

ECOLOGY OF *GLAUCOMYS SABRINUS*: HABITAT, DEMOGRAPHY, AND COMMUNITY RELATIONS

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A common arboreal rodent of boreal and montane coniferous forests, the northern flying squirrel (*Glaucomys sabrinus*) has several life-history traits typical of K-selected species. Density varies among forest types, with core areas of use centering on food patches. Density is largely limited by food, and to a lesser extent, suitable natal dens, but also is influenced by potential competitors and predators. Local abundance of *G. sabrinus* frequently is correlated with density of large trees and snags, shrub and canopy cover, prevalence of old-forest features (e.g., coarse woody debris), and abundance of hypogeous mycorrhizal fungi (truffles). Diet varies seasonally and among habitats, but truffles (spring and autumn) and lichens (winter) are most often reported. In some parts of its geographic range, *G. sabrinus* has a more diverse diet and lower reliance on truffles in forests with a depauperate arboreal small mammal community. *G. sabrinus* is a keystone species in the Pacific Northwest, because its diet facilitates an obligate mutualistic relationship between mycorrhizal fungi and some trees and shrubs and because it is essential prey for mesocarnivores and avian predators. *G. sabrinus* achieves its highest densities in old growth, but also occurs in secondary forests. Disturbance that reduces structural complexity, canopy cover, or the availability of large, decadent trees typically results in smaller populations through effects on food, den sites, or risk of predation. The fundamental niche of *G. sabrinus* may be broader than suggested by early research in the Pacific Northwest. Sustaining viable and well-distributed populations in heavily modified landscapes will depend on the capability of remaining forest habitat to sustain breeding populations without immigration, or functional connectivity among fragmented populations such that viable metapopulations will persist. Future research should focus on identifying habitat conditions that sustain breeding populations in modified habitats and determining whether *G. sabrinus* can migrate freely through a matrix of unsuitable habitat.

Key words: demography, *Glaucomys sabrinus*, habitat relations, home range, interspecific interactions, limiting factors, movements, northern flying squirrel, persistence, population dynamics

The northern flying squirrel (*Glaucomys sabrinus*) is a common arboreal rodent of boreal and montane coniferous forests. Its geographic range (Arbogast 2007:843, figure 2) extends to southern portions of the Appalachian Mountains in the east and the Rocky Mountain and Sierra Nevada Ranges in western North America and includes the San Bernardino Mountains of southern California (Hall 1981; Wells-Gosling and Heaney 1984). This species is active year-round, in air temperatures as low as -26°C (Mowrey and Zasada 1984); is primarily nocturnal, especially in more southern latitudes; and typically has 2 peaks of daily activity (Weigl and Osgood 1974; but see Wilson et al., in press), but adjusts timing and duration of activity according to the onset of darkness and air

temperature (Cotton and Parker 2000a). *G. sabrinus* has several life-history traits typical of K-selected species (sensu MacArthur and Wilson 1967): it inhabits late-seral habitat, it is relatively long-lived (≥ 7 years—Villa et al. 1999), it has delayed development and age at 1st reproduction, it is a seasonal breeder with small litters (average 2 or 3 young) after a relatively long (37- to 42-day) gestation (Wells-Gosling and Heaney 1984), and it undergoes density-dependent population growth (Fryxell et al. 1998; Lehmkühl et al. 2006). Females seem to invest substantial energy (during gestation and lactation) in each offspring, presumably to produce larger young with greater competitive ability (MacArthur and Wilson 1967).

Glaucomys sabrinus is considered a keystone species in the Pacific Northwest because it is an important link in the food chain and dynamics of coniferous forests. It is important prey for several predators (Forsman et al. 1984; Rosenberg et al. 2003; Wilson and Carey 1996) and facilitates an obligate symbiotic relationship between mycorrhizal fungi and domi-

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TABLE 1.—Densities of northern flying squirrels (*Glaucomys sabrinus*) among forested habitats of western North America (adapted from Smith et al. 2003).

Forest type	Age and disturbance history	Season	Densities (number/ha)		Source
			\bar{X}	Range	
Douglas-fir	Young growth, clear-cut	Spring	1.1	0.7–1.6	Carey et al. 1992
Douglas-fir	Young growth, clear-cut	Autumn	0.5	0.3–0.7	Carey et al. 1992
Douglas-fir	Young growth, clear-cut	Autumn	1.9	1.1–2.5	Rosenberg and Anthony 1992
Douglas-fir	Old growth, natural	Spring	1.8	1.1–2.2	Carey et al. 1992
Douglas-fir	Old growth, natural	Autumn	1.9	1.8–2.2	Carey et al. 1992
Douglas-fir	Old growth, natural	Autumn	2.3	1.4–3.3	Rosenberg and Anthony 1992
Douglas-fir	Old growth, natural	Annual	1.0	0.5–1.8	Witt 1992
Douglas-fir	Second growth, clear-cut	Annual	0.1	0–0.2	Witt 1992
Western hemlock–Sitka spruce	Young growth, clear-cut	Autumn	0.2	NA ^a	Carey et al. 1992
Western hemlock–Sitka spruce	Old growth, natural	Autumn	0.5	NA	Carey et al. 1992
Western hemlock–Sitka spruce	Old growth, natural	Spring	1.8	1.6–2.0	Smith and Nichols 2003
Western hemlock–Sitka spruce	Old growth, natural	Autumn	3.2	2.2–4.0	Smith and Nichols 2003
Mixed conifer	Old growth, natural	Spring	1.7	0.9–3.2	Carey et al. 1992
White fir–red fir	Mature, fire replacement	Summer	2.3	2.2–2.4	Waters and Zabel 1995
White fir–red fir	Old growth, natural	Summer	3.3	2.8–3.5	Waters and Zabel 1995
White fir–red fir	Old growth, shelterwood cut	Summer	0.4	0.2–0.6	Waters and Zabel 1995
Ponderosa pine	Second growth, selective harvest	Autumn	1.2	0.9–1.6	Lehmkuhl et al. 2006
Mixed conifer	Young growth, selective harvest	Autumn	1.8	1.4–2.2	Lehmkuhl et al. 2006
Mixed conifer	Mature, natural	Autumn	2.3	1.9–2.6	Lehmkuhl et al. 2006

^a NA = not available.

nant tree species (Maser and Maser 1988). *G. sabrinus* feeds on sporocarps of hypogeous fungi and deposits fecal pellets with fungal spores and nitrogen-fixing bacteria across the forest floor (Caldwell et al. 2005). The spores germinate and establish new colonies or contribute new genetic material to existing colonies. The mycorrhizae facilitate the tree's ability to absorb water and nutrients. Whether *G. sabrinus* plays a similar role in other forest biomes across its range is uncertain, but Smith et al. (2005) suggest that its habitat relations and specialized mycophagous diet in the Pacific Northwest may be attributable (at least in part) to the diverse ecological community of arboreal rodents (Carey 1989, 1991, 1995, 1996; Verts and Carraway 1998).

Glaucomys sabrinus was the focus of considerable research during the past 2 decades, especially in the Pacific Northwest where it is recognized as an essential prey species throughout much of the range of the spotted owl (*Strix occidentalis*—Carey et al. 1992; Forsman et al. 2001) and because of its keystone role in western coniferous forests (Maser et al. 1986; Maser and Maser 1988). In the southern and central Appalachians, federal listing of 2 subspecies renewed and increased interests in the demography and habitat relations of several isolated endemic populations (Payne et al. 1989; Weigl et al. 1999). A fundamental issue underlying much of the research during this period has been whether the habitat of *G. sabrinus* is an emergent property of old-growth forest (Carey 2000; Carey et al. 1999). With few exceptions (Rosenberg and Anthony 1992), the findings of several studies suggest that optimal conditions for *G. sabrinus* occur in mature or old-growth forests (e.g., Carey 1995), which led to its prominence as an indicator species (Smith et al. 2005). However, recent retrospective or manipulative experiments (e.g., Ransome and Sullivan 2003) have produced evidence that challenges any generalization that *G. sabrinus* relies on old-growth forest.

The purpose of this paper is to develop a conceptual ecological model of factors that shape the local and regional distribution of *G. sabrinus* throughout its geographic range, based on a summary of information from the scientific literature. Specific objectives include linking demography to habitat (at multiple spatial scales) and community relations to identify factors (particularly land-use patterns) that may be limiting distribution and abundance. A preponderance of evidence is used to evaluate multiple hypotheses regarding the role of cumulative disturbance, forest structure, specific resources, or interspecific interactions in limiting abundance, and whether factors constraining local populations vary across forest communities.

HABITAT

Influence on distribution.—*Glaucomys sabrinus* occupies a broad range of habitats, mostly coniferous forests (Smith et al. 2003), but it can occur in deciduous forests and is common in mixed forests including spruce (*Picea*)–northern hardwood and other mixed-coniferous–hardwood forest types (Ford et al. 2004; Holloway 2006; Holloway and Malcolm 2006; Payne et al. 1989; Weigl 1978; Weigl et al. 1999). *G. sabrinus* apparently shows little preference for coniferous or hardwood forest types in the Appalachians (Weigl 1978), suggesting that factors other than habitat selection might play a role in determining distribution in portions of its range. Population density varies across portions of its range (Wells-Gosling and Heaney 1984) and among forest types within a region (Smith et al. 2003). In the Pacific Northwest, population density in mature or old-growth forests may vary among sites by an order of magnitude (Table 1). Interestingly, both the lowest (0.5/ha) and highest (4.0/ha) mean densities recorded in the region were in coastal temperate rain forests (Smith et al. 2003; Smith and

Nichols 2003). There are few estimates of density for populations in the eastern portion of its range (Bowman et al. 2005).

