Graham red squirrel population in southeastern Arizona using vital rate data from pine squirrel populations throughout the species' range. Buenau and Gerber (2004) used a Leslie matrix, stage-based approach with three age classes (juvenile, yearling, and >2 year old females) and parameterized the model with data from published studies (**Table 1**). Their elasticity analysis suggests that pine squirrel populations were particularly sensitive to changes in adult survivorship (**Figure 4**). These results were corroborated by a spatially-explicit model applied to Mt. Graham by Harding et al. (in review). Catastrophic fire and variable tree seed crops were also implicated by the model as important external variables influencing dynamics of pine squirrels based on interpretation of the elasticity analyses (Harding et al. in review).

Anthropogenic sources of direct mortality on pine squirrels are generally from three sources: trapping (Obbard 1987), hunting (Flyger and Gates 1982), and motor vehicles (Hatt 1929, Hamilton 1939). Starvation has been reported as the most likely cause for a small number (<3 percent) of adults and juveniles over several years in the Yukon (Stuart-Smith and Boutin 1995a). Death due to malocclusion of incisors

Table 1. Demographic parameters used for pine squirrel sensitivity analysis (Buenau and Gerber 2004). Condition refers to the range of values used in the analysis. Low conditions represent the lower range of values reported in the literature for the parameter, and high conditions refer to the upper range of values.

		Age class		
Condition	**Parameter**	**Juvenile**	**Year 2**	**Year 3**
Low	Litter Size	0.00	1.00	1.00
	% Breeding	0.00	0.29	0.29
	Survival	0.21	0.44	0.39
Average	Litter Size	0.00	1.50	1.50
	% Breeding	0.00	0.50	0.63
	Survival	0.33	0.57	0.73
High	Litter Size	2.00	2.00	2.00
	% Breeding	0.43	0.63	0.80
	Survival	0.45	0.66	0.74

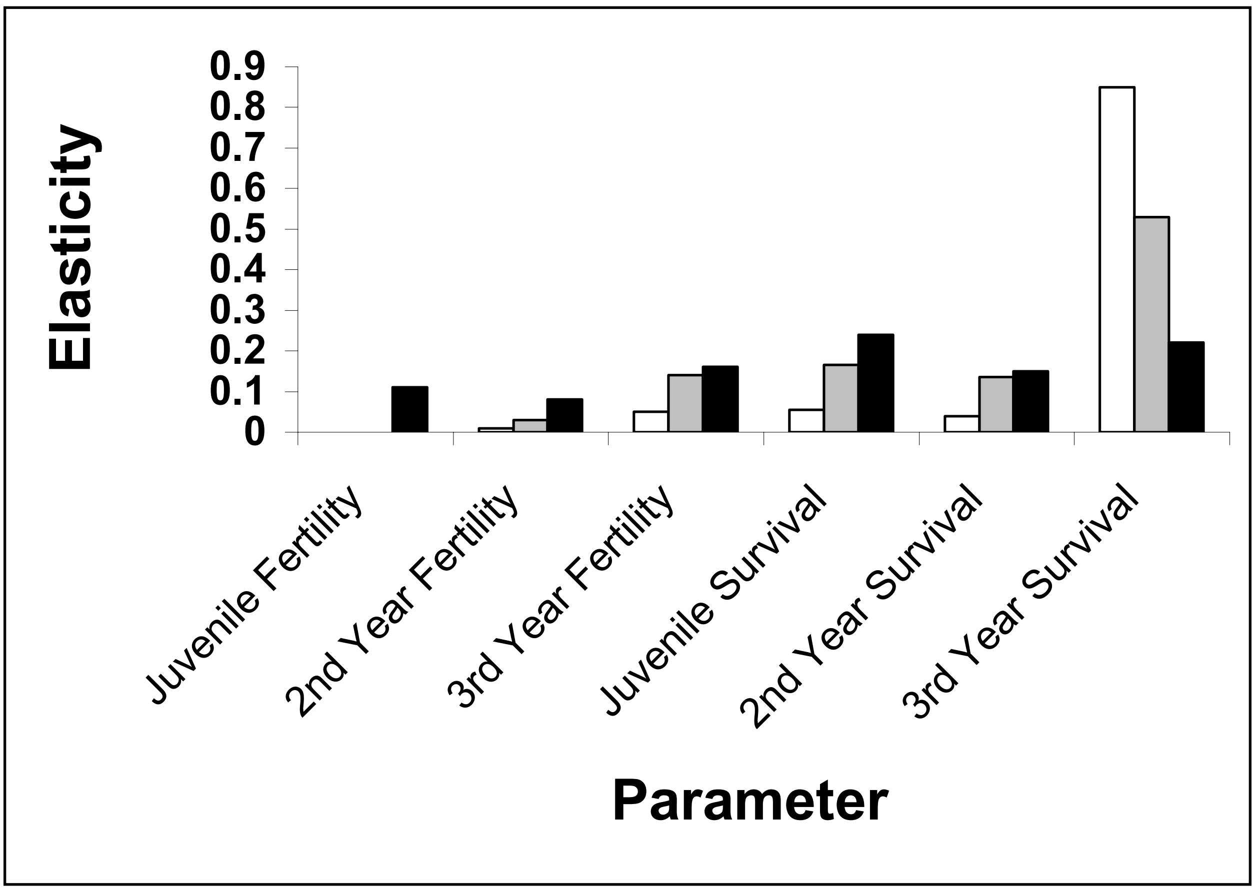

Figure 4. Elasticity values for population growth in response to variations in demographic parameters under three conditions: low ☐, average ☐, and high ■, after Buenau and Gerber 2004. Low, average, and high ranges for demographic parameters used in the analysis are provided in **Table 1**.

has also been reported (Emmons 1840 in Hatt 1929). Mortality directly caused by pathogens has not been well documented and is complicated by the fact that individuals in poor condition due to another cause may be more susceptible to infection. For instance, Hamilton (1939) reports finding two nearly dead, emaciated adult male red squirrels that had large burdens of fleas.

Social structure and space use

The social system of pine squirrels clearly influences population regulation. Pine squirrels are territorial in coniferous forests of western and northern North America; however, some populations in the deciduous and mixed forests of the eastern United States do not demonstrate territorial defense (Munroe et al. in press). A single resident vigorously defends its territory through aggressive chases and vocalizations (Smith 1968, 1978, Gurnell 1984). As a result, social limitations of immigration and recruitment strongly influence population density. Removal experiments demonstrate that vacant territories are very quickly occupied although the source of the floaters is not known (Boutin and Schweiger 1988, Klenner and Krebs 1991, Larsen and Boutin 1995).

Nearly all young disperse from their natal territory (Price et al. 1986, Boutin et al. 1993, Kreighbaum and Van Pelt 1997); however, most juveniles settle within 500 m from the natal area (Larsen and Boutin 1994). In a small number of cases, adult females bequeath their midden and associated territory to their offspring through a short-distance, post-breeding dispersal event (Price et al. 1986, Boutin et al. 1993, Price and Boutin 1993). Such breeding dispersal of adults is uncommon especially among females but does occur when vacancies result from natural or experimental removal of residents (Boutin and Schweiger 1988, Klenner 1991, Larsen and Boutin 1994, 1995).

Spatial aspects of pine squirrel demography, including both source-sink and metapopulation dynamics, are poorly known. Second-growth forests have been considered 'sinks' based on rapid turnover rates (Sullivan and Moses 1986). However, the application of this pattern to the disturbance-prone forests of the central Rocky Mountains is unknown. Pine squirrels appear to often be less common in edges of mixed forest woodlots in New Hampshire and Alberta (King et al. 1998, Cotterill and Hannon 1999), and densities are greater in small woodlots in boreal forests of Saskatchewan (Bayne and Hobson 2000). Dispersing individuals often explore and settle at distances of 500 to 900 m from their natal areas (Larsen and Boutin 1994). Furthermore, pine squirrels demonstrate a very strong homing ability and can return to their midden without prior experience in the matrix that they must cross (Bovet 1984, 1991). This suggests that individuals are adapted to cope with movements outside of their normal home range or territory.

Population regulation

Population growth may be food limited during extraordinarily poor food crops (M.C. Smith 1968, Erlien and Tester 1984) as density often, but not always, increases with food supplementation (Sullivan 1990, Klenner and Krebs 1991, Boutin and Larsen 1993) and territory size is related to available food (M.C. Smith 1968, Sullivan 1990). Removal experiments also suggest that social factors can be a mechanism for population regulation (Boutin and Schweiger 1988, Klenner 1991, Larsen and Boutin 1994, 1995), at least at high densities when territories become densely packed but a minimal territory size is required for survival (Rusch and Reeder 1978). Poor body condition predisposes individuals to predation as a proximate mechanism for mortality (Wirsing et al. 2002); cover from predation may also be limiting, as predation often accounts for the vast majority of mortality in a local population (Kemp and Keith 1970, Rusch and Reeder 1978, Stuart-Smith and Boutin 1995a,b, Kreighbaum and Van Pelt 1996, Wirsing et al. 2002). Response of pine squirrels to fragmentation with an apparent avoidance of edge habitats suggests that in fragmented landscapes, loss of available habitat may be greater than suggested by the extent of forest removal due to edge effects (King et al. 1998, Cotterill and Hannon 1999, Bayne and Hobson 2000). Furthermore, midden densities are reduced in residual forest fragments and corridors, relative to intact forest (Cote and Ferron 2001). Despite the reduction in middens, demographic parameters did not differ in fragments and corridors three to five years post-harvest (Cote and Ferron 2001). Populations of pine squirrels appear to be competitively excluded by Abert's squirrels in Colorado (Ferner 1974, Gurnell 1987) and Arizona (Hoffmeister 1956, Minckley 1968) suggesting that habitat that could be occupied is not available.

