Management and Conservation of Tree Squirrels: The Importance of Endemism, Species Richness, and Forest Condition

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Abstract—*Tree squirrels are excellent indicators of forest health yet the taxon is understudied. Most tree squirrels in the Holarctic Region are imperiled with some level of legal protection. The Madrean Archipelago is the epicenter for tree squirrel diversity in North America with 5 endemic species and 2 introduced species. Most species of the region are poorly studied in keeping with an international dearth of data on this taxon; 3 of the 5 native species are the subject of <3 publications. Herein, I review literature on the response of squirrels to forest management from clearcutting to less comprehensive operations. Major threats to squirrel diversity in the Madrean Archipelago's Sky Islands are the introduction of species, altered fire regimes, and inappropriate application of forestry practices.*

Introduction

The Madrean Archipelago is renown for its biodiversity (Lomolino et al. 1987). The area is considered a hotspot of evolution (Spector 2002) and contains the greatest diversity of mammals in the United States (Turner et al. 1995). Despite this megadiversity, the fauna is poorly represented in peer-reviewed scientific literature (Koprowski et al., this proceedings). The dearth of knowledge is an impediment to effective conservation and management. The persistence of mammalian diversity in relictual forests is dependent on the development of prudent and efficacious management strategies.

Tree squirrels are excellent indicators of forest health and structure (Carey 2000; Steele and Koprowski 2001) due to a dependence on mature forests for seed, nest sites, cover, and microclimates for food storage (Gurnell 1987; Steele and Koprowski 2001). The presence, demographics, and habitat use of tree squirrels can indicate the status of forested ecosystems. Herein, I review the unique nature of tree squirrel diversity in the Madrean Archipelago and address major issues of import to conservation in our forests through a literature review of the effects of forest condition on tree squirrels.

Species Diversity and Endemism

Tree squirrels across the globe are considered at risk (Koprowski and Steele 1998). Holarctic squirrels are of precarious conservation status with 88 % of 9 *Sciurus*, 67% of 3 *Tamiasciurus*, and 100% of 2 *Glaucomys* receiving legal protection due to concerns about persistence in a portion of the species' range (table 1). Fully 85% of squirrels are potentially imperiled. Furthermore, the ecology of squirrels is poorly known. I queried Web of Science (1945-2000; Thomson ISI, Stamford, CT) for all *Sciurus* (n = 28), *Tamiasciurus* (n = 3), and *Glaucomys* (n =2) species. Of 33 species, only 32% were the focus of ≥1 publication. A similar search for all species of arboreal Sciuridae world-wide yielded a bleak picture with 13% of known species the subject of ≥1 publication.

Five *Sciurus* and *Tamiasciurus* are native to the Sky Islands; 2 *Sciurus* were introduced (table 1), the greatest diversity in the Holarctic Region. When including 16 unique subspecies, the Madrean Archipelago's diversity doubles that found elsewhere. Most forms diverged in isolation in the Madrean Archipelago (Brown 1984) and are endemic to the Madrean Archipelago (81%, 13 of 16 forms). Thus, the area serves as an epicenter of tree squirrel diversity in North America. This diversity is at risk, and each native species receives legal protection. Furthermore, while squirrels of Arizona are poorly represented in the scientific literature (Koprowski et al., this proceedings), native tree squirrels of the region are especially so. No publications occur on the ecology of two endemic species, *Sciurus arizonensis* or *Tamiasciurus mearnsi*. *S. nayaritensis* has only 2 ecological papers on its ecology.

The unique diversity of squirrels in the Madrean Archipelago and its continued persistence are influenced by exotic species, forestry practices, and fire. Three tree squirrels were introduced to the Madrean Archipelago region. Fox squirrels (*S. niger*) were introduced to eastern New Mexico, dispersed, and are vagile to continue to do so (Frey and Campbell 1997). Eastern gray squirrels were released in Sierra San Pedro Martir in Baja California in 1946 (Huey 1964). Abert's squirrels were introduced to Sky Islands in Arizona and New Mexico in the 1940s (Davis and Brown 1988) and may have contributed to decline in native species in Arizona (Hoffmeister 1986).