Regional and landscape scales.—The contemporary distribution of *G. sabrinus* may be largely determined by factors associated with regional land-use and recent climate change, particularly at the southern limit of its geographic range. In the southern and central Appalachians, the distribution of *G. sabrinus* is naturally disjunct (Payne et al. 1989), with the species occurring as relict populations among islands of montane coniferous forests that were restricted to higher elevations after glacial retreat because of post-Pleistocene climatic shifts. Boreal-type relict forests are among the rarest in the eastern United States (Hackett and Pagels 2003; Schuler et al. 2002). However, post-European settlement land use has dramatically altered landscape and stand-level composition of forests in the region. Forests dominated by red spruce (*Picea rubens*) have been reduced by 90% (Ford et al. 2004), and Appalachian montane coniferous forest communities of red spruce, eastern hemlock (*Tsuga canadensis*), and Fraser fir (*Abies fraseri*) are considered among the most threatened forested ecosystems in the United States (Schuler et al. 2002). Extensive logging followed by widespread fires changed the overstory composition and destroyed much of the humus layer and coarse woody debris in the understory, which reduced habitat quality for hypogean fungi or altered the composition of local fungal communities (Loeb et al. 2000). Thus, human-caused disturbances have degraded coniferous forests and facilitated expansion of oak (*Quercus*) and hickory (*Carya*) forest communities to higher elevations (Odom et al. 2001; Payne et al. 1989; Weigl 2007; Weigl et al. 1999). Although ecotones between coniferous and hardwood forests are considered optimal habitat for both subspecies of *G. sabrinus* in the Appalachians (Payne et al. 1989; Weigl et al. 1999), continued disturbance and global warming likely will replace conifer-dominated stands with hardwood forest communities and further reduce, fragment, and isolate populations of *G. sabrinus* (Payne et al. 1989; Weigl 2007).

Similarly, post-European settlement land use converted the Great Lakes region from landscapes of largely “frontier” forests to mostly nonforest landcover or different forest communities (Cole et al. 1998; Frelich 1995), with the greatest changes occurring in a reduction of white pine (*Pinus strobus*) and red pine (*P. resinosa*—Leadbitter et al. 2002). Ordinarily, modified landscapes return to native forest types through ecological succession, but climate change may retard or interrupt ecological processes that reestablish forest communities after disturbance (Flannigan et al. 1998; Hennon and Shaw 1997). One significant consequence to *G. sabrinus* has been the fragmentation of populations amid an agricultural matrix (Bowman et al. 2005). In addition, climate change apparently has facilitated the expansion northward (or to higher elevations) of hardwood forest communities typical of more southern latitudes (or lower elevations), with potential negative impacts to federally listed populations of *G. sabrinus* in the region (Ford et al. 2004; Holloway 2006; Menzel et al. 2006a; Payne et al. 1989).

In western North America, habitat of *G. sabrinus* also has undergone substantial modification, but for shorter periods and over smaller portions of its range. Type, intensity, and frequency of broad-scale disturbances that western forests experience (e.g., fire, logging, and windthrow) changed dramatically after European settlement (Dale et al. 2001; Nowacki and Kramer 1998). Consequences of climate warming to ecological succession or patterns of forest cover might not seem as apparent as in eastern North America, but the projected redistribution of climate space because of global warming is substantial, with subboreal and montane climate regions in British Columbia, for example, rapidly disappearing (Hamann and Wang 2006). Furthermore, history has shown that interactions between disturbance and climate change can accelerate changes in landcover and forest communities (Ford et al. 2004; Odom et al. 2001; Payne et al. 1989) that could possibly limit the distribution of *G. sabrinus* in the region. Although broad-scale replacement of coniferous forest types from climatic shifts likely is not imminent, a continued warming trend could significantly affect forest composition and structure (Hamann and Wang 2006; Hennon and Shaw 1997), shift forests toward more xeric types with significant consequences for fungal and understory plant communities (Lehmkuhl et al. 2004; Meyer and North 2005), or change the pattern of natural disturbance across an entire biome (Flannigan et al. 1998), with profound repercussions for the distribution of *G. sabrinus* in western North America, particularly in the southern extent of its range (Meyer and North 2005).

Broad-scale changes in native forest vegetation directly and indirectly influence the distribution of *G. sabrinus* (Menzel et al. 2006a). Across landscapes in eastern North America, the probability of occurrence of *G. sabrinus* is positively correlated with the density of large spruce (*Picea*) and northern hardwood trees and amount of downed woody debris (Holloway 2006). In this region, density of *G. sabrinus* is inversely correlated with the density of the southern flying squirrel (*G. volans*—Bowman et al. 2005; Weigl et al. 1999) and distance to coniferous forest (Menzel et al. 2006a; Odom et al. 2001) or to mixed-spruce-hardwood forests (Menzel et al. 2006a). Furthermore, the extent to which forested landscapes are fragmented influences the northward range expansion and distribution of *G. volans* (Bowman et al. 2005). In the more southeastern portion of its range, *G. sabrinus* has ≥ 0.9 probability of occurrence in forested landscapes where the relative importance value of conifer overstory (especially red spruce) is ≥ 50 (maximum score of 90—Ford et al. 2004). A similar relationship between spruce forests and the distribution of *G. sabrinus* was reported for central Ontario (Holloway 2006; Holloway and Malcolm 2006). Hypogean fungi are an essential resource associated with coniferous forests (Loeb et al. 2000) and decayed standing and coarse woody debris (Carey et al. 1999, 2002; Clarkson and Mills 1994; Colgan et al. 1999; Gomez et al. 2003; Lehmkuhl et al. 2004, 2006; North et al. 1997; Pyare and Longland 2001a, 2002; Smith et al. 2000, 2002; Waters et al. 1997, 2000). Furthermore, in mixed-hardwood-conifer forest or at the ecotone of hardwood and coniferous forests *G. sabrinus* uses dreys (i.e., external leaf

necks) almost exclusively in conifers (Menzel et al. 2004; Mowrey and Zasada 1984; Stihler et al. 1987). Dreys are especially important where *G. sabrinus* is sympatric with *G. volans* and competition for cavities can be intense (Hackett and Pagels 2003; Holloway 2006; Holloway and Malcolm 2006; Muul 1968; Weigl 1978, 2007).

Thus, landscapes where hardwood forest communities (especially hard mast-producing species) are increasing (through land-use or climate change) will probably experience declining populations of *G. sabrinus*, not because hardwood forests are unsuitable, but because oak and hickory forests are ideal habitat for *G. volans* (Payne et al. 1989), an aggressive competitor (Muul 1968; Weigl 1978, 2007) and vector of a pathological nematode (Pauli et al. 2004; Weigl et al. 1999). In recent years, the range of *G. volans* has expanded northward (Bowman et al. 2005; Holloway 2006) and to higher elevations in more southern latitudes (Odom et al. 2001; Weigl et al. 1999), with concomitant declines in populations of *G. sabrinus* (Holloway 2006; Weigl et al. 1999). As more landscapes in the southeastern portion of the range of *G. sabrinus* experience change in land cover or a shift in forest composition, a greater proportion of regional populations will become fragmented and isolated (Payne et al. 1989). At more northern latitudes, climate warming could facilitate migration of boreal forest northward but it is unclear to what extent *G. sabrinus* could shift its range to higher latitudes.

The response of populations of *G. sabrinus* to habitat fragmentation has not been widely studied, but evidence from central Ontario suggests that populations of *G. sabrinus* can occur in forest fragments within an agricultural matrix (Bayne and Hobson 1998; Bowman et al. 2005; Côté and Ferron 2001). In heavily modified landscapes of the Olympic Peninsula, *G. sabrinus* was captured in only 3 of 20 old-growth fragments (ranging from ≈ 3 to 60 ha) that were < 40 ha in size and within 2.5 km of old-growth rain forest (Lomolino and Perrault 2001). Further study revealed that the distribution and size of high-quality habitat fragments determines the genetic diversity of source populations and the likelihood of empty suitable patches becoming recolonized (Wilson 2003). In southeastern Alaska, Smith and Person (2007) used simulations of a birth-death process model developed from empirical estimates of demographic parameters (Smith and Nichols 2003; Villa et al. 1999) to examine the persistence of populations of *G. sabrinus* in hypothetical old-growth reserves isolated in managed landscapes. Based on the results of their population model, the estimated probability that populations of *G. sabrinus* can persist in small (< 100 -ha), high-quality habitat patches for 25 years without migration was ≤ 0.90 in rain forest of southeastern Alaska. According to model predictions (which have not been rigorously tested), the minimum area of primary habitat to confidently ($P \approx 0.90$) sustain populations for at least 100 years without migration was estimated to be about 5,000 ha (Smith and Person 2007). The persistence of populations of *G. sabrinus* in heavily managed landscapes likely depends on the ability of individuals to move freely through the matrix (Smith and Person 2007; Taylor et al. 1993; Wilson 2003), taking

advantage of the spatial arrangement of landscape elements and any available suitable habitat (Selonen and Hanski 2006).

The most effective means of achieving functional connectivity remains unclear, but Wilson (2003) proposed focusing on the spatial and temporal scale of heterogeneity in the matrix (stand age, rotation, and juxtaposition) rather than relying on narrow corridors. This view requires understanding how individuals respond to disturbance at different scales (Desrochers et al. 2003; Reunanen et al. 2000). With the Siberian flying squirrel (*Pteromys volans*), fine-scale fragmentation poses a greater risk to landscape connectivity than comparable habitat reduction occurring in a coarser pattern (Reunanen et al. 2000). Furthermore, landscape character has little effect on decisions of young squirrels to remain philopatric or to become short- or long-distance dispersers (Selonen and Hanski 2003). The home ranges of flying squirrels (*Glaucomys* and *Pteromys*) in fragmented habitat typically are larger (Menzel et al. 2006b; Selonen and Hanski 2003) than those of individuals in continuous forests, consequences of which are a greater association with and more frequent movements along forest edges and a higher risk to predation (Desrochers et al. 2003; Wilson 2003; Wilson and Carey 1996). Still, maintaining physical connectivity between optimal breeding habitats is deemed essential for the persistence of *P. volans* in managed boreal forests of Finland (Reunanen et al. 2000). Despite the ability of juveniles to move long distances in modified landscapes or opportunities in the short term for migration between populations (Selonen and Hanski 2003, 2004), cumulative disturbances that fragment populations into isolated patches, if unchecked, can ultimately lead to the extirpation of flying squirrels from an entire region (Hokkanen et al. 1982; Reunanen et al. 2000).