Community ecology

Pine squirrels have been reported as prey for a large number of vertebrates (Flyger and Gates 1982, Gurnell 1987, Obbard 1987, Steele 1998). Weasels (*Mustela erminea* and *M. frenata*; Rusch and Reeder 1978), fishers (*M. pennanti*), martens (*M. americana*), red fox (*Vulpes vulpes*), lynx (*Lynx lynx*), and bobcat

(*L. rufus*; Schauffert et al. 2002) are known to prey or attempt to prey on pine squirrels. Significant avian predators include great horned owls (*Bubo virginianus*), great gray owls (*Strix nebulosa*), spotted owls (*S. occidentalis*; Schauffert et al. 2002), red-tailed hawks (*Buteo jamaicensis*), broad-winged hawks (*B. platypterus*; Rusch and Reeder 1978), goshawks (*Accipiter gentilis*; Meng 1959, Squires 2000, Schauffert et al. 2002), Cooper's hawks (*A. cooperii*; Meng 1959) and bald eagles (*Haliaeetus leucocephalus*; Flyger and Gates 1982). Pine squirrels composed less than 5 percent of the diet of the raptors for which such data are presented (Meng 1959, Rusch and Reeder 1978); however, goshawks may prey upon pine squirrels more frequently, with 31 percent of 185 food items reported to be *Tamiasciurus hudsonicus* (Meng 1959). Predation on pine squirrels may be seasonal in some populations; squirrels increase in frequency as a prey item during winter although lynx take fewer red squirrels in winter (2 percent of diet) than in summer (9 percent; Flyger and Gates 1982, Obbard 1987). Little is known about reptilian predation on red squirrels; however, one report of such predation occurred by a timber rattlesnake (*Crotalus horridus*; Linzey and Linzey 1971).

Several infectious agents have been reported for pine squirrels (Flyger and Gates 1982, Steele 1998) including tularemia, *Haplosporangium*, adiaspiromycosis, silverwater virus, California encephalitis, and Powasson virus. A diversity of parasites has been reported from pine squirrels in various parts of their range (reviewed by Flyger and Gates 1982).

Interspecific competition has not been well studied. Due to pine squirrels' reliance on conifer seed that is relatively inaccessible to most other granivores, the major competitors for food are likely other forest-dwelling squirrels (*Sciurus*, *Glaucomys*) and possibly chipmunks (Gurnell 1987, Guerra and Vickery 1998, Steele 1998). Competitive exclusion of pine squirrels by other tree squirrels (*Tamiasciurus douglasii*, C.C. Smith 1968; *Sciurus aberti*, Hoffmeister 1956, Minckley 1968, Ferner 1974) and competitive exclusion by pine squirrels of other tree squirrels (*S. carolinensis*, Riege 1991) may be influential in determining the distribution of pine squirrels at local and geographic scales. Crossbills (*Loxia curvirostra*) possess beak and behavioral adaptations that enable them to efficiently access seeds within closed cones and likely are strong competitors. The morphology of cones, crossbills, and perhaps squirrels are evolving in concert due to the strong selective pressures resulting from granivory on trees and food harvesting (crossbills and pine squirrels) and hoarding (pine squirrels) behaviors (reviewed in Benkman et al. 2003).

Middens of pine squirrels are used by a number of other species such a grizzly bear (*Ursus arctos horribilis*; Mattson and Reinhart 1997), martens (Sherburne and Bissonette 1993, Ruggerio et al. 1998), and a number of small sciurids, arvicolids, and cricetids (Pearson and Ruggiero 2001). Pine squirrels may serve as a keystone species in boreal forests due to their larderhoarding behavior (Pearson and Ruggiero 2001). Middens serve as repositories of tree seed through stored cones, structure in even-aged and managed forests, and nutrient stores in the form of decaying matter. The impact of middens on local biodiversity or ecosystem function has not been experimentally examined; however, pine squirrels are likely important in the succession of young forests due to their propensity to modify surrounding environments.

Pine squirrels are believed to have influenced the evolution of conifers and conifer-dominated ecosystems in North America (Smith 1970, 1975, Smith and Reichman 1984, Siepielski and Benkman 2004). Larderhoarding habits of pine squirrels that result in the placement of cones within cool, moist environments that delay opening of cones (Shaw 1936, Finley 1969) likely reduce the number of seeds available because cached cones do not germinate (Brink and Dean 1966, Burns and Honkala 1990, DeLong et al. 1997). Pine squirrels are often described as the primary seed predator and selective agent in occupied coniferous forest because they can reduce cone and seed levels by more than 50 percent (Adams 1950, Squillace 1953, Adams 1955, Burns and Honkala 1990, Benkman 1995, Benkman et al. 2003, Peters et al. 2003, Siepielski and Benkman 2004). Masting of conifer species is believed to be a strategy to saturate the environment with more seeds than can be consumed by satiated seed predators. Furthermore, the irregular and unpredictable nature of mast years may decrease the likelihood of seed predators cueing on an overabundance of cones (Janzen 1971, Silvertown 1980). This appears to be the case in several conifer species (Waldron 1965, Silvertown 1980, Dale et al. 2001). Larderhoarding of cones in middens is considered a strategy by pine squirrels to capitalize on the massive fluctuations in the abundance of cones produced by most tree species (Smith 1970, 1975, Smith and Reichman 1984, Vander Wall 1990).

In addition to the immediate loss of seed to ingestion and hoarding of cones (Adams 1950, Lotan and Perry 1983, Alexander 1987, Peters et al. 2003), pine squirrels reduce cone crops by clipping branch tips and buds by as much as 55 percent (Adams 1955, Allred et al. 1994). Pine squirrels feed on the vascular tissues of trees after stripping bark and occasionally girdle trees (Pike 1934, Sullivan and Sullivan 1982, Brockley and Elmes 1987, Sullivan and Klenner 1993). Young vigorous stems (Sullivan and Vyse 1987, Brockley and Sullivan 1988, Sullivan and Klenner 1996) and dense stands (>1000 stems per ha) of young lodgepole pine (Sullivan et al. 1994, Sullivan and Klenner 1996) are preferentially damaged.

Cone morphology also appears responsive to selection pressure from pine squirrels for both conifer and pine squirrel morphology appears to have coevolved (Smith 1970, Benkman et al. 2001, Siepielski and Benkman 2004). In areas with pine squirrels, the number of seeds per cone is reduced, the degree of serotony is increased, cone size is increased, the number of sterile basal scales is increased, and seed coats are thickened; all of these characteristics make the energy extraction more difficult for squirrels (Smith 1970, Benkman 1995, Benkman et al. 2001). Although not well documented, tree squirrels in western coniferous forests also likely are important in the dispersal and inoculation of sites with fungal spores, and fungi likely possess adaptations to take advantage of this relationship including the ease of detection by scent (Kotter and Farentinos 1984, Allred and Gaud 1999, Carey et al. 2002). Clearly, pine squirrels play a significant role in the evolution and function of coniferous forests (**Figure 5**).

Conservation

Threats

Pine squirrels typically rely upon mature forests that produce large quantities of tree seed, shaded microclimates for fungal growth and long-term cone storage, and cavities for nesting (Smith 1968, Rusch and Reeder 1978, Vahle and Patton 1983). Natural and anthropogenic disturbances that disrupt these conditions reduce persistence of the pine squirrel populations in a local area in the short term; management schemes that do not promote the return of forests to these conditions following disturbance will not favor re-establishment and long-term persistence of pine squirrels.

Roads

Small forest roads appear to have minimal direct impact on microclimate beyond the road margins and thus at the scale that pine squirrels interact with the environment (Young 1995, Trombulak and Frissel 2000, Young 2000, Gucinski et al. 2001). Mortality due to vehicular traffic can be significant in some areas of the eastern United States (Hamilton 1939), but roads are not likely to significantly impact populations in the western United States.

Indirect effects of roads that influence forest health may occur. In reviews of possible impacts of roads on wildlife, little evidence for the influence of road formation on forest disease was found; however, the spread of the root disease, *Phythoptera lateralis*, was facilitated by roads (Zobel et al. 1985, Trombulak and Frissell 2000, Gucinski et al. 2001). Roads also influence fire behavior in a myriad of ways by serving as fire breaks, increasing access of fire suppression crews, enhancing access to reduce fuels, increasing the frequency of human fire starts, and facilitating penetration of light and increases in ground and ladder fuels (Gucinski et al. 2001).

The greatest effects of roads on pine squirrels are likely those associated with fragmentation of forests. Road building and widening that reduce connectedness of the canopy likely results in decreased connectivity of habitat and may increase vulnerability to predation due to increased visibility and the facilitation of carnivore travel (Gucinski et al. 2001). Fragmentation of forests appears to impact pine squirrels as they avoid edges (King et al. 1998, Cotterill and Hannon 1999), become less active near edges (Anderson and Boutin 2002), and are found in high densities within isolated fragments (Bayne and Hobson 2000). In residual strips and blocks of unthinned black spruce (*Picea mariana*) forest following clearcutting, midden numbers were reduced from those found in control sites (Cote and Ferron 2001).

Sport harvest

As noted previously, hunting pressure appears relatively low in most of Region 2. The most likely exceptions to this would be relictual populations of pine squirrels in northeastern South Dakota and neighboring North Dakota where the range of pine squirrels is not well defined, yet a rather liberal hunting season and bag limit are retained.

Cone harvesting by humans

In some regions, human harvest of conifer cones is permitted primarily for arts and crafts or tree propagation, and most guides suggest capitalizing on the cone clipping and hoarding behavior of pine squirrels (Brener and Cunningham 1989, Mahalovich and Hoff 2000). Commercial collection of seed occurs

WEB				CENTRUM
4	3	2	1	
				RESOURCES
		Water, weather	Cone-producing conifers	**Food:** Conifer seeds
	Water	Large live trees	Cone-producing conifers	**Food:** Phloem
Water	Large live trees	Mature forest cover	Cones and cool moist sites	**Food Storage Sites:** Middens
	Water	Large live trees	Mature forest cover	**Food:** Arboreal lichens
Water	Large live trees	Mature forest cover	Woody debris and organic soils	**Food:** Epi- and hypogeous fungi
		Insects and other foods	Primary cavity nesting birds	**Nest Cavities**
	Water	Large live trees	Snags and live trees with rot	**Nest Cavities**
				MALENTITIES
	Water	Large live trees	Mature forest cover	**Predators**
Water	Large live trees	Mature forest cover	Clearing of forests Stand-replacing fire	**Habitat Loss**
Water	Large live trees	Clearing of forests Stand-replacing fire	Habitat fragmentation	**Accessibility of Mates**
Water	Large live trees	Mature forest cover	Cone-producing conifers	**Competition:** Food
	Water	Large live trees	Snags and live trees with rot	**Competition:** Nest cavities

Figure 5. Envirogram representing the linkages between the pine squirrels (*Tamiasciurus hudsonicus*) and their ecosystem with the USDA Forest Service Region 2.

in association with regeneration using mechanized approaches that typically collect 10 to 45 bushels per hour for the conifers found in Region 2 (Copes 1985, Fandrich 1986). Large seeded pines, particularly piñon pine, are also collected to obtain edible pine nuts (Lanner 1981, Food and Agriculture Organization of the United Nations 1995). Because cones stores in middens serve as the major food source for overwinter survival of pine squirrels, large scale removal of cones during the fall and winter are likely detrimental to a small number of animals in the local population. Strategies to minimize impacts include prohibiting the taking of cones at middens, limiting the number of permittees within an area, and restricting collection to early fall and spring when squirrels may replenish supplies or switch food sources.