Squirrel Responses to Forest Management Strategies: A Review

Squirrels rely on mature forests that produce quantities of seed, shaded microclimates for fungal growth and seed storage, and nest cavities (Gurnell 1987; Steele and Koprowski 2001). Disturbance of such conditions is not conducive to short-term

Table 1—Tree squirrel species of special concern in the Holarctic Region including the species of the Madrean Archipelago.

Species	Range	Status	Number of subspecies
Abert's Squirrel (*Sciurus aberti*)	Wyoming, Utah, Colorado, New Mexico, Arizona, Northern Mexico	Threatened in Mexico Kaibab Plateau Arizona IUCN	8
Persian Squirrel (*S. anomalus*)	Middle East Western Asia	Threatened in Israel	3
Arizona Gray Squirrel (*S. arizonensis*)	Arizona, New Mexico, Sonora	Threatened in Mexico USFS Sensitive	3
Western Gray Squirrel (*S. griseus*)	Washington, Oregon, California, Baja California	Threatened in Washington	3
Japanese Squirrel (*S. lis*)	Japan	Threatened	1
Mexican Fox Squirrel (*S. nayaritensis*)	Arizona, Sierra Madre Occidental	USFS Sensitive in Arizona	3
Fox Squirrel (*S. niger*)	Eastern United States	Endangered in Maryland, Delaware, Virginia	10
Eurasian Red Squirrel (*S. vulgaris*)	Europe and Asia	United Kingdom Protected	>20
Mearns's Squirrel (*Tamiasciurus mearnsi*)	Baja California	Threatened	1
Red Squirrel (*Tamiasciurus hudsonicus*)	North America	Endangered in southeastern Arizona	25
Southern Flying Squirrel (*Glaucomys volans*)	North and Central America	Threatened in Nebraska	10
Northern Flying Squirrel (*Glaucomys sabrinus*)	North America	Endangered in Appalachian Mountains	25

persistence of populations in a local area; management schemes that do not promote return of forests to such conditions after disturbance will impede reestablishment and persistence of squirrels. Unfortunately, few studies have been conducted specifically to quantify impacts of forestry practices.

Impacts of clearcuts

Clearcuts remove habitat directly, degrade habitat by edge effects, decrease squirrel activity, and potentially increase vulnerability to predation (Wolff 1975; Anderson and Boutin 2002). Squirrel densities are often significantly higher in mature forests compared to clearcuts (Nixon et al. 1980a; Bayne and Hobson 1997; King et al. 1998). Red squirrel densities decreased from 1.2 to 0/ha in clearcut blocks of spruce (Wolff 1975). Seed predation declines greatly in single seed tree cut blocks due to decrease in use by red squirrels (Peters et al. 2003). The scale of clearcutting operations appears important. Red squirrels persist for $\geq$3 to 5 y in residual forest and corridors in clearcuts and cutblocks (Cote and Ferron 2001). Small (<8 ha), narrow clearcuts (<160 m) did not change densities or demographics in eastern gray squirrels, a non-territorial species (Nixon et al. 1980b).

Impacts of thinning regimes

Squirrel densities decline in thinned sites that include a significant (>50%) reduction in stems (Nixon et al. 1980b; Sullivan and Moses 1986; Sullivan et al. 1996). Red squirrels decreased from 1.5 to 0.5 squirrels/ha in thinned blocks (83% removal), while edge and interior habitats of uncut forest did not change in density (Wolff 1975). Thinning of lodgepole pine (*Pinus contorta*) by 73% resulted in an 80% decline of red squirrels compared to unthinned sites (Sullivan and Moses 1986). Heavily thinned stands of juvenile lodgepole pine had reduced densities of pine squirrels (Sullivan et al. 1996). Sites with post-thinning densities of 1,000 to 2,000 stems/ha had more immigrants than intensively thinned (500 stems/ha) sites; populations in these treatments did not differ consistently in demography (Sullivan et al. 1996). Red squirrel demographics did not differ in second growth or old growth spruce-fir and lodgepole pine forests (Ransome and Sullivan 1997). Douglas's squirrel (*Tamiasciurus douglasii*) abundance was similar in young, mature, and old growth forests (Anthony et al. 1987; Carey 2000, 2001). Douglas's squirrels were most common in 80 to 100 y mature fir (*Abies*) forest compared to shelterwood cut (harvested in 2 stages with regeneration under partial canopy) or old growth forests (Waters and Zabel 1998).