Correlates of occupancy, density, and habitat use.—*Glaucomys sabrinus* is more abundant in mature or old forest than in 2nd-growth forests (Carey 1989, 1995; Lehmkuhl et al. 2006; Waters and Zabel 1995; Witt 1992; but see Rosenberg and Anthony 1992). Furthermore, Carey et al. (1999) reported that variation in population density of *G. sabrinus* across regions in the Pacific Northwest could not be explained by individual habitat features; rather, habitat of *G. sabrinus* was multifactorial. The abundance of *G. sabrinus* among stands varied directly with multivariate factors such as “decadence,” which was positively correlated with density of large snags and fallen tree cover, or “crown class diversification,” which was directly correlated with conifers > 50 cm in diameter at breast height, herbaceous cover, midstory cover, and foliage height diversity (Carey et al. 1999). Consequently, habitat of *G. sabrinus* in the Pacific Northwest became viewed as an emergent property of old-growth forest (Carey et al. 1999), and the northern flying squirrel became an indicator species for ecosystem management (Carey 2000).

More recently, Smith et al. (2005) concluded that the habitat of *G. sabrinus* in southeastern Alaska was not multifactorial because individual habitat variables were more effective in explaining variation in population density and individual captures than were multivariate factors. Across unmanaged rain-forest habitats, 77% of the variation in population density was explained by the volume of decayed downed wood on the

forest floor, whereas 65% of the variation was attributable to the density of large-diameter (≥ 74 -cm) trees (Fig. 1; Smith et al. 2004). In fact, numerous studies conducted across the range of *G. sabrinus* have established a direct relationship between population density and several individual features typical of mature or old forest, including large-diameter trees (Gomez et al. 2005; Holloway 2006; Lehmkuhl et al. 2006; Smith et al. 2004), large snags (Carey 1995; Carey et al. 1999; Holloway and Malcolm 2006; Smith et al. 2004), coarse woody debris, particularly decayed downed logs (Carey et al. 1999; Smith et al. 2004), and measures of truffle abundance (Fig. 2; Gomez et al. 2005; Lehmkuhl et al. 2006; Waters and Zabel 1995). Not surprisingly, retaining "legacy" (e.g., snags or coarse woody debris) in logged stands reduces the disparity in population density between mature and 2nd-growth forests (Carey 1995; Rosenberg and Anthony 1992).

Many of the features that explain variation in abundance among landscapes and across stands also are significant predictors of capture sites or microhabitat use (Carey et al. 1999; Payne et al. 1989; Smith et al. 2004). However, evidence from multiple studies suggests that resource selection by *G. sabrinus* can be scale dependent (Carey et al. 1999; Holloway and Malcolm 2006; Smith et al. 2004). Within drier forest types, microhabitat use is inversely related to distance from streams (Meyer et al. 2005a, 2007); in mesic forests, which typically support higher population densities than xeric forests (Lehmkuhl et al. 2006; Smith et al. 2003), microhabitat use is not as biased toward riparian areas (Carey et al. 1999; Smith et al. 2003). And in rain forest, the odds of capturing *G. sabrinus* are either unaffected by or inversely related to the amount of surface water (Smith et al. 2004). Similarly, in more-productive (greater basal area) stands of old-growth rain forest, large trees are uniformly abundant and large-tree density, a significant correlate of population density, explained little variation in microhabitat use (Smith et al. 2004). But in less-productive rain forest with much lower (order of magnitude) densities and clumped distributions interspersed among sparsely forested muskegs, large trees had the greatest ecological impact (17-fold) in increasing the odds of capturing *G. sabrinus* (Smith et al. 2004). Carey et al. (1999) and Meyer et al. (2007) reported similar patterns for populations of *G. sabrinus* in the Pacific Northwest and in the Sierra Nevada, respectively. Still, in portions of its range where essential resources are less abundant, *G. sabrinus* may depend on suitable conditions occurring uniformly across multiple spatial scales. In the Appalachians, Payne et al. (1989) reported not only that stands with red spruce were likely to be occupied by *G. sabrinus*, but that all capture sites had red spruce in the overstory.

Nest site selection.—Types and attributes of nests vary geographically, likely reflecting differences in climatic conditions (Bakker and Hastings 2002; Mowrey and Zasada 1984) and energetic demands (Stapp 1992). *G. sabrinus* typically uses 2 types of nests: external leaf nests (dreys) constructed on branches and boles, or nests in cavities (Cowan 1936). Witches' broom, a branch deformity caused by dwarf mistletoe (*Arceuthobium*) or spruce rust (*Chrysomyxa arctostaphyli*)

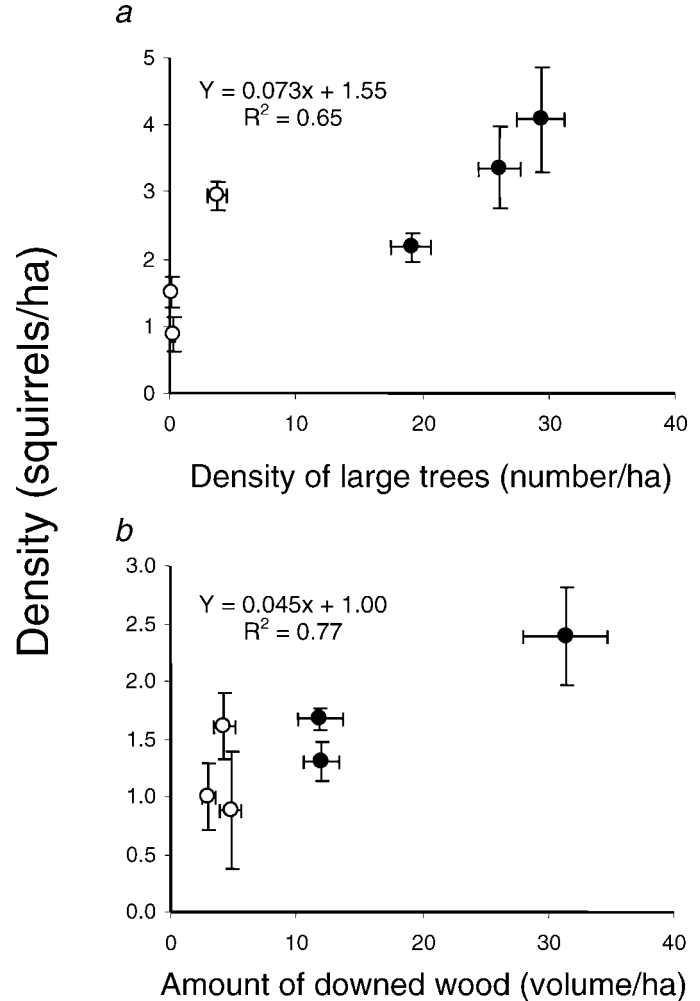


FIG. 1.—Relationship between a) autumn density of *Glaucomys sabrinus* and density of large (>74 -cm)-diameter trees and b) spring population density and abundance of downed wood in decay class III (i.e., bark sloughing or absent, heartwood mostly sound, and large branches longer than log diameter present). Decay class based on Sollins (1982). Data points constitute average values ($\bar{X} \pm SE$) for upland old-growth (●) and peatland-mixed-conifer (○) habitats. Standard error bars denote variation in both the predictor (x) and response (y) variables. (Adapted from Smith et al. 2004.)

infection, is commonly used as an external nesting substrate (Bakker and Hastings 2002; Cotton and Parker 2000b; Gerrow 1996; Mowrey and Zasada 1984). Also, use of subterranean structures (Bakker and Hastings 2002; Gerrow 1996; Hackett and Pagels 2003) may be more prevalent than previously recognized (Hackett and Pagels 2003). Carey et al. (1997) suggested that this behavior may be more common among females seeking solitary nests in circumstances where cavities may be limited (e.g., young secondary forests). However, Hackett and Pagels (2003) reported that only males used below-ground nests, which did not differ between old and 2nd-growth forests. Within a population, the number of nest trees regularly used by individual *G. sabrinus* can vary from 1 to as many as 11 (Mowrey and Zasada 1984) but the mean number used per month (range 2.3–4.8) is similar between males and females, and differences throughout the range of this species

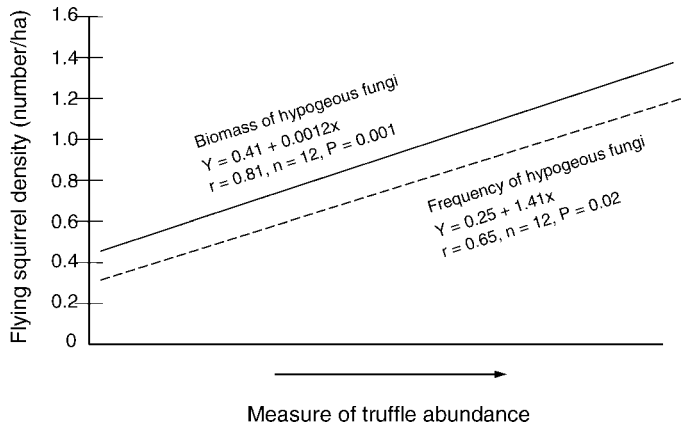


FIG. 2.—Relationship of population density of *Glaucomys sabrinus* with 2 measures of truffle abundance, biomass (solid curve) and frequency (dashed curve), among 12 stands in the northern Oregon Coast Range. (Adapted from Gomez et al. 2005.)

are relatively minor (Carey et al. 1997; Cotton and Parker 2000b; Hackett and Pagels 2003; Menzel et al. 2004; Meyer et al. 2005a; Weigl et al. 1999). Some individuals show strong fidelity to 1 or 2 nests, whereas others have a more uniform utilization distribution (Hackett and Pagels 2003). Number of consecutive nights at a nest (range 1–16) can vary substantially (Mowery and Zasada 1984); however, the majority of individuals remain ≥ 2 days in the same den (Carey et al. 1997; Cotton and Parker 2000b) and mean values ranged from 4.2 to 9.8 days (Hackett and Pagels 2003; Menzel et al. 2004).