Timber harvest

Of 13.98 million acres of forested land in Region 2, about 1.77 million acres, or 12.7 percent of the suitable forested lands, are managed to emphasize timber value (USDA Forest Service 2001). The most isolated populations of pine squirrels found in the Black Hills of Wyoming and South Dakota and the Bighorn Mountains of Wyoming occur in landscapes where the greatest proportions of forested lands are managed to emphasize timber production (44.2 percent and 16.3 percent, respectively; USDA Forest Service 2001). Reforestation efforts are required by law within Region 2 and are necessary for the long-term persistence of these forest-dependent squirrels.

Clearcutting techniques remove habitat directly for these arboreal squirrels, degrade habitat by creating edge effects near openings, and potentially increase vulnerability to predation (Wolff 1975). In interior spruce forests, squirrel densities decreased from 1.2 to 0 squirrels per ha in clearcut blocks and from 1.5 to 0.5 squirrels per ha in thinned blocks (83 percent of stems removed), whereas edge habitats of uncut forest and interior uncut forest showed little change in density (1.6 to 1.3 squirrels per ha and 1.3 to 1.5 squirrels per ha, respectively; Wolff 1975). Seed predation does decline greatly in single seed tree cut blocks apparently due to the dramatic decrease in use of these areas by pine squirrels (Peters et al. 2003). Pine squirrels persisted for at least three to five years in residual forests and corridors through clear cuts and cutblocks (Cote and Ferron 2001).

Pine squirrel densities are often significantly higher in mature forests compared to clearcuts (Bayne and Hobson 1997a, 1997b, King et al. 1998) and conventionally thinned sites that include a significant (>50 percent) reduction in stems (Sullivan and Moses 1986, Sullivan et al. 1996). Pine squirrel populations did not differ in density, survivorship, recruitment, body mass, or prevalence of reproduction in second growth and old growth spruce-fir and lodgepole pine forests in interior British Columbia (Ransome and Sullivan 1997). Thinning of lodgepole pine to densities of 850 to 2304 stems per ha in British Columbia resulted in a nearly 80 percent decline of pine squirrels compared to unthinned sites (20,000 to 34,778 stems per ha; Sullivan and Moses 1986). In a replicated study in British Columbia, heavily thinned stands of juvenile lodgepole pine (post-thinning densities of 500 to 1000 stems per ha) had reduced densities of pine squirrels (Sullivan et al. 1996). Sites with post-thinning densities of 1000 to 2000 stems per ha had more immigrants into the populations than the intensively thinned (500 stems per ha) sites; the populations in these three treatments did not differ consistently in body mass, prevalence of reproduction, recruitment of young, or survivorship (Sullivan et al. 1996). In black spruce, density, survivorship, recruitment, and body mass of pine squirrels did not differ between the treatments of residual untreated forest strips (250 to 800 m and connected to contiguous forest), residual untreated blocks (19 to 50 ha), or control sites in continuous forest for three to five years post harvest, suggesting that they minimally impacted squirrel species in the short term; however, middens densities were significantly less common in residual forests (Cote and Ferron 2001).

Similar results have been obtained for the congener, Douglas squirrel, in the Pacific Northwest. In western Oregon and a portion of Washington, Douglas squirrel abundance did not differ amongst young, mature, and old growth forests (Anthony et al. 1987, Carey 1989). In western Washington, densities did not differ greatly between commercially thinned (224 to 236 stems per ha) Douglas-fir forests and old growth legacy retention Douglas-fir treatments (598 to 642 stems per ha; Carey 2000, 2001). Douglas squirrels were most common in 80 to 100 year old mature fir forest in northern California compared to shelterwood cut (harvested in two stages with regeneration under partial canopy) or old growth forests (Waters and Zabel 1998).

Seed tree and shelterwood tree cuts may retain some habitat components but often the density of trees is too low to provide habitat (Waters and Zabel 1998, Peters et al. 2003). Selection cuts that remove a low number of the largest trees or thinning from below with the removal of pole size ladder fuels may provide the least impact by retaining snags and mature overstory seed producers. For Douglas squirrels, Carey (1995) suggests the retention of at least 20 snags per ha for the management of arboreal sciurids in thinned forests. Retention of biological legacies and management for decadence and variable stem densities are promising approaches to region wide management of forests for mature and old-growth conditions favorable to pine squirrels while also permitting extraction of resources and management for forest health and fire (Carey 1995, 2000, 2001).

Wildfire

In the western United States, fire is often considered the major disturbance under heavy anthropogenic influence (Pyne 1982, Brown and Smith 2000, Flannigan et al. 2000, Smith 2000). Policies of fire suppression for nearly a century in most of the United States have resulted in significant changes in cool fire frequency, catastrophic fire frequency, and forest structure in some forest types (Pyne 1982, Brown and Smith 2000). Since 1970, only three years have exceeded 100,000 acres of wildfire on lands in Region 2 (1972, 1988, and 2000); the 186,115 acres burned in 2000 was the second highest total recorded in this period. Ponderosa pine and Douglas-fir forests in southern portions of Region 2 typically are characterized by frequent, low-intensity ground fires or mixed fire regimes and rarely stand replacement fires (**Table 2**; Brown and Smith 2000). Conversely, mixed and stand replacing fires are the most likely occurrence in higher elevation lodgepole pine, whitebark pine, and spruce-fir forests. Stand replacing fires occur only every 100 to 400 years (Brown and Smith 2000) with particularly moist spruce-fir forests burned only once every 800 to 2000 years in British Columbia (Brown and Smith 2000). These temporal scales suggest that fire cycles for high elevation species may have been much less impacted by human disturbances and suppression. Restoration of natural fire frequencies is perhaps desirable but difficult; forest thinning practices must avoid the impacts noted in the Timber harvest section above.

Response of pine squirrels to fire is poorly known, and no studies have examined explicitly the relationships between fire and squirrel populations. No direct mortality due to fire has been reported (Smith 2000). Stand replacement fires result in the loss of middens and habitat, while pine squirrels continue to use areas of less intensive fire and on the fringe of the burns (King and Koprowski in review). The short-term loss of habitat and concomitant changes in midden microclimates that result from ground and mixed fires must be considered in relation to the long-term gains in habitat quality due to retention of open forest structure, increased productivity and cone production, and decreased risk of catastrophic fire (Brown and Smith 2000). Pine squirrel population responses to habitat fragmentation appear to be similar to that resulting from fire (Bayne and Hobson 1997b). Because pine squirrels routinely move distances of 1 km and have high biotic potential, displacement or loss of individuals due to ground fires or patchy mixed fire regimes is not likely to be a significant problem for pine squirrel persistence. Stand replacement fires and less patchy mixed fire regimes, however, are likely to have greater impact because these fires are effectively

Table 2. Summary of fire cycles and fire regime types for common forest types in Region 2 (after Brown and Smith 2000:98-99)

Forest Type	Fire Regime Type						No Fire
	Understory		Mixed		Stand Replacing		
	Extent[1]	Freq[2]	Extent	Freq	Extent	Freq	
Ponderosa pine							
Black Hills	Minor	<35	Major	35 to 200	Major	35 to 200	
Southern Rockies	Major	1 to 25	Minor	35 to 200			
Douglas-fir	Minor	<35 to 200	Major	25 to 100			
Lodgepole pine			Major	25 to 75	Major	100 to 300	
Whitebark pine			Major	50 to 200	Major	150 to 300	
Engelmann spruce-Subalpine fir					Major	100 to 400	Minor
White fir-Blue spruce-Douglas-fir			Major	35 to 200	Major	35 to 200	

[1]Percentage of stand: Major = >25%, minor = <25%

[2]Frequency of occurrence in years

experienced as clearcuts by squirrel populations. In addition, the high temperatures of some burns can result in less productive soils and a greater refractory period in recovery than is experienced in more patchy and ground fires (Brown and Smith 2000). Seed producing trees that are common to Region 2 typically require at least 15 years to begin producing seeds (**Table 3**) with the most productive age classes typically 50 to 200 years of age (Burns and Honkala 1990). Given the lengthy associations and coevolution of coniferous forest and pine squirrels, historical temporal and spatial patterns of fire are unlikely to adversely influence persistence of squirrel populations. Significant changes in the frequencies, intensities, and spatial scale of fires resulting from the influence of human activities are the major challenge.

Insect infestation

During recent decades, forest insect infestations have increased in most national forests within Region 2 (USDA Forest Service Region 2 2000). All of the major insects influencing forest health in Region 2 (e.g., bark beetles [*Dendroctonus* spp., *Dryocetes* spp.], engraver beetles [*Ips* spp.], and budworms [*Choristoneura* spp.]) degrade certain characteristics of habitat for pine squirrels by directly influencing forest structure, increasing risk of catastrophic fire, and decreasing seed crops. The major insect of consequence in Region 2 at present is the mountain pine beetle (*Dendroctonus ponderosae*) with increased levels of damage reported in Wyoming and Colorado over the period 1995 to 2000 by Region 2 Forest Health Specialists. Estimated tree kills in 2000 were 273,400 trees over 139, 400 infested acres in Colorado, 13,700 trees over 9,000 infested acres in Wyoming, and 34,300 trees over 13,900 infested acres in South Dakota.