Seed and shelterwood tree cuts may retain habitat components but often stem density is too low to provide squirrel habitat (Waters and Zabel 1998). In black spruce (*Picea mariana*), red squirrel demography did not differ between residual uncut forest strips or blocks and controls in continuous forest for 3-5 years post harvest suggesting minimal impact; however, middens were less common in residual forests (Cote and Ferron 2001). Thinned sites that become open and permit increased ground and shrub cover are avoided by *Sciurus vulgaris* (Gurnell et al. 2002).

Stringers of habitat often along riparian areas appear important. Eastern gray squirrels are less common in even-aged pine stands compared to mixed aged stands and mixed forests, especially those with hardwood stringers (Fischer and Holler 1991; Lurz et al. 1995). Similarly, southern flying squirrels did not use young (<15 y) and immature (15-40 y) pine plantations and harvest sites except if 10 to 20 m wide riparian forest strips were retained (Taulman 1999). Use of linear habitats and stringers may be important for other squirrels including red squirrels (Goheen et al. 2003), Eurasian red squirrels (Verbeylen et al. 2003), and fox squirrels (Goheen 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. The retention of biological legacies and the management for decadence and variable stem densities are promising approaches to region wide management of forests for mature and old-growth conditions favorable to red squirrels while also permitting extraction of resources and management for forest health and fire (Carey 1995, 2000, 2001).

Nest availability is important for some species. Douglas's squirrels benefit from retention of ≥20 snags/ha in thinned forests (Carey 1995). At least 1 den/0.8 ha is required to maintain densities of >1 eastern gray squirrel/1.6 ha (Sanderson 1975). Artificial nests increase eastern gray squirrel and southern flying squirrel densities (Burger 1969; Nixon and Donohoe 1979; Goertz et al. 1975), but only impact male fox squirrels (Nixon et al. 1984).

Forestry practices in the Madrean Archipelago

Sorely little is known about management of most tree squirrels. Abert's squirrels are likely to be negatively impacted by forestry practices that include widespread thinning (Dodd et al. 2003). The impact appears to occur due to reduction of an interlocking canopy and decreased production of fungi (Dodd et al. 2003). These impacts led Dodd et al. to suggest that squirrels would be negatively impacted by traditional large-scale restoration methods, and that a large landscape mosaic that retains 35% of the area in high quality habitat patches with multiple management schemes applied to the matrix would be most beneficial. Red squirrels in the White and Pinaleno Mountains of Arizona prefer dense patches of moderately sized trees and high levels of canopy closure for storage and nest sites (Vahle and Patton 1983; Mannan and Smith 1994; Young et al. 2002). Linear riparian habitats appear crucial to nesting in Mexican fox squirrels (Pasch and Koprowski, this proceedings). Little work on the relationships between forest condition and tree squirrels exists for the Archipelago.

Fire

In the Western United States, fire is considered the major disturbance under heavy anthropogenic influence (Smith 2000; Brown and Smith 2000). Policies of suppression for nearly 100 y in the United States have resulted in significant changes in cool and catastrophic fire frequencies, as well as forest structure (Brown and Smith 2000). Ponderosa pine and Douglas-fir forests are typically characterized by frequent, low intensity ground fires, or mixed fire regimes; rarely stand replacement fires (table 2: Brown and Smith 2000). Conversely, mixed and stand replacing fires most likely occur in high elevation spruce-fir forests only every 100 to 400 y with particularly moist spruce-fir forests burned only once every 800 to 2000 years (Brown and Smith 2000). Such temporal scales suggest that human disturbances and suppression may have had much less impact on fire cycles for high elevation species. Restoration of natural fire frequencies is likely desirable but difficult.