The propensity to use cavities varies considerably among (Fig. 3a) and within (Fig. 3b) regions, and seems to be influenced largely by factors that affect the suitability of nest sites (Cotton and Parker 2000b; Hackett and Pagels 2003; Meyer et al. 2005a) or the availability of suitable nesting structures (Carey et al. 1997; Lehmkuhl et al. 2006). In Alaska's coastal rain forests, *G. sabrinus* mostly uses cavities (Bakker and Hastings 2002) but in interior boreal forests external nests are used 3 times more often than cavities (Mowrey and Zasada 1984:353). Within southeastern Alaska, use of external nests (Fig. 3b) can vary from as much as 27% (Bakker and Hastings 2002) to virtually zero (S. Pyare and W. P. Smith, in litt.). Similarly, relatively few external nests were used in the southern Appalachian (Weigl and Osgood 1974) and Sierra Nevada ranges (Wilson et al., in press) and during winter in subboreal forests of British Columbia (Cotton and Parker 2000b). In young forests, however, opportunities to nest in cavities likely are limited in many regions. In the eastern Cascades, the proportion of external nests in mistletoe was higher (and number of cavities lower) in young mixed-conifer stands than in mature forests (Lehmkuhl et al. 2006). Across the range of *G. sabrinus*, cavities typically represent <60% of nests (Fig. 3a; Carey et al. 1997; Gerrow 1996; Hackett and Pagels 2003; Lehmkuhl et al. 2006; Menzel et al. 2004; Rosenberg et al. 1996; Weigl et al. 1999; Wilson and Carey 1996).

Macro- and microhabitat characteristics of den sites vary depending on type of nests, ecological community, and land use or management history (Carey et al. 1997; Cotton and

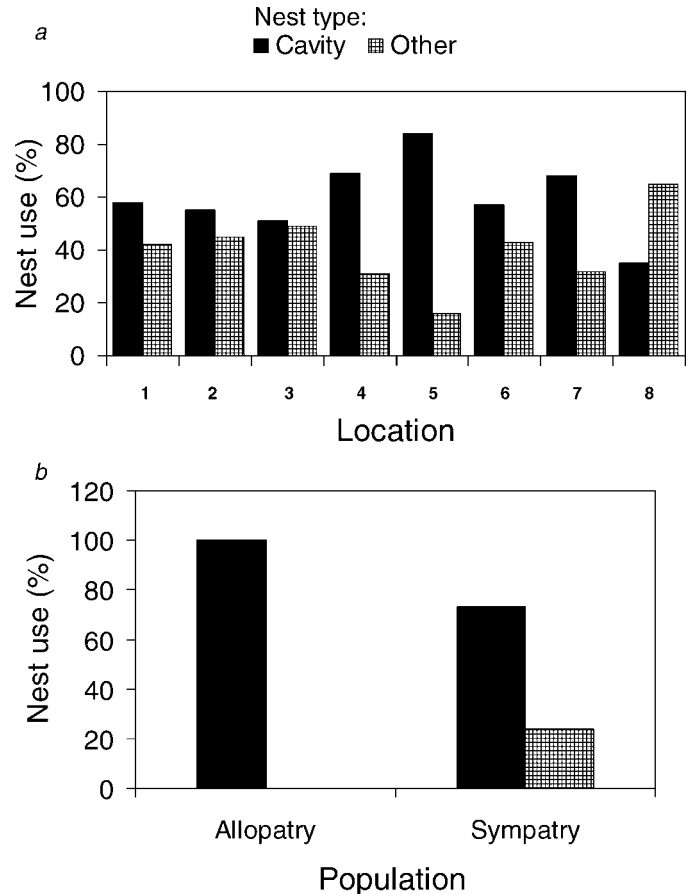


FIG. 3.—Relative use of cavities and external nests (= other) by *Glaucomys sabrinus* a) among various locations in its geographic range: 1 = New Brunswick, Canada (Gerrow 1996); 2 = Cascade Range, Oregon (Rosenberg et al. 1996); 3 = Puget Trough, Washington (Carey et al. 1997); 4 = central Appalachians, United States (Menzel et al. 2004); 5 = interior British Columbia, Canada (Cotton and Parker 2000b); 6 = southern Appalachians, United States (Weigl et al. 1999); 7 = Ontario, Canada (Holloway 2006); 8 = interior Alaska (Mowrey and Zasada 1984); and b) in allopatry (Prince of Wales Island, southeastern Alaska) and in sympatry with *Tamiasciurus hudsonicus* (Mitkof Island, southeastern Alaska).

Parker 2000b; Hackett and Pagels 2003; Menzel et al. 2004; Weigl and Osgood 1974). In the central Appalachians, nests were located within 100 m of the ecotone between pure conifer and mixed northern hardwood–conifer stands (Menzel et al. 2004). *G. sabrinus* invariably selected hardwoods, mostly beech (*Fagus*), birch (*Betula*), or maple (*Acer*), as nest trees in the southern Appalachians (Weigl and Osgood 1974) and as cavity trees in central Ontario (Holloway and Malcolm 2007). However, leaf nests are almost exclusively found in conifers (Holloway and Malcolm 2007; Weigl et al. 1999), high in the canopy (Stihler et al. 1987). Elevation, tree height, nest height, and mean diameter at breast height of overstory trees were all greater at leaf nest sites than at cavity sites in the central Appalachians (Menzel et al. 2004). Large hardwood snags are a common nesting structure in eastern forests (Gerrow 1996; Hackett and Pagels 2003; Holloway and Malcolm 2006, 2007), which likely is related to their higher decay rates and the

preferences of primary excavators (Holloway 2006). Nest sites in eastern forests often occur on cooler, more mesic sites such as in spruce stands (Holloway and Malcolm 2007; Menzel et al. 2004; Weigl and Osgood 1974), on northern slopes (Menzel et al. 2004; Payne et al. 1989; but see Hackett and Pagels 2003), in "coves" (Payne et al. 1989), or in areas with large amounts of downed wood (Hackett and Pagels 2003), all of which are favorable conditions for higher decay rates and fungal growth (Loeb et al. 2000). Selection for mesic to wet conditions (Cotton and Parker 2000b) or riparian areas (Meyer et al. 2005a, 2007) also occurs in western coniferous forests. In xeric forests, truffle abundance, biomass, and species composition are highest in riparian areas (Meyer and North 2005).

In western forests, live conifers are the primary structure used for internal and external nests (Carey et al. 1997; Cotton and Parker 2000b; Mowery and Zasada 1984; Wilson et al., in press). This in part might be related to the limited availability of snags of sufficient size because of management history (Bakker and Hastings 2002; Carey et al. 1997; Cotton and Parker 2000b; Lehmkuhl et al. 2006; Meyer et al. 2005a) or growth and decay rates (Mowery and Zasada 1984). One notable exception is in rain forests of southeastern Alaska, where a snag was more than 3 times more likely than a live tree to be a den (Bakker and Hastings 2002). *G. sabrinus* also used more snags than live trees in Alberta (McDonald 1995) and it uses more snags (relative to availability) in the Sierra Nevada (Meyer et al. 2005a). In southeastern Alaska, the more frequent (60%) use (as well as preference) of snags over live trees (Bakker and Hastings 2002) likely is related to availability; the mean density of large (>50-cm) snags in old-growth spruce-hemlock rain forests (18.0/ha, $SE = 2.1$ —W. P. Smith, in litt.) is among the highest recorded in western coniferous forests (Carey et al. 1997).

Nevertheless, there are circumstances of *G. sabrinus* preferring cavities in live trees over snags (Carey et al. 1997; Cotton and Parker 2000b). Furthermore, Carey et al. (1997) suggested that live trees might be more suitable as nesting structures because the dense canopy overhead provides protection from weather, hiding cover and structural complexity for predator avoidance, and because live trees persist longer than snags. In southeastern Alaska, nest sites were characterized by features highly correlated with the presence of cavities (snags, conks, and bole entries), external nesting structures (witches' broom), or large-diameter trees (Bakker and Hastings 2002). In fact, regardless of region or forest type, *G. sabrinus* selects den trees (live and snags) that are older, larger, and taller than what is randomly available throughout the stand (Bakker and Hastings 2002; Cotton and Parker 2000b; Menzel et al. 2004; Wilson et al., in press). Larger live trees and snags likely provide more suitable cavities, greater thermal insulation, reduced predation risk, and greater biomass of arboreal forage lichens (Meyer et al. 2005a).

The benefits of cavities over external nests remain uncertain (Carey et al. 1997). Cavities ostensibly provide better protection from inclement weather (Carey et al. 1997; Maser et al. 1981; Menzel et al. 2004) and are more predator-proof (Carey and Sanderson 1981). Because cavities are more resistant to

wind and precipitation, they are thought to be thermally superior to stick nests (Carey and Sanderson 1981). Bakker and Hastings (2002) reported that *G. sabrinus* in southeastern Alaska selected features associated with more-weatherproof cavities. And in interior British Columbia during winter, *G. sabrinus* mostly used cavities (Cotton and Parker 2000b). However, in interior Alaska *G. sabrinus* on average used external nests ($\bar{X} = 6.4$) more frequently than cavities ($\bar{X} = 2.1$). Moreover, when air temperature drops abruptly, solitary individuals often move from cavity nests to aggregations in witches' broom (Mowery and Zasada 1984). Thus, in forests where tree diameters (and presumably nest chambers) are too small to accommodate cohabitation, perhaps the benefits of reduced energy expenditure from aggregations (Stapp et al. 1991) are greater than what might be expected from differences between external nests and cavities in thermal properties. Den trees in boreal forest of interior Alaska had diameters that averaged <33 cm in diameter at breast height (Mowery and Zasada 1984). In forests where larger (>50 cm in diameter at breast height) trees are available, *G. sabrinus* seems to use primarily cavities (Bakker and Hastings 2002; Carey et al. 1997; Gerrow 1996; Weigl and Osgood 1974), especially during winter (Cotton and Parker 2000b; Maser et al. 1981), and group denning (2–4 squirrels/den) commonly occurs throughout the year (Carey et al. 1997). Nonetheless, in coastal regions where annual precipitation is relatively high and mostly rainfall, *G. sabrinus* uses primarily cavities year-round (Bakker and Hastings 2002; Carey et al. 1997; W. P. Smith and S. Pyare, in litt.) presumably to reduce risk to hypothermia, which seems to be the primary cause of mortality of individuals exposed to wet ambient conditions (W. P. Smith and S. Pyare, in litt.). Thus, heavy precipitation may render exposed outside nests uninhabitable, particularly during winter (Cowan 1936).