Following tree mortality due to insects, forest communities continue to change as wind and ice fell trees and open the canopy. Secondary succession is hastened due to the release of trees suppressed by the dominant trees lost to insects (Veblen et al. 1991, 1994). The spatio-temporal pattern of insect-caused mortality in trees results in a mosaic structure of forest patches (Matsuoka et al. 2001). Levels of insect infestation are also linked to fire dynamics due to increases in fuel that result from tree mortality; however, the mosaic pattern that often results from the plethora of disturbances to conifer forests may reduce the spatial extent of catastrophic crown fires (Baker and Veblen 1990, Veblen et al. 1994, Matsuoka et al. 2001). Pine squirrels have evolved in these ecosystems and were able to cope with historical temporal and spatial patterns of natural disturbance. Issues of anthropogenic changes to scale that were discussed with respect to fire also are germane to the impacts of insect infestation.

Little research has been conducted on how squirrels respond to insect infestation. The level of tree mortality caused by insect infestations is important as a measure of the short-term degradation of habitat. Pine squirrel populations decline significantly in areas with greater than 40 percent mortality of spruce trees due to beetle infestations in Alaska (Matsuoka et al. 2001), and this pattern of decline has been noted elsewhere (Yeager and Riordan 1953, Medicine Bow-Routt National Forests 2002). Importantly, pine squirrels were not observed to completely disappear from areas with high levels of insect infestation and tree mortality, but rather

Table 3. Seed crop characteristics of major conifer species in Region 2. Mean values provided when available, otherwise ranges are provided. Cone crop failures can occur at any time, and data here provide a generalized assessment (Fowells 1965, Burns and Honkala 1990).

Species	Common Name	Age at 1st Seed[1]	Mast Year Interval(yr)
Abies concolor	White fir	40	3 to 9
Abies lasiocarpa	Subalpine fir	20 to 50	3 to 5
Picea engelmannii	Engelmann spruce	15 to 40	2 to 5
Picea glauca	White spruce	10 to 15	2 to 12
Picea pungens	Blue spruce	20	2 to 3
Pinus contorta	Lodgepole pine	5 to 10	1 to 3
Pinus ponderosa	Ponderosa pine	7	3 to 8
Pinus edulis	Piñon pine	25	4 to 7
Pseudotsuga menziesii	Douglas-fir	10 to 30	7

[1]Earliest age at which cones are produced. Most productive age is usually 3 to 5 times older than minimum age.

abundance declined. Pine squirrels exist within patches of the mosaic where conditions remain suitable (Yeager and Riordan 1953, Matsuoka et al. 2001). Abandoned cone caches often serve as food for pine squirrels that remain in insect damaged forests, and many of the insects serve as food for pine squirrels (Steele 1998, Koprowski personal observation). The ability of pine squirrels to use relictual forest patches and persist throughout secondary succession is likely the result of their long evolutionary history of association with coniferous forests.

Miscellaneous human activities

Typically, recreational activities and livestock grazing have minimal impact on pine squirrels. Cattle disturbance of middens is typically minimal, and grazing is less common in high elevation forests; however, thinning of forests to increase available grasslands would reduce quality squirrel habitat. Increases in ambient noise levels do not appear to significantly influence the behavior of squirrels in proximity to human activities (Young 1995, Young 2000). Pine squirrels do not interact with exotic species in Region 2.

Unfortunately, few experimental studies have examined the direct or indirect impacts of natural and anthropogenic disturbances. Such studies are necessary to determine the actual impacts of disturbances and to design effective strategies to minimize and mitigate the loss and degradation of habitat.

Conservation Status of Pine Squirrels in Region 2

Pine squirrel populations appear secure in most of Colorado, Wyoming, and western South Dakota. Populations in the more isolated mountains such as the Bighorn Mountains and Black Hills are not well documented, and speculation concerning their status must be tempered by this lack of information. Distribution in North Dakota and northeastern South Dakota is very poorly documented but range appears to have declined significantly. High elevation spruce and fir forests appear to be to have the highest squirrel densities and smallest home ranges (Gurnell 1987). Territory size appears tightly tied with environmental quality (Smith 1981, Gurnell 1984, 1987) as territories enlarge during periods of food shortage (M.C. Smith 1968) and decrease significantly with the provisioning of supplemental food (Sullivan 1990). Densities also appear to be related to food availability (Erlien and Tester 1984) for they increase significantly with provisioning of supplemental food although this may be an artifact of ingressing animals attracted by food (Sullivan 1990, Sullivan and Klenner 1992). Ponderosa pine forests that are inhabited by Abert's squirrels rarely have pine squirrels in Colorado (Hatt 1943, Ferner 1974, Fitzgerald et al. 1994). Most pine squirrels in pine forests have larger home ranges and lower densities than other coniferous forests, suggesting that these habitats may be of relatively low quality (Gurnell 1987).

As noted in the section on Demography, pine squirrels have a relatively high biotic potential with large litter sizes produced each year typically beginning in the second year of life. This biotic potential and the larderhoarding habits of pine squirrels that provide a buffer against cone failure likely minimize risk to stochastic events except in highly isolated locales (U.S. Fish and Wildlife Service 1993).

Management of Pine Squirrels in Region 2

As with many forest management actions, consequences of prescriptions must be assessed in spatial and temporal contexts. Clearcutting a single isolated fragment would obviously be detrimental to local populations of pine squirrels; however, prescriptions that ensure quality mature forest habitat over broad areas will promote long-term persistence of pine squirrels in the region. Fragmentation of forests negatively impacts pine squirrels because they avoid edges (King et al. 1998, Cotterill and Hannon 1999), become less active near edges (Anderson and Boutin 2002), and are found in high densities within isolated fragments (Bayne and Hobson 2000). Furthermore, retention of single seed trees in clearcuts dramatically reduced squirrel use of cones apparently due to decreased use of such denuded sites (Peters et al. 2003). In residual strips and blocks of unthinned black spruce (*Picea mariana*) forest following clearcutting, midden numbers were reduced from those found in control sites (Cote and Ferron 2001).

Pine squirrels depend heavily on tree seed and the storage of seed in middens; therefore, quality habitat occurs in forests providing shaded environments with mature trees that produce large seed crops as well as high canopy closure to maintain cool and moist microclimates for middens, and cover from predators (Rusch and Reeder 1978, Flyger and Gates 1982, Vahle and Patton 1983, Mahan and Yahner 1992, Steele 1998). Management practices that eliminate or thin forests and disrupt the appropriate microclimates (Shaw 1936, Finley 1969), or practices that fragment forests leading to negative edge effects observed for pine squirrels (Bayne and Hobson 2000), are likely to be detrimental in the short term. Prescriptions that restore conditions of cool, moist ground microclimates and promote cone crop productivity and regularity will likely favor the long-term persistence of pine squirrels. Unfortunately, no guidelines exist on the proper mixture of prescriptions to manage for pine squirrels; however, management schemes that promote rotations wherein significant tracts of mature, closed canopy forests are available during all rotations to avoid edge effects and demographic isolation will likely lead to long-term persistence in any of the forests in Region 2.

The lack of strong differences in treatment effects across a number of studies, geographic areas, and forest types suggests that moderate timber harvest and prescribed thinning levels may be compatible with management for pine squirrels (see earlier sections on Timber Harvest). Silviculturists may use long-standing thinning prescriptions to achieve the desired states and spatial organization of mature forest conditions to achieve long-term persistence of pine squirrels in an area. Recent suggestions to manage for biological legacies, decadence, and variable stem densities (Carey 1995, 2000, 2001) are promising. Carey (1995) recommended the retention of 20 large (>50 cm DBH) snags per ha to promote arboreal squirrel populations in Douglas-fir forests of western Oregon and Washington. Additionally, the use of variable-density thinning on a 0.2 ha scale, retention of between 1:1 and 2:1 relative density (RD 6:RD4) ratios with 15 percent of the stand in patches of RD 2 and RD 8 appears to accelerate late-seral forest characteristics in these Douglas-fir forests (Carey 2001). Variable density thinning alone does not appear to result in all desired conditions and extended rotations (>130 years), legacy retention, and variable retention harvest systems appear necessary to effectively manage the landscape to mimic old-growth Douglas-fir forest conditions (Carey 2001) for this species. Unfortunately, the applicability of these techniques to other forest types in Region 2 has not been examined.

Tools and practices

Inventory and monitoring populations and habitat

Much of the biology of pine squirrels makes them conducive to detection and monitoring. Their diurnal habits, year-round activity, modest size, territorial behaviors such as vocalizations and aggression, feeding sign, nesting habits in forming leaf nests, and conspicuous midden piles in western North America make the species relatively conspicuous. The most common methods of detection employed in western coniferous forests are identification of middens, transects or circular plots for observation of individuals or feeding sign, tracks, live trapping, and listening/eliciting vocalizations (Carey and Witt 1991, Young 1995, Mattson and Reinhart 1996, Koprowski in press). The following sections detail the methods available and the issues encountered in the inventory and monitoring of pine squirrels and their habitat.

Species inventory: Most inventories that have included pine squirrels are not species specific and involve live trapping individuals (Cote and Ferron 2001). Pine squirrel middens are excellent indicators of presence and if checked during late summer, fall, or winter, caches and feeding sign (e.g., cone cores, discarded green cone scales, small branch tips; Rasmussen et al. 1975) and tracks are often quite obvious (Young 1995). There is greater agreement among fall censuses conducted on different areas than during the spring when territoriality breaks down and feeding sign is difficult to assign to pine squirrels (Koprowski and Snow in review). Mattson and Reinhart (1996) found that midden surveys were the best means of detecting pine squirrels in whitebark pine forests. In most of Region 2, pine squirrels are the only diurnal tree squirrel (western South Dakota, northern Wyoming) or sympatric with Abert's squirrels (southern Wyoming, Colorado), and feeding sign is easily distinguishable. Hair tubes have not yet been applied to pine squirrels; however, this remote technique has shown great promise in efficiently detecting the presence of other tree squirrels (Gurnell et al. 2001).