The response of any tree 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 direct and immediate loss of habitat, yet 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 microclimates that result from ground and mixed fires must be considered in relation to the long-term term gains in habitat quality due to retention of open forest structure, increased productivity and seed production, and decreased risk of catastrophic fire (Brown and Smith 2000). Red squirrel population responses to habitat fragmentation appear to be similar to that resulting from fire (Bayne and Hobson 1997). Because 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 squirrel persistence (Gurnell 1987; Steele and Koprowski 2001). Stand replacement fires and less patchy, mixed fire regimes, however, are likely to have greater impact because these fires effectively are experienced as clearcuts by squirrel populations. In addition, the high temperatures at which such fires burn 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 common to the Madrean Archipelago typically require at least 15 years to produce seed (table 3) with the most productive age classes at 50 to 200 y (Burns and Honkala 1991). Given the lengthy associations and coevolution of forests and squirrels, historical temporal and spatial patterns of fire (Swetnam and Baisan 1996) are likely not a problem for the persistence of squirrel populations. Changes in the frequency, intensity, and scale of fires resulting from human activities are the major challenge.

Levels of insect infestation are also linked to fire dynamics due to the fuel increase that results from tree mortality; however, the mosaic pattern that often results may reduce the risk of catastrophic fires (Baker and Veblen 1990; Matsuoka et al. 2001). Little research has been conducted on how squirrels respond to insect infestation. Red squirrel populations decline significantly in areas with >40% mortality of spruce trees due to beetle infestations (Matsuoka et al. 2001), and this pattern of decline has been noted in spruce-fir forests as well (Yeager and Riordan 1953). Importantly, red squirrels did not disappear entirely from areas with high insect infestation and tree mortality. Red squirrels exist within patches of the mosaic where conditions remain suitable (Matsuoka et al. 2001). Red squirrel use of relictual forest patches throughout secondary succession is likely the result of their long association with coniferous forests. Similar results might be expected for other Madrean forest dwelling species.

Table 2—Summary of fire cycles and fire regime types for common forest types in the Madrean Archipelago (after Brown and Smith 2000:98-99; Swetnam and Baisan 1995).

	Fire regime type					
	Understory		Mixed		Stand replacing	
Forest type	Extent[a]	Freq[b]	Extent	Freq	Extent	Freq
Ponderosa Pine						
Southern Rockies	Major	1-25	Minor	35-200		
Southwestern	Major	10	Minor	<35		
Arizona Cypress			Major	<35 to 200	Minor	<35
Douglas-fir	Minor	<35-200	Major	25-100		
Engelmann spruce-Subalpine fir					Major	100-400
White fir-Blue Spruce-Douglas-fir			Major	35-200	Major	35-200
Madrean Pine-Oak	Major	1-25	Minor			

[a] Percentage of stand: Major = >25%, minor = <25%.
[b] Frequency of occurrence in years.

Conclusions

The Madrean Archipelago represents the epicenter of tree squirrel diversity in North America. In agreement with global trends, the diversity of tree squirrels is poorly described and understudied. In the Madrean Archipelago, 5 native species of tree squirrel occur and 3 of these species have not been thoroughly studied. In addition, 3 species have been introduced to sites in the region with the status and impact of these introductions not well documented. This lack of information on the status and ecology of tree squirrels is an impediment to effective conservation and management of some of the mammals most illustrative of the Sky Island region.

Several patterns emerge from a comparison of the response of squirrels in a variety of habitats to thinning. Clearcuts are detrimental to local populations of tree squirrels; however, if part of a large-scale regional plan in a connected landscape, small clearcuts and other management techniques that result in small but temporary fragmentation may have minimal impacts. Thinning treatments that exceed 50% of the stems are nearly always associated with dramatic declines in numbers. Canopy closure is a key factor influencing populations with a number of species favoring dense sites (Gurnell et al. 2002; Vahle and Patton 1983; Dodd et al. 2003; Dodd 2003; Nixon and Hansen 1987). Dense ground cover in open forests is often avoided by squirrels (Gurnell et al. 2002). Retention of biological legacies to increase cavities also appears important (Sanderson 1975; Carey 2000). Our knowledge of the impacts of forestry practices and fire management on squirrels remains scant and we are especially poorly versed in the interactions between multiple disturbances.