Alternatively, cavities may provide better protection from predators, which may explain why females almost exclusively use cavities (or nest boxes) for natal dens when they are available (Carey et al. 1997; Holloway 2006; Ransome and Sullivan 2004). Or, *G. sabrinus* may select den sites because of benefits unrelated directly to the attributes of trees or nest types. Vernes et al. (2004) reported that *G. sabrinus* selected den sites that were near red squirrel (*Tamiasciurus hudsonicus*) middens, and Currah et al. (2000) suggested that the winter overlap in diet between these 2 species was due to *G. sabrinus* raiding the middens of *T. hudsonicus*. Core areas of use in eastern forests were centered on food patches (hypogeous fungi) or foraging areas rather than dens (Holloway 2006; Menzel et al. 2006b), and *G. sabrinus* may select den sites according to the availability of nearby food resources (Hackett and Pagels 2003; Menzel et al. 2004; Payne et al. 1989; Weigl et al. 1999). Also, proximity to a permanent water source is a significant correlate of nest sites in both western coniferous forests (Meyer et al. 2005a) and Appalachian mixed hardwood-coniferous forests (Hackett and Pagels 2003).

Spatial ecology.—Average daily movements determined from successive locations from mark-recapture studies (Ransome and Sullivan 2003; Smith et al. 2003) and from radiotelemetry (Martin and Anthony 1999) typically are <100

m and rarely differ between sexes or among habitats. Mean maximum distance moved can be highly variable among individuals (range 20–240 m—Vernes et al. 2004) and occasionally males (153.4, $SE = 27.7$ m) and females (105.6, $SE = 53.5$ m) will differ (Holloway 2006). In forests of the northern Sierra Nevada, females moved greater distances than males while foraging, although movements were similar across 4 activity periods and distance from the nearest nest tree was similar between sexes (Wilson et al., in press). However, mean maximum distance moved is surprisingly similar across a wide range of habitats regardless of sex, with means varying from 60 to 150 m (Smith et al. 2003).

Distance moved between dens also is highly variable (Cotton and Parker 2000b; Hackett and Pagels 2003) and can be as great as 1 km (Carey et al. 1997). In western forests, both Carey et al. (1997) and Meyer et al. (2005a) reported that mean distance between successive nest sites was smaller for females (range 68–107 m) than for males (range 114–212 m). The combined (male + female) means for populations in the central Appalachians (164 m—Hackett and Pagels 2003) and British Columbia (163 m—Cotton and Parker 2000b) were similar. Movements, home-range size, and use of space appear to be influenced mostly by availability of food resources (Holloway 2006; Menzel et al. 2006b; Smith et al. 2003), primarily the distribution of truffles (Gomez et al. 2005; Pyare and Longland 2002). Captures are higher at sites where truffles are more abundant (Pyare and Longland 2002) and female movements on average (mean maximum distance moved) decline as truffle abundance increases across sites (Gomez et al. 2005). The larger home ranges and a 10-fold difference between core nest area and home-range size in northern Sierra Nevada suggest that *G. sabrinus* must forage over larger areas (Wilson et al., in press). Forays by males can exceed 1.5 km (Weigl et al. 1999), and daily movements of several kilometers have been recorded for males during the breeding season and for juveniles while dispersing (W. P. Smith, in litt.).

The mean ($\pm SE$) size of core nest areas (area enclosed by an animal's nest trees—Cotton and Parker 2000b) ranges from 0.9 ± 0.29 ha to 2.7 ± 0.62 ha, with males having larger (2.2 compared to 0.9 ha—Meyer et al. 2005a) and more variable (range = 0.9 – 8.6 ha—Cotton and Parker 2000b) nest areas than females. Home-range (including forage areas) size varies with habitat quality (based on population density, survival, and recruitment), with the home ranges of individuals occupying poorer habitat averaging 85% larger than individuals in higher-quality habitat (Lehmkuhl et al. 2006). The largest home range (59.8 ha) recorded for this species was recorded in the highly fragmented and degraded habitat of the central Appalachians (Menzel et al. 2006b). Mean sizes of home ranges of males (3.7–59.8 ha) typically are larger than those of females (3.4–15.3 ha), but home-range size also is influenced by season (Weigl et al. 1999) and forest type (Holloway 2006; Lehmkuhl et al. 2006; Menzel et al. 2006b; Smith et al. 2003). Typically, home ranges of females are <5 ha (e.g., Martin and Anthony 1999); home ranges of males usually are <10 ha, except in winter when they can be much larger (Menzel et al. 2006b). Mean core area (50% kernel utilization contour—Holloway

2006) in central Ontario was similar between females (1.6 ha) and males (2.6 ha) and comparable in size to core nest areas reported in other portions of the range of this species, suggesting that the disparity in home-range size that occasionally occurs between sexes is related to movements associated with foraging (Gomez et al. 2005; Holloway 2006; Pyare and Longland 2002) or breeding (W. P. Smith, in litt.).

Foraging ecology.—Although *G. sabrinus* inhabits conifer forests throughout its range, conifer seeds are not a major food item (Smith et al. 2003). Rather, *G. sabrinus* is primarily mycophagous and consumes a wide variety of fungi (Maser et al. 1986), especially hypogeous, mycorrhizal fungi (truffles), particularly during snow-free periods (Hall 1991; Pyare et al. 2002). Furthermore, *G. sabrinus* prefers truffles over other food items in feeding trials (Zabel and Waters 1997) and uses truffles relatively more often than would be expected from availability across the forest (Cazares et al. 1999; Lehmkuhl et al. 2004). Arboreal lichens also are a common ($\leq 49\%$ in central Appalachians) food (Hall 1991; McKeever 1960; Mitchell 2001; Pyare et al. 2002), particularly during winter, but not everywhere (Currah et al. 2000). Diet composition and diversity vary depending on forest type (Holloway 2006; Lehmkuhl et al. 2004; Pyare et al. 2002; Weigl 2007; Weigl et al. 1999), ecological community (Carey et al. 1999; Holloway 2006; Maser and Maser 1988; Weigl 1978), and season (Cazares et al. 1999; Currah et al. 2000; McKeever 1960; Mitchell 2001; Rosentreter et al. 1997; Vernes et al. 2004).

The fundamental food niche of *G. sabrinus* seems quite broad and its diet can include a wide range of plant and animal items (Smith et al. 2003) that change with availability (Mitchell 2001; Pyare et al. 2002; Weigl et al. 1999). In any region, however, the diet or other niche dimensions of *G. sabrinus* can be narrow or highly specialized (Carey 1991, 1996) and differ substantially from other portions of its range (Fig. 4). Individuals in southeastern Alaska consumed truffles less frequently, consumed fewer genera of truffles, and consumed vascular vegetation, lichens, and mushrooms more frequently than did *G. sabrinus* in other geographic areas (Pyare et al. 2002). Moreover, regional variation and diversity of its diet likely have been underestimated because microscopic examination of fecal pellets does not adequately characterize thoroughly digested food items, such as fruits, nuts, seeds, and vegetation (Hall 1991; Thysell et al. 1997). *G. sabrinus* seems to rely on fungi, largely truffles, in western coniferous forests (Cazares et al. 1999; Currah et al. 2000; Meyer and North 2005; Rosentreter et al. 1997), especially in the Pacific Northwest (Carey 1995; Carey et al. 1999; Hall 1991; Maser et al. 1985, 1986; Lehmkuhl et al. 2004; Thysell et al. 1997; Waters et al. 2000). This species depends less on truffles in the eastern portion of its range (Holloway 2006; Mitchell 2001; Vernes et al. 2004), or where plant understories are more diverse (Loeb et al. 2000; Weigl 2007; Weigl et al. 1999) or small mammal communities are less diverse (Pyare et al. 2002). However, factors that determine the diet of local populations remain unknown.

Although much has been learned about the diet of *G. sabrinus*, little is known about its foraging behavior and ecology (Pyare and Longland 2001a); specifically, interrela-

tionships among habitat structure, food resources, and use of space remain poorly understood (Pyare and Longland 2002). Indirect evidence suggests that *G. sabrinus* spends considerable time in search of and digging for truffle fruiting bodies (sporocarps), which typically occur 5–15 cm below the surface of the forest floor. Furthermore, the distribution of truffles within forests is patchy because suitable habitat is patchy (Smith et al. 2000). Truffles are less abundant in xeric forest types (Lehmkuhl et al. 2004), where fungal communities may be concentrated in riparian areas (Meyer and North 2005). In the southern Appalachians, truffles are more abundant at higher elevations or on northerly aspects, where spruce (*Picea*)–fir (*Abies*) or mixed spruce–fir–hardwood forests predominate (Loeb et al. 2000). Truffles (and most fungi) favor cool, mesic to wet microenvironments with relatively large amounts of decayed logs or coarse woody debris across the forest floor (Amaranthus et al. 1994; Carey et al. 1999; Lehmkuhl et al. 2004; Smith et al. 2000; Waters et al. 1997). For that reason, fungal communities purportedly achieve their greatest abundance (total biomass) and highest diversity in old growth, as compared to younger, managed forests (North et al. 1997). Furthermore, a greater percentage of unique taxa occur in old growth than in younger, managed Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest (Smith et al. 2002). However, abundance, species composition, and species richness of fungal communities (especially the prevalence of truffles) vary seasonally, which likely contributes to the temporal variability of diets of *G. sabrinus* (Mitchell 2001; North et al. 1997; Vernes et al. 2004). Still, the consistency with which *G. sabrinus* consumes truffles throughout its range year-round indicates that hypogeous fungi are a vital food resource (Currah et al. 2000; North et al. 1997; Rosentreter et al. 1997; Vernes et al. 2004).