Habitat inventory and monitoring: Current aerial and satellite imagery methods with resolution to detect forest stage and general forest composition are adequate to assess available habitat and spatial distribution/continuity of habitats. Aerial or satellite imagery are typically used to monitor habitat availability and changes in availability due to anthropogenic and natural factors (Hatten 2000, Lynch et al. in press). Systems to monitor habitat quality should include approaches to assess and track insect damage and other related forest health issues (Koprowski et al. in review, Young in review). Biotic features such as biological legacies, management for decadence, and snags are often not inventoried but appear to be important components of pine squirrel biology as previously noted (Carey 2000, 2001, Young et al. 2002); ground truthing that incorporates these features would likely provide a finer scale inventory with respect to the biology of pine squirrels.

Population monitoring: Middens and associated feeding sign are the most detectable means of monitoring population trends and population persistence in western forests where midden formation is the rule (Mattson and Reinhart 1996). Because middens are relatively conspicuous and unique structures created only by pine squirrels, surveys can be conducted by biologists with minimal training. Feeding sign associated with middens, including larders of the current year's crop of cones, fresh cone scales, and cone cores during fall and winter, enable occupancy status to be assessed enabling population persistence and trend to be assessed (Young 1995, Mattson and Reinhart 1996, Snow in press). Middens can be revisited each year to monitor population trends, or randomly placed transects or circular plots can be placed and searched to obtain density estimates (Young 1995, Mattson and Reinhart 1996, Snow in press).

Limitations of this method are several but generally easily minimized. In deciduous forests of the eastern United States where squirrels are not territorial, middens are not constructed and defended (reviewed in Munroe et al. in press). Surveying middens outside of the fall and winter seasons of cone caching and feeding yields the least repeatable results (Koprowski and Snow in press). The method assumes that a single squirrel uses a single active midden. Pine squirrels are highly territorial, and solitary and communal nesting is extremely unusual (Munroe et al. in press) suggesting that midden counts are not likely to be underestimates. Counts could overestimate squirrel abundance if animals provision more than a single midden. Little evidence exists for the occurrence of animals holding two middens in their territory. Adult animals in particular are not likely to move to middens following removal of neighbors, and when such movements occur, the new territory does not contain both middens (Price et al. 1986, Klenner 1991, Larson and Boutin 1995, Larsen et al. 1997). Females, however, may bequeath their territory to young of the year in some populations (Price et al. 1986).

Point counts of squirrels have recently been applied to pine squirrel populations in western forests (Carey 1989, Hayward personal communication). This method uses traditional circular plot techniques applied to monitoring of avian populations (Diefenbach et al. 2003) to monitor pine squirrels. While it has not been rigorously tested for application to pine squirrels, similar methods were applied to other tree squirrels with modest success (Bouffard and Hein 1978, Carey 1989). Pine squirrels are likely to be most conspicuous during fall when harvesting and caching cones and when territorial vocalizations are common (Smith 1978, Price et al. 1986).

More intensive monitoring could include live trapping and marking with uniquely numbered ear tags to identify individuals and assess trends in adult survivorship which appears to be the most important factor influencing the growth trajectory of a population (Buenau and Gerber 2004, Harding et al. in review). Because animals do occasionally change middens and males range very widely during the breeding season, live trapping efforts during fall and winter are most likely to provide the best assessment of the squirrel population. Pine squirrels can be a challenge to trap, and a one to two month period of light prebaiting with peanuts and peanut butter during late spring and summer is recommended (Koprowski in press).

Population or habitat management approaches

As previously noted, few management- oriented studies have been conducted on pine squirrels due in part to state agency beliefs that populations are secure. The few management-oriented studies that have been published focused on short-term responses (1 to 10 years) to various forestry practices (see previous section on Timber harvest). Due to the dependence of pine squirrels on mature forests, it is imperative that the conservation, ecology, and management of this species is considered along with other forest obligates. Management that maintains a diversity of successional stages in a temporal and spatial distribution that permits movement and use by pine squirrels is likely to enable long-term persistence within the native disturbance regime. Management will need to be more rigorous when dealing with small and isolated patches of conifer forest that can lead to changes in density and movements (see previous section on Biology and Ecology).

Information Needs

The distribution of pine squirrels in Region 2 is fairly well documented in Colorado, Wyoming, and western South Dakota.

An understanding of the impact of timber practices on microclimate and pine squirrels is adequate to enable managers to make reliable predictions of the effects of timber management decisions. Additional data are required for most other anthropogenic and natural agents of forest change. Data on sex-specific needs likely to be related to reproductive strategies of the sexes are sorely lacking because most population-level studies have combined the sexes or have failed to report sex-specific responses to treatments. These data would provide a more thorough understanding of factors that limit populations. Recent studies have also demonstrated that predation is an important cause of mortality in pine squirrel populations; however, we have little knowledge of how susceptibility to predation changes with various alterations in habitat.

General activity and movement patterns, territory sizes, and dispersal are reasonably well understood to provide a basis to evaluate the impacts of potential management options. However, knowledge of larger scale movements related to breeding season and dispersal events is lacking. How far animals will travel to mate or to disperse is not adequately known to assess questions related to connectivity of habitats and metapopulation structure. This dearth of data, in combination with little knowledge of age-specific demography over extended periods of time, makes assessments of the likelihood of population persistence at either local or regional scales tenuous.

Current methods of monitoring presence/absence and trends of populations are adequate to collect the necessary population data if carefully applied. The conspicuous nature of middens, vociferous defense by resident animals, and their territorial nature (Gurnell 1987) provide easily recognized sign that permits assessment of pine squirrel presence. Furthermore, the obvious nature of middens enables other monitoring techniques such as live trapping, hair tubes, elicitation of calls, and track surveys to be focused at appropriate locations. These monitoring techniques provide a means of assessing the efficacy of restoration efforts.

Because pine squirrels require mature forests that can produce tree seed and promote appropriate microclimates of larderhoards, silviculturists can use long-standing prescriptions to achieve the desired states of mature forest requested by forest managers. Recent suggestions to manage for biological legacies, decadence, and variable stem densities (Carey 1995, 2000, 2001) are promising. Such strategies focus on sustainable yields of timber harvest while promoting forest conditions that appear conducive to *Tamiasciurus* population persistence. Persistence of ecologically functioning pine squirrel populations is likely achieved because such applications maintain mature canopy trees to produce cones, snags to provide nest cavities, decadent logs to provide microclimates for scatterhoarded cones and fungi, continuous canopies to minimize edge effects and to facilitate movement and avoid predation, and cool and moist microclimates for cone storage.

Research priorities in Region 2 for the conservation of pine squirrels are four-fold:

1) obtain accurate data on the range and distribution of pine squirrels through presence/absence surveys

2) assess the impact of forest fragmentation by anthropogenic and natural causes, in particular the determination of the threshold at which thinning begins to restrict movements and promote edge effects

3) determine the status of populations and minimize risk of loss of pine squirrels in isolated mountains

4) address the gaps in knowledge of pine squirrel biology that are pertinent to conservation of the species and informed management of the habitat.

The extreme dearth of data on metapopulation dynamics and broad scale movement makes such research necessary to understand the implications of forest and region wide decisions on land use. Furthermore, the emergent properties of populations in habitat fragments are poorly known, although of increasing importance given current trends of anthropogenic (timber practices, development, roadways) and natural (wildfires, insect infestations) fragmentation.

References

Adams, L. 1950. Consumption of ponderosa pine seed by small mammals. USDA Forest Service Rocky Mountain Forest and Range Experiment Station Research Note 80.

Adams, L. 1955. Pine squirrels reduce future cone crops of ponderosa pine cones. Journal of Forestry 53:35.

Alexander, R.R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. USDA Forest Service, Agriculture Handbook 659. Washington, D.C. 144 p.

Allred, W.S. and W.S. Gaud. 1999. Abert squirrel (*Sciurus aberti*) as a soil excavator. Southwestern Naturalist 44: 88-89.

Allred, W.S., W.S. Gaud, and J.S. States. 1994. Effects of herbivory by Abert squirrels (*Sciurus aberti*) on cone crops of Ponderosa pine. Journal of Mammalogy 75:700-703.

Anderson, E.M. and S. Boutin. 2002. Edge effects on survival and behaviour of juvenile red squirrels (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 80:1038-1046.

Andrewartha, H.G. and L.C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago, IL.

Anthony, R.G., E.D. Forsman, G.A. Green, G. Witmer, and S.K. Nelson. 1987. Small Mammal populations in riparian zones of different-aged coniferous forests. Murrelet 68:94-102.

Arbetan, P.T. 1993. The mating system of the red squirrel, (*Tamiasciurus hudsonicus*). M.S. Thesis, University of Kansas, Lawrence, KS.

Arbogast, B.S., R.A. Browne, and P.D. Weigl. 2001. Evolutionary genetics and Pleistocene biogeography of North American tree squirrels (*Tamiasciurus*). Journal of Mammalogy 82:302-319.

Armstrong, D.M. 1972. Distribution of mammals in Colorado. Mongraph, Museum of Natural History, University of Kansas 3:1-415.

Bailey, V. 1926. A biological survey of North Dakota. I. Physiography and life zones. II. The mammals. North American Fauna No. 49.

Bailey, V. 1931. Mammals of New Mexico. North American Fauna 53.

Baker, W.L. and T.T. Veblen. 1990. Spruce beetles and fire in the nineteenth-century subalpine forests of western Colorado, USA. Arctic Alpine Research 22:65-80.

Bakker, V.J. and D.H. Van Vuren. 2004. Gap-crossing decisions by the red squirrel, a forest dependent small mammal. Conservation Biology 18:389-397.

Bayne, E. and K. Hobson. 1997a. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. Conservation Biology 11:1418-1429.

Bayne, E. and K. Hobson. 1997b. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixed wood forest. Canadian Journal of Zoology 76:62-69.

Bayne, E. and K. Hobson. 2000. Relative use of contiguous and fragmented boreal forest by red squirrels (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 78:359-365.

Becker, C.D. 1993. Environmental cues of estrus in the North American red squirrel (*Tamiasciurus hudsonicus* Bangs). Canadian Journal of Zoology 71:1326-1333.