Working on different species in diverse habitats in different regions of North America (Carey 2000, 2001; Dodd et al. 2003; Taulman 1999; Nixon and Hansen 1987) and Europe (Gurnell et al. 2002), researchers concluded that the most successful approach to conservation of tree squirrels is the promotion of a mosaic landscape. The mosaic should contain patches of dense vegetation (high canopy cover, stem densities, interlocking canopies) while the matrix contains thinning regimes that serve as lower quality habitat, fire breaks, corridors for movement, and/or timber extraction depending on management goals. Perhaps most clear is that successful management and conservation of the unique tree squirrel diversity of the Madrean Archipelago will require that we increase our knowledge of this diverse assemblage and the impacts of management schemes on their demography and persistence.

Table 3—Seed crop characteristics of major conifer species in Madrean Archipelago. 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 Honkala1990).

Species	Common name	Age at 1st seed[a]	Mast year interval (yr)
Abies concolor	White fir	40	3 to 9
A. lasiocarpa	Subalpine fir	20 to 50	3 to 5
Picea engelmannii	Engelmann spruce	15 to 40	2 to 5
P. pungens	Blue spruce	20	2 to 3
P. ponderosa	Ponderosa pine	7	3 to 8
P. edulis	Piñon pine	25	4 to 7
Pseudotsuga menziesii	Douglas-fir	10 to 30	7

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

References

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

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

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

Bayne, E.; Hobson, K. 1997. 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.

Brown, David. E. 1984. Arizona's tree squirrels. Phoenix: Arizona Game and Fish Department. 114 p.

Brown, James K.; Smith, J. K., eds. 2000. Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-GTR-42-Vol.2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Burger, George V. 1969. Response of gray squirrels to nest boxes at Remington Farms, Maryland. Journal of Wildlife Management 33: 796-803.

Burns, Russell M.; Honkala, Barbara H., tech. coords. 1990. Silvics of North America: 1. Conifers. Agric. Handb. 654, Vol.2. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.

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

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

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

Cote M, Ferron J. 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.

Davis, Russell; Brown, D. E. 1988. Documentation of the transplanting of Abert's squirrels.Southwestern Naturalist 33: 490-492.

Dodd, Norris L. 2003. Landscape-scale habitat relationships to tassel-eared squirrel population dynamics in north-central Arizona. Arizona Game and Fish Department Technical Guidance Bulletin 6: 1-28.

Dodd, Norris L.; States, J. S.; Rosenstock, S. S. 2003. Tassel-eared squirrel population, habitat condition, and dietary relations in north-central Arizona. Journal of Wildlife Management 67: 622-633.

Fischer, Robert A.; Holler, N. R. 1991. Habitat use and relative abundance of gray squirrels in southern Alabama. Journal of Wildlife Management 55: 52-59.

Frey, Jennifer K.; Campbell, M. L. 1997. Introduced populations of fox squirrel (Sciurus niger) in the Trans-Pecos and Llano Estacado regions of New Mexico and Texas. Southwestern Naturalist 42: 356-358.

Goertz, J. W.; Dawson, R. M.; Mowbray, E. E. 1975. Response to nest boxes and reproduction by Glaucomys volans in northern Louisiana. Journal of Mammalogy 56: 933-939.

Goheen, Jacob R.; Swihart, R.K.; Gehring, T. M.; Miller, M. S. 2003. Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. Oikos 102: 95-103.

Gurnell, John 1987. The natural history of squirrels. New York: Facts on File. 201 p.

Gurnell, John; Clark, M. J.; Lurz, P. W. W.; Shirley, M. D. F.; Rushton, S. P. 2002. Conserving red squirrels (Sciurus vulgaris): mapping and forecasting habitat suitability using a Geographic Information System approach. Biological Conservation 105: 53-64.

Hoffmeister, Donald F. 1986. Mammals of Arizona. Tucson: University of Arizona Press. 602 p.