Furthermore, movements (Gomez et al. 2005; Menzel et al. 2006b) and patterns of habitat use at multiple spatial scales (Ford et al. 2004; Meyer et al. 2005a; Pyare and Longland 2002) suggest that *G. sabrinus* tracks short-term temporal and spatial dynamics of truffle fruiting bodies (sporocarps), and perhaps other food resources. Indirect evidence comes from observations that captures of *G. sabrinus* are predicted by habitat conditions (e.g., coarse woody debris) typical of abundant fungal communities (Carey et al. 1999; Meyer et al. 2007). In at least 1 study, however, captures of *G. sabrinus* were unrelated to habitat correlates of abundant fungal communities (Pyare and Longland 2002). Rather, individuals were captured more often where there was direct evidence (i.e., animal diggings or sampled plots) of sporocarps in the immediate vicinity of understory cover. Truffles are an ephemeral food resource, and at any time not all favorable habitats will have fruiting bodies available (Fogel 1976). Nonetheless, flying squirrels choose to forage in microhabitats with abundant understory cover (Pyare and Longland 2002; Rosenberg and Anthony 1992; Smith et al. 2005), presumably to reduce predation risk or to opportunistically feed on other food items (Smith et al. 2005).

The mechanisms that underlie truffle detection remain unclear, but recent field study and laboratory experiments suggest that there may be 3 interacting elements: cognitive

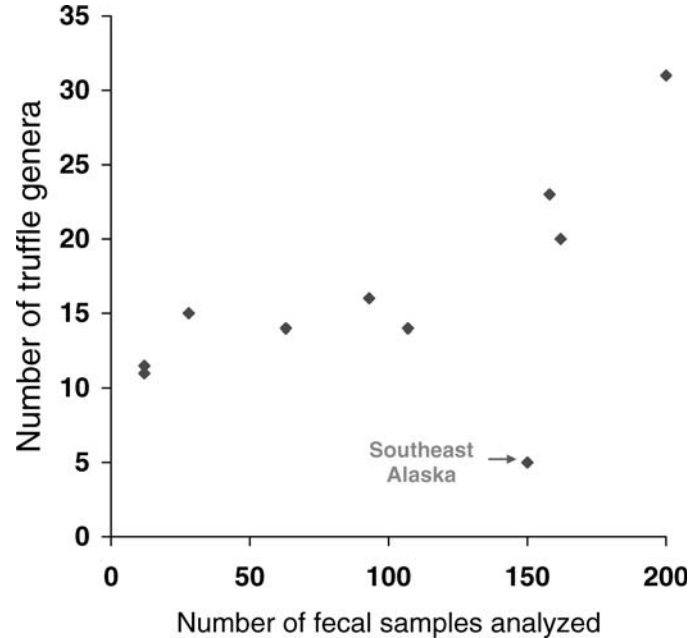


FIG. 4.—Comparison of truffle diversity in diet (number of truffle genera detected in fecal samples) of *Glaucomys sabrinus* in southeastern Alaska with other populations in western North America. The correlation coefficient (r) excluding data from southeastern Alaska is 0.90. Data are from Carey et al. (1999), Cazares et al. (1999), Colgan et al. (1997), Hall (1991), Maser et al. (1985, 1986), Pyare and Longland (2001b), Pyare et al. (2002), and Rosentreter et al. 1997. (Adapted from Pyare et al. 2002.)

mapping or ability to recall locations of food patches, olfactory capability that facilitates detecting hypogeous fungi with specific chemical signatures, and microhabitat features (coarse woody debris) that serve as fine-scale cues for locating sporocarps (Pyare and Longland 2001a, 2002). Feeding trials demonstrated that *G. sabrinus* spends the vast majority of time searching sites where truffles are buried. Also, time allocated to a treatment condition was consistently higher at sites where a decayed log was present (truffle + log) than at sites with truffles alone. And detection rate (truffles/min) was significantly higher at truffle + log treatment sites than at sites with just buried truffles. Furthermore, chemical analysis revealed that truffles used in the feeding trials possessed highly volatile compounds capable of attracting mammals (Pyare and Longland 2001a). The capacity to memorize or recall locations has not been demonstrated conclusively; however, several lines of indirect evidence suggest that *G. sabrinus* has some cognitive mapping ability, including fine-scale patterns of habitat use (Pyare and Longland 2002) and the capacity to consistently relocate other key resources (e.g., den sites—Mowrey and Zasada 1984). Nevertheless, the expected benefits of timely visits to fungal-rich microhabitats are quite high, because >80% of locations with fruiting bodies in one year have sporocarps present at about the same time (± 2 weeks) in following years (Pyare and Longland 2001a). That *G. sabrinus* uses decayed logs as a microhabitat cue for locating sporocarps is not surprising given the ecological association between

TABLE 2.—Sex ratio (males/females) and recruitment (number of young per adult female) in populations of *Glaucomys sabrinus*.

Forest type	Sex ratio	Percentage females reproductive	Recruitment ^a	Source
Douglas-fir (2nd growth)	1.0	0.90	0.72 ^b	Villa et al. 1999.
Conifer–northern hardwood	1.4	0.83	1.4	Reynolds et al. 1999
Conifer–northern hardwood	1.2	0.59 ^b	0.33 ^b	Weigl et al. 1999
Aspen–black spruce	1.2	NA ^c	1.30 ^b	Davis 1963
Peatland–mixed conifer	1.7	0.75	0.41 ^b	Smith and Nichols 2003
Sitka spruce–western hemlock	1.1	0.75	0.50 ^b	Smith and Nichols 2003
Fir (old)	1.0	NA	0.97 ^b	Waters and Zabel 1995
Fir (young)	1.2	NA	0.84 ^b	Waters and Zabel 1995
Douglas-fir (old growth)	0.9 ^b	NA	0.40 ^b	Rosenberg and Anthony 1992
Douglas-fir (2nd growth)	0.6 ^b	NA	0.33 ^b	Rosenberg and Anthony 1992
Ponderosa pine	1.1	NA	0.28	Lehmkuhl et al. 2006
Mixed conifer (young)	1.0	NA	0.35	Lehmkuhl et al. 2006
Mixed conifer (old)	1.0	NA	0.37	Lehmkuhl et al. 2006
Western hemlock (young)	1.0	0.29	1.62 ^b	Carey 1995
Western hemlock (old)	0.8	0.31	0.62 ^b	Carey 1995

^a Ratio of juveniles to adults in the autumn population (includes births and immigration).

^b Estimated from data in source.

^c NA = not available.

fungus-rich communities and coarse woody debris (Amaranthus et al. 1994; Carey et al. 1999, 2002; Smith et al. 2000).

POPULATION AND COMMUNITY DYNAMICS

Population attributes.—Much of what is known about populations of *G. sabrinus* comes from the upper Pacific coast (Carey 1995; Carey et al. 1999; Lehmkuhl et al. 2006; Ransome and Sullivan 2003; Smith and Nichols 2003; Villa et al. 1999; Waters and Zabel 1995) and the Appalachians (Reynolds et al. 1999; Weigl et al. 1999). *G. sabrinus* typically produces 1 litter/year, typically in late spring–early summer (Cowan 1936; Well-Gosling and Heaney 1984). Litter size averaged 2.5 ± 0.82 SE in the Appalachians (Reynolds et al. 1999) and 2.3 ± 0.19 in the Pacific Northwest (Villa et al. 1999), where younger females gave birth to smaller litters ($\bar{X} = 1.6 \pm 0.24$) than older females ($\bar{X} = 2.9 \pm 0.29$). Sex ratios

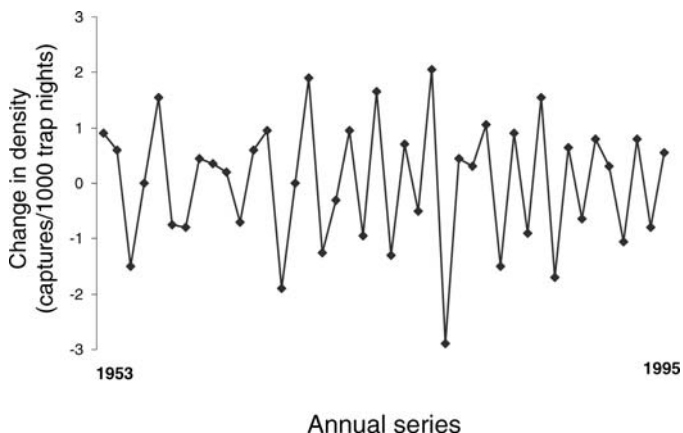


FIG. 5.—Annual changes in population density of *Glaucomys sabrinus* as indexed by live captures per 1,000 trap nights in Algonquin Park, Ontario, Canada, between 1952 and 1995 (Fryxell et al. 1998). (No captures were recorded in 1952.)

usually do not depart from unity (Table 2), but Smith and Nichols (2003) recorded male-biased ratios in old-growth peatland–mixed-conifer rain forest of southeastern Alaska and Rosenberg and Anthony (1992) reported female-biased sex ratios in 2nd-growth Douglas-fir forest of western Oregon. Although *G. sabrinus* undergoes density-dependent population growth (Fryxell et al. 1998; Lehmkuhl et al. 2006), populations can fluctuate widely among years (Fig. 5). Furthermore, there is evidence of autocorrelation between population densities (4-year lag), indicative of periodic population dynamics (Fryxell et al. 1998). Little is known about dispersal (Smith et al. 2003; Wells-Gosling and Heaney 1984). In heavily managed landscapes of southeastern Alaska, many juveniles remain near their apparent natal area through the winter and into the following spring, whereas some move straight-line distances of several hundred meters during autumn (W. P. Smith and S. Pyare, in litt.). Adult males in breeding condition will make daily long-distance (≥ 2 -km) movements during spring, presumably in search of estrous females. In unmanaged landscapes, juveniles have the ability in early autumn of moving several kilometers per day; in intensively managed landscapes, straight-line movements of juveniles (based on radiotelemetry) from putative natal areas were < 2 km (W. P. Smith and S. Pyare, in litt.).