Benkman, C.W. 1995. The impact of tree squirrels (*Tamiasciurus*) on limber pine seed dispersal adaptations. Evolution 49:585-592.

Benkman, C.W., W.C. Holimon, and J.W. Smith. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine Evolution 55:282-294.

Benkman, C.W., T.L. Parchman, A. Favis, and A.M. Siepielski. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. American Naturalist 162:182-194.

Bouffard, S.H. and D. Hein. 1978. Census methods for eastern gray squirrels. Journal of Wildlife Management 42: 550-557.

Boutin, S. and K.W. Larsen. 1993. Does food availability affect growth and survival of males and females differently in a promiscuous small mammal, *Tamiasciurus hudsonicus*? Journal of Animal Ecology 62:364-370.

Boutin, S. and S. Schweiger. 1988. Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. Canadian Journal of Zoology 66:2270-2274.

Boutin, S., Z. Tooze, and K. Price. 1993. Post-breeding dispersal by female red squirrels (*Tamiasciurus hudsonicus*). Behavioral Ecology 4:151-155.

Bovet, J. 1984. Strategies of homing behavior in the red squirrel (*Tamiasciurus hudsonicus*). Behavioral Ecology and Sociobiology 16:81-88.

Bovet, J. 1991. Route-based visual information has limited effect on the homing performance of red squirrels, Tamiasciurus hudsonicus. Ethology 87:59-65.

Bowles, J.B. 1975. Distribution and biogeography of mammals of Iowa. Special Publication, Museum, Texas Tech University 9:1-184.

Brener, W.H. and G.R. Cunningham. 1989. Collecting and planting seeds of cone-bearing trees. University of Wisconsin Extension Service Publication G1649.

Brink, C.H. and F.C. Dean. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. Journal of Wildlife Management 30:503-512.

Brockley, R.P. and E. Elmes. 1987. Barking damage by red squirrels in juvenile-spaced lodgepole pine stands in south-central British Columbia. Forestry Chronicle 63:28-31.

Brockley, R.P. and T.P. Sullivan. 1988. Impact of feeding damage by small mammals on cultural treatments in young stands of lodgepole pine. Pages 322-329 in Proceedings of future forests of the mountain west: a stand culture symposium. USDA Forest Service General Technical Report INT-243.

Brown, J.K. and J.K. Smith, editors. 2000. Wildland fire in ecosystems: effects of fire on flora. USDA Forest Service General Technical Report RMRS-GTR-42-Volume 2.

Buenau, K.E. and L.R. Gerber. 2004. Developing recovery and monitoring strategies for the endemic Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in Arizona. Animal Conservation 7:1-6.

Burns, R.M. and B. H. Honkala, technical coordinators. 1990. Silvics of North America: 1. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture Forest Service, Washington, D.C. Volume 2. 877 pp.

Carey, A.B. 1989. Wildlife associated with old-growth forests in the Pacific Northwest. Natural Areas Journal 9:151-162.

Carey, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications 5:648-661.

Carey, A.B. 2000. Effects of new forest management strategies on squirrel populations. Ecological Applications 10: 248-257.

Carey, A.B. 2001. Experimental manipulation of spatial heterogeneity in Douglas-fir forests: effects on squirrels. Forest Ecology and Management 152:13-30.

Carey, A.B. and J.W. Witt. 1991. Track counts as indices to abundances of arboreal rodents. Journal of Mammalogy 72:192-194.

Carey, A.B., W. Colgan, J.M. Trappe, and R. Molina. 2002. Effects of forest management on truffle abundance and squirrel diets. Northwest Science 76:148-157.

Chamberlain, T.C. 1897. The method of multiple working hypotheses. Journal of Geology 5:837-848.

Clark, T.W. and M.R. Stromberg. 1987. Mammals in Wyoming. University of Kansas Press, Lawrence, KS.

Cook, D.B. 1954. Susceptibility of larch to red squirrel damage. Journal of Forestry 52:491-492.

Copes, D.L. 1985. Effect of leader topping and branch pruning on efficiency of Douglas-fir cone harvesting with a tree shaker. USDA Forest Service Research Note PNW-431.

Cote, M. and J. Ferron. 2001. Short-term use of different residual forest structures by three sciurid species in clear-cut boreal landscape. Canadian Journal of Forest Research 31:1805-1815.

Cotterill, S.E. and S.J. Hannon. 1999. No evidence of short-term effects of clear-cutting on artificial nest predation in boreal mixed wood forests. Canadian Journal of Forest Research 29:1900-1910.

Dale, M., S. Francis, C.J. Krebs, and V. Nams. 2001. Trees. Pages 116-137 *in* C.J. Krebs, S. Boutin, R. Boonstra, editors. Ecosystem dynamics of the boreal forest: the Kluane Project. Oxford University Press, New York, NY.

Davis, D.W. 1969. The behavioral and population dynamics of the red squirrel, *Tamiasciurus hudsonicus*, in Saskatchewan. Ph.D. Dissertation, University of Arkansas, Fayetteville, AK.

Davis, D. and J.A. Sealander. 1971. Sex ratio and age structure in two red squirrel populations in northern Saskatchewan. Canadian Field-Naturalist 85:303-308.

DeLong, H.B., V.J. Lieffers, and P.V. Blenis. 1997. Microsite effects on first year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Canadian Journal of Forest Research 27: 1452-1457.

Deutch, R.S. 1978. Seasonal activity budget of the red squirrel (*Tamiasciurus hudsonicus*) in a southern Ohio deciduous forest. M.S. Thesis, University of Dayton, Dayton, OH.

Diefenbach, D.R., D.W. Brauning, and J.A. Mattice. 2003. Variability in grassland bird counts related to observer differences and species detection rates. Auk 120:1168-1179.

Dolbeer, R.A. 1973. Reproduction in the red squirrel (*Tamiasciurus hudsonicus*) in Colorado. Journal of Mammalogy 54:536-540.

Erlien, D.A. and J.R. Tester. 1984. Population ecology of sciurids in northwestern Minnesota. Canadian Field-Naturalist 98:1-6.

Fandrich, H.E. 1986. Collecting cones by helicopter. Journal of Forestry 84:18-19.

Fancy, S.G. 1980. Nest-tree selection by red squirrels in a boreal forest. Canadian Field Naturalist 94:198.

Ferner, J.W. 1974. Habitat relationships of *Tamiasciurus hudsonicus* and *Sciurus aberti* in the Rocky Mountains. Southwestern Naturalist 18:470-473.

Ferron, J. and J. Prescott. 1977. Gestation, litter size and number of litters of the red squirrel (*Tamiasciurus hudsonicus*) in Quebec. Canadian Field Naturalist 91:385-391.

Finley, R.B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Miscellaneous Publications of the University of Kansas Museum of Natural History 51:233-273.

Fitzgerald, J.P., C.A. Meaney, and D.M. Armstrong. 1994. Mammals of Colorado. Denver Museum of Natural History and University Press of Colorado, Denver, CO.

Flannigan, M.D., B.J. Stocks, and B.M. Wotton. 2000. Climate change and forest fires. Science of the Total Environment 262:221-229.

Flyger, V. and J.E. Gates. 1982. Pine squirrels: *Tamiasciurus hudsonicus*, *T. douglasii*. Pages 230-237 *in* J.A. Chapman and G.A. Feldhamer, editors. Wild mammals of North America. John Hopkins University Press, Baltimore, MD. 1147 pp.

Food and Agriculture Organization of the United Nations. 1995. Non-wood forest products from conifers. Non-Wood Forest Products 12.

Fowells, H.A., technicial editor. 1965. Silvics of forest trees of the United States. U.S. Department of Agriculture Handbook 271. 762 pp.

Goheen, J.R., R.K. Swihart, and J.H. Robins. 2003. The anatomy of a range expansion: changes in cranial morphology and rates of energy extraction for North American red squirrels from different latitudes. Oikos 102:33-44.

Gray, A. 1972. Mammalian hybrids. Farnham, Royal Commonwealth Agricultural Bureau.

Gucinski, H., M.J. Furniss, R.R. Ziemer, and M.H. Brookes. 2001. Forest roads: a synthesis of scientific information. USDA Forest Service General Technical Report PNW-GTR-509.

Guerra, B. and W.L. Vickery. 1998. How do red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, coexist? Oikos 83:139-144.

Gurnell, J.C. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine forest. Animal Behaviour 32:1119-31.

Gurnell, J.C. 1987. The natural history of squirrels. Facts on File, New York, NY. 201 pp.

Gurnell, J.C., P. Lurz, and H. Pepper. 2001. Practical techniques for surveying and monitoring squirrels. Forestry Commission Practice Note 11:1-12.

Hall, E.R. 1981. The mammals of North America. Second edition. John Wiley and Sons, New York, NY. 1:1-600 + 90.

Halvorson, C.H. and R.M. Engeman. 1983. Survival analysis for a red squirrel population. Journal of Mammalogy 64:332-336.

Hamilton, W.J. 1939. Observations on the Life History of the Red Squirrel in New York. American Midland Naturalist 22:732-745.

Harding, E.K., D.F. Doak, C. Hartway, T.M. Frederick, and G. Froehlich. In review. A risk assessment of multiple impacts on the endangered Mt. Graham red squirrel. *In*: R. Sanderson, and J.L. Koprowski, editors. Trapped on a Sky Island: Ecology and Conservation of endangered Mt. Graham Red Squirrels. (tentative title). University of Arizona Press, Tucson, AZ.

Hatt, R.T.1929. The red squirrel: its life history and habits. Roosevelt Wildlife Annual 2:1-146.

Hatt, R.T. 1943. The pine squirrel in Colorado. Journal of Mammalogy 24:311-345.

Hatten, J.R. 2000. A pattern recognition model for the Mount Graham red squirrel. Technical Report 160. Arizona Game and Fish Department, Phoenix, 32 pp.

Hatton, L.E., Jr. and R.S. Hoffmann. 1979. The distribution of red squirrels (*Tamiasciurus*) in eastern Oregon. The Murrelet 60:23-25.

Heinrich, B. 1992. Maple sugaring by red squirrels. Journal of Mammalogy 73:51-54.