Huey, Lawrence M. 1964. The mammals of Baja California, Mexico. Transactions of the San Diego Society of Natural History 13: 85-168.

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

Koprowski, John L.; Steele, M. A. 1998. Future directions: Research on the ecology of tree squirrels. In: M. A. Steele; J. F. Merritt; D. A. Zegers, eds. Ecology and Evolutionary Biology of Tree Squirrels. Special Publication 6. Virginia Museum of Natural History: 309-310.

Lomolino, Mark V.; Brown, J. H.; Davis, R. 1989. Island biogeography of montane forest mammals in the American Southwest. Ecology 70: 180-194.

Lurz, Peter W.W.; Garson, P. J.; Rushton, S. P. 1995. The ecology of squirrels in spruce dominated plantations: Implications for forest management. Forest Ecology and Management 79: 79-90.

Matsuoka, S. M.; Handel, C. M.; Ruthrauff, D. R. 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.

Nixon, Charles M.; Donohoe, R.W. 1979. Squirrel nest boxes—are they effective in young hardwood stands. Wildlife Society Bulletin 7: 283-284.

Nixon, Charles M.; Hansen, L. P. 1987. Managing forests to maintain populations of gray and fox squirrels. Illinois Department of Conservation Technical Bulletin 5: 1-35.

Nixon, Charles M.; Havera, S. P.; Hansen, L. P. 1980a. Initial response of squirrels to forest changes associated with selection cutting. Wildlife Society Bulletin 8: 298-306.

Nixon, Charles M.; Havera, S. P.; Hansen, L. P. 1984. Effects of nest boxes on fox squirrel demography, condition and shelter use. American Midland Naturalist 112: 157-171.

Nixon, Charles M.; McClain, M. W.; Donohoe, R. W. 1980b. Effects of clear-cutting on gray squirrels. Journal of Wildlife Management 44: 403-412.

Patton, David R.; Vahle, J. R. 1986. Cache and nest characteristics of the red squirrel in an Arizona mixed-coniferous forest. Western Journal of Applied Forestry. 1: 48-51.

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

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

Sanderson, H. R. 1975. Den-tree management for gray squirrels. Wildlife Society Bulletin 3: 125-131.

Smith, Andrew A.; Mannan, R. W. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. Journal of Wildlife Management. 58(3): 437-445.

Smith, James K., ed. 2000. Wildland fire in ecosystems: effects of fire on fauna. Gen. Tech. Rep. RMRS-GTR-42-Vol 1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Spector, S. 2002. Biogeographic crossroads as priority areas for biodiversity conservation. Conservation Biology. 16: 1480-1487.

Steele, Michael A.; Koprowski, J. L. 2001. North American tree squirrels. Washington, DC: Smithsonian Institution Press. 225 p.

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

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

Swetnam, Thomas, W.; Baisan, C. H. 1996. Fire histories of montane forests in the Madrean Borderlands. In: Effects of fire on Madrean Province ccosystems. Gen. Tech. Rep. GTR-RM-289. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 15-36.

Taulman, J. F. 1999. Selection of nest trees by southern flying squirrels (Sciuridae : Glaucomys volans) in Arkansas. Journal of Zoology 248: 369-377.

Turner, Dale S.; Brandes, S.; Fishbein, M.; Hirt, P. W. 1995. Preserve design for maintaining biodiversity in the Sky Island Region. In: Biodiversity and management of the Madrean Archipelago: the Sky Islands of Southwestern United States and Northwestern Mexico. Gen. Tech. Rep. GTR-RM-264. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 669 p.

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

Verbeylen, Goedele; De Bruyn, L.; Matthysen, E. 2003. Patch occupancy, population density and dynamics in a fragmented red squirrel Sciurus vulgaris population. Ecography 26: 118-128.

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

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

Yeager, Lee E.; Riordan L. E. 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, Paul J.; Greer, V. L.; Six, S. K. 2002. Characteristics of bolus nests of red squirrels in the Pinaleño and White Mountains of Arizona. The Southwestern Naturalist 47: 267-275.