The population density of *G. sabrinus* is not a reliable indicator of habitat quality. Smith and Nichols (2003) concluded that peatland–mixed-conifer forests likely sustain populations of *G. sabrinus* because densities were comparable to those in old-growth forests in the Pacific Northwest (Table 1). In addition, select population attributes in peatland–mixed conifer were generally similar to those in Sitka spruce–western hemlock forest, the primary habitat of this species in southeastern Alaska (Figs. 6a and 6b; Smith and Nichols 2003). However, when demographic variability was explicitly considered in simulations of a simple birth–death population model (Smith and Person 2007), the majority of per capita

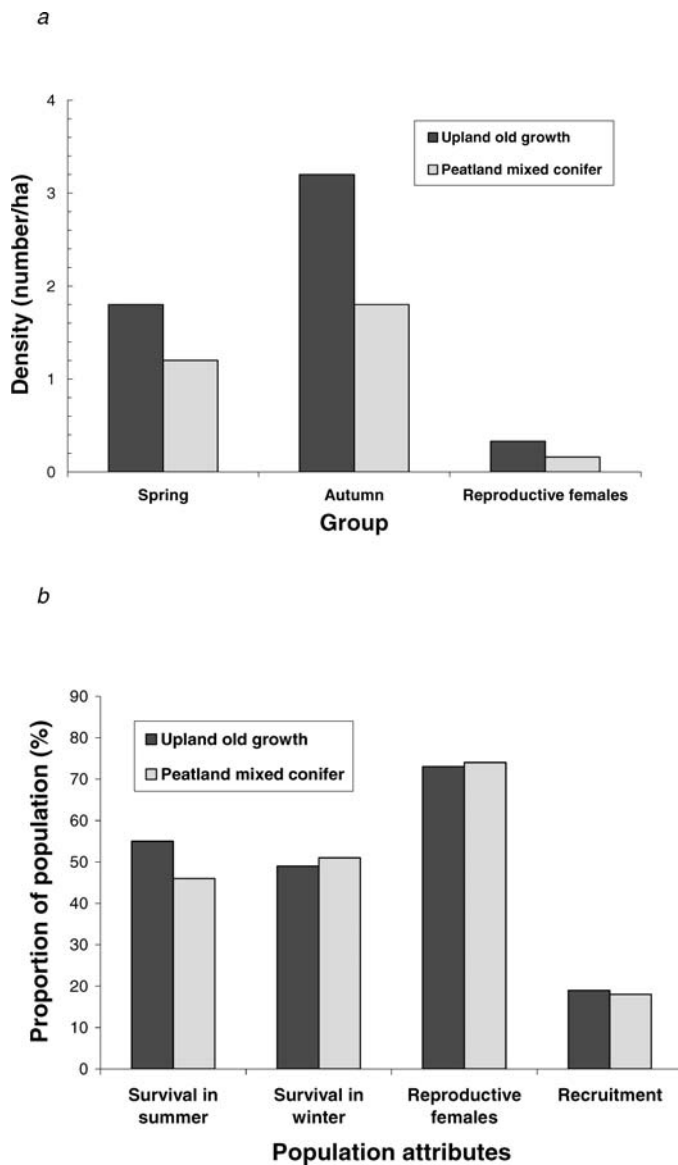


FIG. 6.—a) Spring and autumn population density and density of reproductive females $\times 10$ and b) winter and summer survival, percentage reproductive females, and recruitment of *Glaucomys sabrinus* in old-growth Sitka spruce–western hemlock (upland old growth) and peatland–mixed-conifer forests in southeastern Alaska between 1998 and 2000.

population growth values (r) were <0 , suggesting that in some years peatland–mixed conifer was a sink (sensu Pulliam 1988). Lehmkuhl et al. (2006) reported similar findings for ponderosa pine (*Pinus ponderosa*) forest of the eastern Cascades, which had population densities of *G. sabrinus* comparable to that reported for some old-growth forests of western Oregon and Washington (Table 1), but which had finite rates of growth (λ) that were <1 . Furthermore, according to simulations of a population model based strictly on demographic parameters, the probability of *G. sabrinus* persisting (without immigration) in fragments of primary habitat is much more sensitive to demographic variability than to population size (Fig. 7). The modeled effect of demographic variability on population

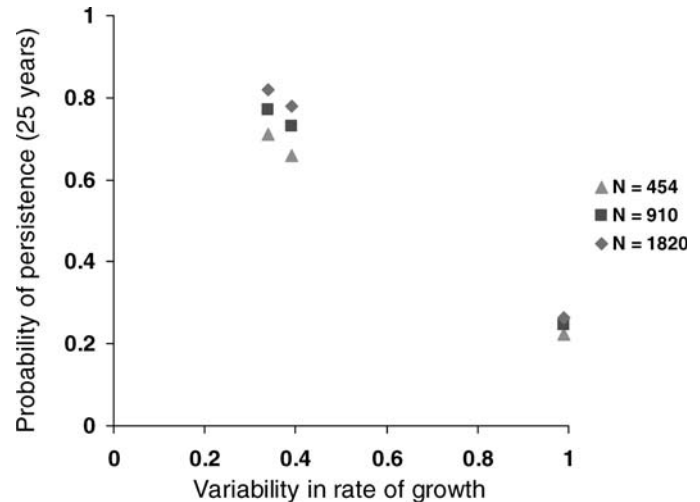


FIG. 7.—Probability of persistence (without immigration) for a period of 25 years of populations of *Glaucomys sabrinus* in fragments of old-growth Sitka spruce–western hemlock forests for 3 population sizes (N) relative to demographic variability (v) or total population size (adapted from Smith and Person 2007).

viability increases disproportionately as the time horizon increases (Smith and Person 2007).

Dispersal.—The state of knowledge regarding dispersal of *G. sabrinus* includes mostly information about flying squirrel anatomy (Scheibe et al. 2007), or about habitat and landscape structure and how they influence locomotor ability or performance (Scheibe et al. 2006, 2007; Vernes 2001). There are a few accounts of *G. sabrinus* moving several kilometers over relatively short time periods, but little is known about long-distance movements (Weigl et al. 1999). In the Pacific Northwest, adult males evidently move great lengths in search of mates (Wilson 2003). However, large clear-cuts and dense, young 2nd-growth stands are barriers to *G. sabrinus* undergoing natal dispersal or searching for females for at least 20–35 years after harvest (Wilson 2003). Ongoing studies in southeastern Alaska (on cost of transport, behavior, and movement capability) have documented daily movements of several kilometers for males during the breeding season and for juveniles while dispersing from putative natal areas (W. P. Smith, in litt.). Movement rates through recent (<5 -year-old) clear-cuts (≈ 10 m/min) averaged an order of magnitude lower than in old-growth forest, which was 2 times higher than in young, 2nd-growth stands (W. P. Smith and S. Pyare, in litt.). In the southern Appalachians, typical movement rates ranged from 1,080 to 1,440 m/h for males and 1,008 m/h for females (Weigl et al. 1999).

Most of what is known regarding flying squirrel dispersal comes from studies of *P. volans*, which is somewhat more arboreal than *G. sabrinus*. Unlike *G. sabrinus*, which spends considerable time foraging on the forest floor (Pyare and Longland 2001a, 2002), *P. volans* obtains its essential resources in the forest canopy (Reunanen et al. 2000). It rarely visits the forest floor, only running along the ground for short distances when canopy gaps exceed its gliding capability (Selonen and Hanski 2003). Still, *P. volans* is capable of

dispersing long distances in fragmented landscapes (Selonen and Hanski 2004). It uses woodland strips for interpatch movements, but also uses the matrix with trees and is able to cross narrow, treeless gaps (Selonen and Hanski 2003). Individual behavioral differences suggest decisions to disperse short or long distances occur before the onset of dispersal. Surprisingly, long-distance dispersers explored the area around their natal site less than short-distance dispersers; exploration by philopatric individuals was similar to dispersers (Selonen and Hanski 2006).

Community relations.—Throughout its range, *G. sabrinus* performs an essential ecological function within forest communities (Caldwell et al. 2005), most notably in the Pacific Northwest (Maser and Maser 1988). The extent to which this facultative role is unique within a community depends on the assortment of ectomycorrhizal fungi the squirrel consumes and the small mammal assemblage (Pyare and Longland 2001b). Interspecific variation among mycophagists in patterns of home range, habitat use, fungal consumption, vagility, and digestive physiology facilitate nonredundant dispersal of ectomycorrhizal fungi. Still, *G. sabrinus* consumes the greatest variety of ectomycorrhizal fungi and therefore has the greatest potential to influence forest community dynamics (Pyare and Longland 2001b). Furthermore, where ecological communities of arboreal and semiarboreal rodents are diverse, such as in the Pacific Northwest (Carey 1991; Verts and Carraway 1998), *G. sabrinus* is a highly specialized mycophagist and its population density and microhabitat use are correlated with structural features (e.g., coarse woody debris) typical of old forest and fungal-rich communities (Amaranthus et al. 1994; Carey et al. 1999; Smith et al. 2000; Waters et al. 1997). In contrast, southeastern Alaska has a depauperate small mammal fauna (Smith 2005), *G. sabrinus* has a less specialized diet (Pyare et al. 2002), and its habitat relations differ from those of populations in the Pacific Northwest (Smith et al. 2004, 2005). Similarly, Mitchell (2001) reported a more varied diet (compared to populations in the Pacific Northwest) for *G. sabrinus* in forest communities of the Appalachians, where the diversity of arboreal rodents is notably less than that in forest communities of the Pacific Northwest (Smith et al. 2003, 2004; Weigl et al. 1999). The extent to which fungal community diversity is directly linked to arboreal small mammal diversity remains unclear, but biological variation among mycophagists that facilitates nonredundant dispersal of fungal spores presumably promotes ecological opportunities for radiation among ectomycorrhizal fungi. Clearly, the number of truffle genera sampled by *G. sabrinus* in southeastern Alaska (5) was much less than that (32) recorded for populations in the Pacific Northwest (Fig. 4; Pyare et al. 2002). This apparent relationship between small mammal assemblages, ectomycorrhizal fungal communities, and diet and habitat use of *G. sabrinus* suggest a coevolved forest community structure that underpins the ecology of populations of *G. sabrinus* throughout its range.