Higgins, K.F., G. Dowd-Stukel, J.M. Goulet, and D.C. Backlund. 2000. Wild Mammals of South Dakota. South Dakota Department of Game, Fish, and Parks, Pierre, SD.

Hillborn, R. and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.

Hoffmeister, D.F. 1956. Mammals of the Graham (Pinaleno) Mountains, Arizona. American Midland Naturalist 55: 257-288.

Hoffmeister, D.F. 1989. Mammals of Illinois. University of Illinois Press, Urbana, IL.

Hosley, N.W. 1928. Red squirrel damage to coniferous plantations and its relation to changing food habits. Ecology 9:43-49.

Hurly, T.A. and R.J. Robertson. 1986. Scatter-hoarding by territorial red squirrels: a test of the optimal density model. Canadian Journal of Zoology 65:1247-1252.

Janzen, D.H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465-492.

Jones, J.K., Jr., D.M. Armstrong, R.S. Hoffmann, and C. Jones. 1983. Mammals of the Northern Great Plains. University of Nebraska, Lincoln, NE.

Kemp, G.A. and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology 51:763-779.

Kilham, L. 1954. Territorial behavior of red squirrel. Journal of Mammalogy 35:252-253.

King, D.I., C.R. Griffin, and R.M. DeGraaf. 1998. Nest predator distribution among clearcut forest, forest edge and forest interior in an extensively forested landscape. Forest Ecology and Management 104:151-156.

King, S.R.B. and J.L. Koprowski. In press. Effect of human and non-human disturbance on the Mt. Graham red squirrel. *In*: R. Sanderson and J.L. Koprowski, editors. Trapped on a Sky Island: Ecology and conservation of endangered Mt. Graham Red Squirrels. (tentative title). University of Arizona Press, Tucson, AZ.

Klenner, W. 1991. Red squirrel population dynamics. 2. Settlement patterns and the response to removals. Journal of Animal Ecology 60:979-993.

Klenner, W. and C.J. Krebs. 1991. Red squirrel population dynamics. 1. The effect of supplemental food on demography. Journal of Animal Ecology 60:961-978.

Klugh, A.B. 1927. Ecology of the red squirrel. Journal of Mammalogy 8:1-32.

Koford, R.R. 1982. Mating system of a territorial tree squirrel (*Tamiasciurus douglasii*) in California. Journal of Mammalogy 63:274-283.

Koprowski, J.L. 2005. The response of tree squirrels to fragmentation: a review and synthesis. Animal Conservation 8: In press.

Koprowski, J.L. In press. Review of capture and marking methods for tree squirrels with special reference to endangered Mt. Graham red squirrels. *In*: R. Sanderson and J.L. Koprowski, editors. Trapped on a Sky Island: Ecology and Conservation of endangered Mt. Graham Red Squirrels. (tentative title). University of Arizona Press, Tucson, AZ.

Koprowski, J.L. and T. Snow. In press. Comparison of methods used to census endangered Mt. Graham red Squirrels. *In*: R. Sanderson and J.L. Koprowski, editors. Trapped on a Sky Island: Ecology and Conservation of endangered Mt. Graham Red Squirrels. (tentative title). University of Arizona Press, Tucson, AZ.

Kotter, M.M. and R.C. Farentinos. 1984. Tassel-eared squirrels as spore dispersal agents of hypogenous mycorrhizal fungi. Journal of Mammalogy 65:684-687.

Kreighbaum, M.E. and W.E. Van Pelt. 1996. Mount Graham red squirrel juvenile dispersal telemetry study. Nongame and Endangered Wildlife Program Technical Report 89. Arizona Game and Fish Department, Phoenix, AZ.

Lair, H. 1985. Length of gestation in the red squirrel (*Tamiasciurus hudsonicus*). Journal of Mammalogy 66:809-810.

Lair, H. 1987. Estimating the location of the focal center in red squirrel home ranges. Ecology 68:1092-1101.

Lanner, R.M. 1981. The piñon pine, a natural and cultural history. University of Nevada Press, Reno, NV.

Larsen, K.W. and S. Boutin. 1994. Movements, survival and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75:214-223.

Larsen, K.W. and S. Boutin. 1995. Exploring territory quality in the North American red squirrel through removal experiments. Canadian Journal of Zoology 73:1115-1122.

Larsen, K.W., C.D. Becker, S. Boutin, and M. Blower. 1997. Effects of hoard manipulations on life history and reproductive success of female red squirrels (*Tamiasciurus hudsonicus*). Journal of Mammalogy 78:192-203.

Layne, J.N. 1954. The biology of the red squirrel *Tamiasciurus hudsonicus loquax* in central New York. Ecological Monographs 24:227-267.

Lindsay, S.L. 1982. Systematic relationship of parapatric tree squirrel species (*Tamiasciurus*) in the Pacific Northwest. Canadian Journal of Zoology 60:2149-2156.

Linzey, A.V. and D.W. Linzey. 1971. Mammals of Great Smokey Mountains National Park. University of Tennessee Press.

Long, C.A. 1965. The mammals of Wyoming. University of Kansas Publications, Museum of Natural History 14: 493-758.

Lotan, J.E. and D.A. Perry. 1983. Ecology and regeneration of lodgepole pine. U.S. Department of Agriculture, Agriculture Handbook 606. Washington, D.C.

Lynch, A.M. In press. Spruce aphid, *Elatobium abietinum* (Walker): Life history and damage to Engelmann spruce in the Pinaleno Mountains, Arizona. R. Sanderson and J.L. Koprowski, editors. Trapped on a Sky Island: Ecology and Conservation of endangered Mt. Graham Red Squirrels. (tentative title). University of Arizona Press, Tucson, AZ.

Mahalovich, M.F. and R.J. Hoff. 2000. Whitebark pine operational cone collection instructions and seed transfer guidelines. Nutcracker Notes 11:10-13.

Mahan, C. and R.H. Yahner. 1992. Microhabitat use by red squirrels in central Pennsylvania. Transactions of the Northeast Section of the Wildlife Society 49:49-56.

Matsuoka, S.M., C.M. Handel, and D.R. Ruthrauff. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. Canadian Journal of Zoology 79: 1678-1690.

Mattson, D.J. and D.P. Reinhart. 1996. Indicators of red squirrel (*Tamiasciurus hudsonicus*) abundance in the whitebark pine zone. Great Basin Naturalist 56:272-275.

Mattson, D.J. and D.P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology 34:926-940.

McKeever, S. 1964. Food habits of pine squirrels in northeastern California. Journal of Wildlife Management 28: 402-404.

Medicine Bow-Routt National Forests. 2002. Bark beetle analysis: final environmental impact statement. USDA Forest Service, Steamboat Springs, CO.

Meng, H. 1959. Food habits of nesting Cooper's hawks and goshawks in New York and Pennsylvania. Wilson Bulletin 71:169-174.

Millar, J.S. 1970. The breeding season and reproductive cycle of the western red squirrel. Canadian Journal of Zoology 48:471-473.

Minckley, W.L. 1968. Possible extirpation of the spruce squirrel from the Pinaleno (Graham) Mountains, south-central Arizona. Journal of the Arizona Academy of Science 5:110.

Mumford, R. and J.O. Whitaker, Jr. 1982. Mammals of Indiana. Indiana University Press, Bloomington, IN.

Munroe, K.E., J.L. Koprowski, and V.L. Greer. In press. The Social and Mating Systems of Red Squirrels: Do Mt. Graham Red Squirrels Fit the Pattern? *In*: R. Sanderson, and J.L. Koprowski, editors. Trapped on a Sky Island: Ecology and Conservation of endangered Mt. Graham red squirrels. (tentative title). University of Arizona Press, Tucson, AZ.

Nice, M.M., Nice, C., and D. Ewers. 1954. Comparison of behavioral development in snowshoe hares and red squirrels. Journal of Mammalogy 37:64-74.

Obbard, M.E. 1987. Red Squirrel. Pages 265-281 *in* M. Novack, M.E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, Canada. 1150 pp.

Over, W.H. and E.P. Churchill. 1941. Mammals of South Dakota. The Museum and The Department of Zoology of the University of South Dakota, Vermillion, SD.

Pauls, R.W. 1978. Behavioural strategies relevant to the energy economy of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 56:1519-1525.

Pauls, R.W. 1979. Body temperature dynamics of the red squirrel (*Tamiasciurus hudsonicus*): adaptations for energy conservation. Canadian Journal of Zoology 57:1349-1354.

Pearson, D.E. and L.F. Ruggiero. 2001. Test of the prey-base hypothesis to explain use of red squirrel midden sites by American martens. Canadian Journal of Zoology 79:1372-1379.

Peters, S., S. Boutin, and E. Macdonald. 2003. Pre-dispersal seed predation of white spruce cones in logged boreal mixedwood forest. Canadian Journal of Forest Research 33:33-40.

Peterson, C.J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. Science of the Total Environment 262:287-311.

Pike, G.W. 1934. Girdling of ponderosa pine by squirrels. Journal of Forestry 32:98-99.

Platt, J.R. 1964. Strong inference. Science 146:347-353.

Prescott, J. and J. Ferron. 1978. Breeding and behaviour development of the American red squirrel. International Zoo Yearbook 18:125-130.

Prescott, J. 1979. Contribution a l'etude des vocalisations des jeunes chez l'ecureuil roux (*Tamiasciurus hudsonicus*). Behavioural Processes 4:359-373.

Price, K. and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. Behavioral Ecology 4:144-150.

Price, K., K. Broughton, S. Boutin, and A.R.E. Sinclair. 1986. Territory size and ownership in red squirrels: response to removals. Canadian Journal of Zoology, 64:1144-1147.

Pruitt, W.O. and C.V. Lucier. 1958. Winter activity of red squirrels in interior Alaska. Journal of Mammalogy 39: 443-444.

Pyne, S.J. 1982. Fire in America: a cultural history of wildland and rural fire. University of Washington Press, Seattle, WA.

Ransome, D.B. and T.P. Sullivan. 1997. Food limitation and habitat preferences of Glaucomys sabrinus and Tamiasciurus hudsonicus. Journal of Mammalogy 78:538-549.

Rasmussen, D.I., D.E. Brown, and D. Jones. 1975. Use of Ponderosa Pine by Tassel-eared squirrels and a key to determine evidence of their use from that of red squirrels and porcupines. Arizona Game and Fish Dept Wildlife Digest 10:1-12.

Rathcke, B.J. and R.W. Poole. 1974. Red squirrel attacks pileated woodpecker. Wilson Bulletin 84:465-466.

Riege, D.A. 1991. Habitat specialization and social factors in the distribution of red and gray squirrels. Journal of Mammalogy 72:152-162.

Rothwell, R.H. 1977. The effects of forest type and mast crop on winter territories and population of red squirrels (*Tamiasciurus hudsonicus baileyi*) in the Laramie Range of southeastern Wyoming. M.S. Thesis, University of Wyoming, Laramie, WY.

Rothwell, R.H. 1979. Nest sites of red squirrels (*Tamiasciurus hudsonicus*) in the Laramie Range of southeastern Wyoming. Journal of Mammalogy 60:404-405.

Ruggiero, L.F., D.E. Pearson, and S.E. Henry. 1998. Characteristics of American marten den sites in Wyoming. Journal of Wildlife Management 62:663-673.

Rusch, D.A. and W.G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology 59:400-420.

Salt, J.R. and C.A. Roth. 1980. Bark of pine galls eaten by red squirrels. Canadian Field-Naturalist 94:196.

Schauffert, C.A., J.L. Koprowski, V.L. Greer, K.H. Hutton, M. Alanen, and P. Young. 2002. Interactions between predators and Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*). Southwestern Naturalist 47:498-501.

Shaw, W.T. 1936. Moisture and its relation to the cone-storing habit of the western pine squirrel. Journal of Mammalogy 17:337-349.

Siepielski, A. and C.W. Benkman. 2004. Interactions among moths, crossbills, squirrels, and lodgepole pine in a geographic selection mosaic. Evolution 58:95-101.

Silvertown, J. 1980. Evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14: 235-250.

Smith, A.A. and R.W. Mannan. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. Journal of Wildlife Management 58:437-445.

Smith, C.C. 1965. Interspecific competition in the genus of tree squirrels, *Tamiasciurus*. Ph.D. dissertation, University of Washington, Seattle.

Smith, C.C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs 38:31-63.

Smith, C.C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349-371.

Smith, C.C. 1975. The coevolution of seeds and seed predators. Pages 53-77 in L.E. Gilber and P.H. Raven, editors. Coevolution of animals and plants. University of Texas Press, Austin, TX.

Smith, C.C. 1978. Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). Journal of Mammalogy 59:793-808.

Smith, C.C. 1981. The indivisible niche of *Tamiasciurus*: an example of non-partitioning of resources. Ecological Monographs 51:343-363.

Smith, C.C. and O.J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329-351.

Smith, J.K., editor. 2000. Wildland fire in ecosystems: effects of fire on fauna. USDA Forest Service General Technical Report RMRS GTR 42-Volume 1.

Smith, M.C. 1968. Red squirrel responses to spruce cone failure. Journal of Wildlife Management 32:305-316.

Snow, T. In press. Interagency census results for the Mt. Graham red squirrel. R. Sanderson and J.L. Koprowski, editors. Trapped on a Sky Island: Ecology and Conservation of endangered Mt. Graham red squirrels. (tentative title). University of Arizona Press, Tucson, AZ.

Squillace, A.E. 1953. Effect of squirrels on supply of ponderosa pine seed. USDA Forest Service Northern Rocky Mountain Forest and Range Experiment Station Research Note 131.

Squires, J.R. 2000. Food habits of Northern goshawks nesting in south central Wyoming. Wilson Bulletin 112:536-539.

Steele, M.A. 1998. Tamiasciurus hudsonicus. Mammalian Species 586:1-9.

Stuart-Smith, A.K. and S. Boutin. 1995a. Behavioral differences between surviving and depredated juvenile red squirrels. Ecoscience 2:34-40.

Stuart-Smith, A.K. and S. Boutin. 1995b. Predation on red squirrels during a snowshoe hare decline. Canadian Journal of Zoology 73:713-722.

Sullivan, R.M. and T.L. Yates. 1995. Population genetics and conservation biology of relict populations of red squirrels. Pages 193-208 *in* C. Istock and R.S. Hoffman, editors. Storm over a Mountain Island. University of Arizona Press, Tucson, AZ.

Sullivan, T.P. 1990. Response of red squirrels (*Tamiasciurus hudsonicus*) populations to supplemental food. Journal of Mammalogy 71:579-590.

Sullivan, T.P. and W. Klenner. 1993. Influence of diversionary food on red squirrel populations and damage to crop trees in young lodgepole pine forest. Ecological Applications 3:708-718.

Sullivan, T.P. and R.A. Moses. 1986. Red squirrel populations in natural and managed stands of lodgepole pine. Journal of Wildlife Management 50:595-601.

Sullivan, T.P. and D.S. Sullivan. 1982. Barking damage by snowshoe hares and red squirrels in lodgepole pine stands in central British Columbia. Canadian Journal of Forest Research 12:443-448.

Sullivan, T.P. and A. Vyse. 1987. Impact of red squirrel feeding damage on spaced stands of lodgepole pine in the Cariboo region of British-Columbia. Canadian Journal of Forest Research 17:666-674.

Sullivan, T.P., H. Coates, A. Jozsa, and P.K. Diggle. 1993. Influence of feeding damage by small mammals on tree growth and wood quality in young lodgepole pine. Canadian Journal of Forest Research 23:799-809.

Sullivan, T.P., W. Klenner, and P.K. Diggle. 1996. Response of red squirrels and feeding damage to variable stand density in young lodgepole pine forest. Ecological Applications 6:1124-1134.

Sullivan, T.P., J.A. Krebs, P.K. Diggle. 1994. Prediction of stand susceptibility to feeding damage by red squirrels in young lodgepole pine. Canadian Journal of Forest Research 24:14-20.

Sullivan, T.P., J.R. Sutherland, T.A.D. Woods, and D.S. Sullivan. 1984. Dissemination of the conifer seed fungus *Caloscypha fulgens* by small mammals. Canadian Journal of Forest Research 14:134-137.

Sun, C. 1997. Dispersal of young in red squirrels (*Tamiasciurus hudsonicus*). American Midland Naturalist 138:252-259.

Tackle, D. 1957. Protection of Ponderosa pine cones from cutting by the red squirrel. Journal of Forestry 55:446-447.

Trombulak, S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

Turner, R.W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. University of Kansas Museum of Natural History, Misc. Publications 60:1-178.

U.S. Fish and Wildlife Service. 1993. Mount Graham red squirrel recovery plan. U.S. Fish and Wildlife Service, Albuquerque, NM.

Vahle, J.R. and D.R. Patton. 1983. Red squirrel cover requirements in Arizona mixed conifer Forests. Journal of Forestry 81:115-127.

Vander Wall, S.B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, IL.

Veblen, T.T., K.S. Hadley, M.S. Reid, and A.J. Rebertus. 1991. The response of subalpine forest to spruce beetle outbreak in Colorado. Ecology 72:213-231.

Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M. Reid, and R.Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology 82:125-135.

Waldron, R.M. 1965. Cone production and seedfall in a mature white spruce stand. Forestry Chronicle 41:316-329.

Walton, M.A. 1903. A hermit's wild friends. D. Estes, Boston, MA.

Warren, E.R. 1942. The mammals of Colorado. University of Oklahoma Press, Norman, OK.

Waters, J.R. and C.J. Zabel. 1998. Abundances of small mammals in fir forests in northeastern California. Journal of Mammalogy 79:1244-1253.

Wirsing, A.J., T.D. Steury, and D.L. Murray. 2002. Relationship between body condition and vulnerability to predation in red squirrels and snowshoe hares. Journal of Mammalogy 83:707-715.

Wolff, J.O. 1975. Red squirrel response to clearcut and shelterwood systems in interior Alaska. U.S. Department of Agriculture Forest Service Research Note PNW-255.

Wood, T.J. 1967. Ecology and population dynamics of the red squirrel (*Tamiasciurus hudsonicus*) in Wood Buffalo National Park. M.S. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Wrigley, R.E. 1969. Ecological notes on the mammals of southern Quebec. Canadian Field-Naturalist 83:201-211.

Yahner, R.H. 1980. Burrow system use by red squirrels. American Midland Naturalist 103:409-411.

Yahner, R.H. 1986. Microhabitat use by small mammals in even-aged forest stands. American Midland Naturalist 115: 174-180.

Yahner, R.H. 1987. Feeding site use by red squirrels, *Tamiasciurus hudsonicus*. Canadian Field-Naturalist 101:586-589.

Yamamoto, O., B. Moore, and L. Brand. 2001. Variation in the bark call of the red squirrel (*Tamiasciurus hudsonicus*). Western North American Naturalist 61:395-402.

Yeager, L.E. and L.E. Riordan. 1953. Effects of beetle-killed timber on range and wildlife in Colorado. Transactions of the North American Wildlife and Natural Resources Conference 18:596-616.

Young, P. 1995. Monitoring the Mt. Graham red squirrel. Pages 226-246 *in* C. Istock and R.S. Hoffman, editors. Storm over a Mountain Island. University of Arizona Press, Tucson, AZ.

Young, P.J. 2000. Ten year report on the Red Squirrel Monitoring Project. University of Arizona Vice President for Research Office, Tucson, AZ.

Young, P.J., V.L. Greer, and S. Six. 2002. Characteristics of bolus nests of red squirrels in the Pinaleño and White Mountains of Arizona. Southwestern Naturalist 47:267-275.

Zirul, D.L. and W.A. Fuller. 1970. Winter fluctuations in size of home range of red squirrel (*Tamiasciurus hudsonicus*). Transactions of the North American Wildlife and Natural Resource Conference 70:115-127.

Zobel, D.B., L.F. Roth, and G.M. Hawk. 1985. Ecology, pathology, and management of Port Orford cedar (*Chamaecyparis lawsoniana*). USDA Forest Service General Technical Report PNW GTR 184.