Glaucomys sabrinus also is an essential link in the food chain of forest communities (Carey 2000). In the Pacific Northwest, it is the primary prey of the northern spotted owl (*Strix occidentalis caurina*—Carey et al. 1992; Forsman et al.

2001) and California spotted owl (*S. o. occidentalis*—Munton et al. 1998; Verner et al. 1992) and common prey of weasels (*Mustela*—Wilson and Carey 1996) and American marten (*Martes americana*—Bull 2000). In central Ontario, the population dynamics of American marten are closely linked to population density of *G. sabrinus* (Fryxell et al. 1999). *G. sabrinus* also is common prey of northern goshawks (*Accipiter gentilis*) during breeding in the Pacific Northwest (Reynolds and Meslow 1984), and there is little reason to doubt that it is a regular prey item of goshawks and other forest specialists elsewhere, especially across more northern latitudes where the daylight regime facilitates hunting throughout much of the day (e.g., Lewis 2001). The ecological community of small mammals and other vertebrate prey species likely influences the population dynamics of *G. sabrinus*, which can change with seasonal differences in predation pressure (Bull 2000) or have a stabilizing influence on predator populations that ultimately determines interannual variation in predation pressure (Fryxell et al. 1999). Abundant and diverse prey communities likely facilitate specialization by predators, as in the example of northern spotted owls in the Pacific Northwest (Carey et al. 1992; Forsman et al. 2001). Prey-rich forest communities likely have a greater diversity of mammalian or avian predators, which ostensibly reinforces food partitioning and prey specialization to reduce competition (Reynolds and Meslow 1984). Nevertheless, the persistence of viable and well-distributed populations of *G. sabrinus* has significant implications for fundamental ecological processes in many forest communities, which is why it was proposed as an indicator of ecosystem management in the Pacific Northwest (Carey 2000).

Direct interspecific competition has not been widely reported, but because of similarities in behavior and shared vital resources, *G. volans* potentially is a formidable competitor (Weigl 2007; Weigl et al. 1999). Although the ranges of *G. volans* and *G. sabrinus* overlap in eastern North America (Arbogast 1999, 2007:figure 2; Hall 1981), coexistence varies in time and space (Bowman et al. 2005) and the 2 species are rarely syntopic in the Appalachians (Weigl 2007; Weigl and Osgood 1974; Weigl et al. 1999). It is unlikely that habitat preferences completely explain their distributions (Weigl 1978, 2007; Payne et al. 1989). Some investigators suggest that *G. sabrinus* in the southern Appalachians might require both conifer and hardwood forest components (Payne et al. 1989; Weigl et al. 1999). There are multiple examples where *G. sabrinus* occupies hardwood forest when *G. volans* is absent (Bowman et al. 2005; Holloway 2006; Weigl 2007; Weigl et al. 1999). Furthermore, *G. volans* reputedly interferes with use of key resources by *G. sabrinus* in hardwood forests of the southern Appalachians (Muul 1968; Weigl 1978; Weigl et al. 1999). More importantly, habitat segregation is not uniform across the entire region of overlap; the probability of syntopy increases with increasing latitude (Bowman et al. 2005; Holloway 2006; Pagels et al. 1990). Still, there is evidence of competitive interactions at northern latitudes, because densities appear to be inversely related across the region of overlap (Bowman et al. 2005; Holloway 2006; Holloway and Malcolm 2006; Weigl 2007; Weigl et al. 1999).

The distributional patterns suggest it may be the presence of *G. volans* that determines the relative abundance of *G. sabrinus* (Bowman et al. 2005; Weigl et al. 1999). *G. sabrinus* seems more tolerant of cold temperatures than *G. volans* (Weigl et al. 1999), which likely explains the latter's reliance on cavities for nesting (Muul 1968; but see Holloway and Malcolm 2006), its propensity for aggregating to reduce winter energy expenditure (Stapp 1992), and its northern range limit (Bowman et al. 2005). But it likely is not cold temperature alone that defines the northern limit of *G. volans*, but rather, an energetic bottleneck that occurs as a result of periods of concurrent cold temperature and mast failure. This phenomenon appears to underpin a range boundary dynamic that also influences the local and regional abundance of *G. sabrinus* in Ontario (Bowman et al. 2005). In fact, it probably is one example of a broader-scale pattern precipitated by a warming trend that affects northern and elevational limits of *G. volans* at more southern latitudes, such as in the Appalachians (Payne et al. 1989; Weigl 2007; Weigl et al. 1999).

However, the distribution and relative abundance of *G. sabrinus* in the region of range overlap are only indirectly related to factors constraining the range of *G. volans*. Arguably, additional ecological factors must be responsible for the observed reciprocal relationship in density in Ontario (Bowman et al. 2005) and the exclusion of *G. sabrinus* from hardwood forests at more southern latitudes (Weigl 2007; Weigl et al. 1999). One proposed mechanism is through interference competition of essential resources (Weigl 2007). *G. volans* is more aggressive than *G. sabrinus* and likely prevents the latter from using cavities in hardwood forests through agonistic interactions (Muul 1968; Weigl 1978). Female *G. sabrinus* rely on cavities for natal dens (Carey et al. 1997), and the availability of suitable natal dens likely limits reproduction by females (Carey 2002; Ransome and Sullivan 2004; Smith et al. 2004). In southeastern Alaska, lower densities of populations and breeding females of *G. sabrinus* occurred in peatland-mixed-conifer forest (Smith and Nichols 2003), a habitat in which large tree and snag density and population growth were an order of magnitude lower than in its primary habitat (Smith et al. 2004).

Alternatively, *G. sabrinus* may be excluded from hardwood forests through parasite-mediated competition (Weigl 2007; Weigl et al. 1999). Furthermore, aggressive evictions of *G. sabrinus* by *G. volans* likely further reduce the availability of cavities by displacing *G. sabrinus* from cavities (Muul 1968; Weigl 2007; Weigl et al. 1999) that subsequently become unsuitable because of the risk of infection (Pauli et al. 2004). Nonetheless, a significant difference between congeners in their tolerance of infection could produce a pattern of increasing syntopy with increasing latitude because the parasitic nematode *Strongyloides robustus* has a low tolerance for cold (Weigl et al. 1999). At more northern latitudes, where coexistence occurs more often (Bowman et al. 2005; Holloway 2006), the frequency of infections with *S. robustus* in flying squirrels is lower, especially in *G. sabrinus* (Pauli et al. 2004). Overall, patterns of varying and reciprocal densities across landscapes of boreal forest (e.g., Bowman et al. 2005;

Holloway 2006) likely are a result of interactions among energetic bottlenecks and range boundary dynamics of *G. volans*, which determines when and where sympatry occurs and ultimately the subsequent interspecific interactions that reduce survival or reproduction in *G. sabrinus*.

The potential for competition also exists with several other arboreal rodents, especially in the Pacific Northwest (Carey 1989, 1991, 1995). Yet, relatively little resource overlap occurs because species segregate according to forest type (Carey 1989) or microhabitat (Carey et al. 1999; Holloway and Malcolm 2006). In the southern Sierra Nevada (where small mammal communities are relatively depauperate), substantial dietary overlap of fungi occurs throughout the year between *G. sabrinus* and *Tamias speciosus*, the lodgepole chipmunk, particularly in frequently consumed taxa (Meyer et al. 2005b). The American red squirrel (*T. hudsonicus*), which overlaps much of the northern and eastern range of *G. sabrinus*, and Douglas's squirrel (*T. douglasii*), in the Pacific Northwest (Hall 1981), likely share resources with *G. sabrinus* (Maser and Maser 1988; Pyare and Longland 2001b; Smith et al. 2003). *T. douglasii*, in particular, uses fungi extensively (Maser and Maser 1988), and in the Sierra Nevada its consumption of hypogeous fungi is similar to that of *G. sabrinus* (Pyare and Longland 2001b). However, of the many studies that included both species (Carey 1989, 1995, 2001; Carey et al. 1999; Holloway 2006; Holloway and Malcolm 2006; Ransome and Sullivan 2002, 2003, 2004; Ransome et al. 2004) few reported evidence of competition between either species of *Tamiasciurus* and *G. sabrinus*. Carey (1995) recorded the greatest abundance of *G. sabrinus* where densities of *T. douglasii* were lowest, but abundance of *T. douglasii* might have been influenced also by the low density of the chipmunk *Tamias townsendii*, a species that specializes on conifer seeds and fungi (Carey 1995).

In southeastern Alaska, populations of *G. sabrinus* that were sympatric with *T. hudsonicus* (Mitkof Island) had lower spring and autumn population densities, fewer reproductive females, and lower recruitment than in similar habitat where red squirrels were absent (W. P. Smith, in litt.). The density of *G. sabrinus* explained 76% of the variation in density of *T. hudsonicus*, suggesting that the 2 species had similar habitat requirements. This conclusion is corroborated by observations in Ontario that the 2 species show a strong affinity for similar key habitat features (Holloway and Malcolm 2006). Although the underlying mechanism for patterns in southeastern Alaska remains unclear, the 2 species might compete for cavities, which *G. sabrinus* uses exclusively on Prince of Wales Island. On Mitkof Island, up to 27% of the dens used by *G. sabrinus* were external nests, which provide a poorer thermal microenvironment, especially in coastal rain forests (Bakker and Hastings 2002), and are probably less secure for females with young (Carey et al. 1997). Females of *G. sabrinus* prefer cavities as natal dens, which when limited can reduce the density of reproductive females (Smith et al. 2004) and population growth rate (Smith and Person 2007).

Limiting factors.—Carey (2002) suggested that 3 factors potentially limit populations of *G. sabrinus*: predation;

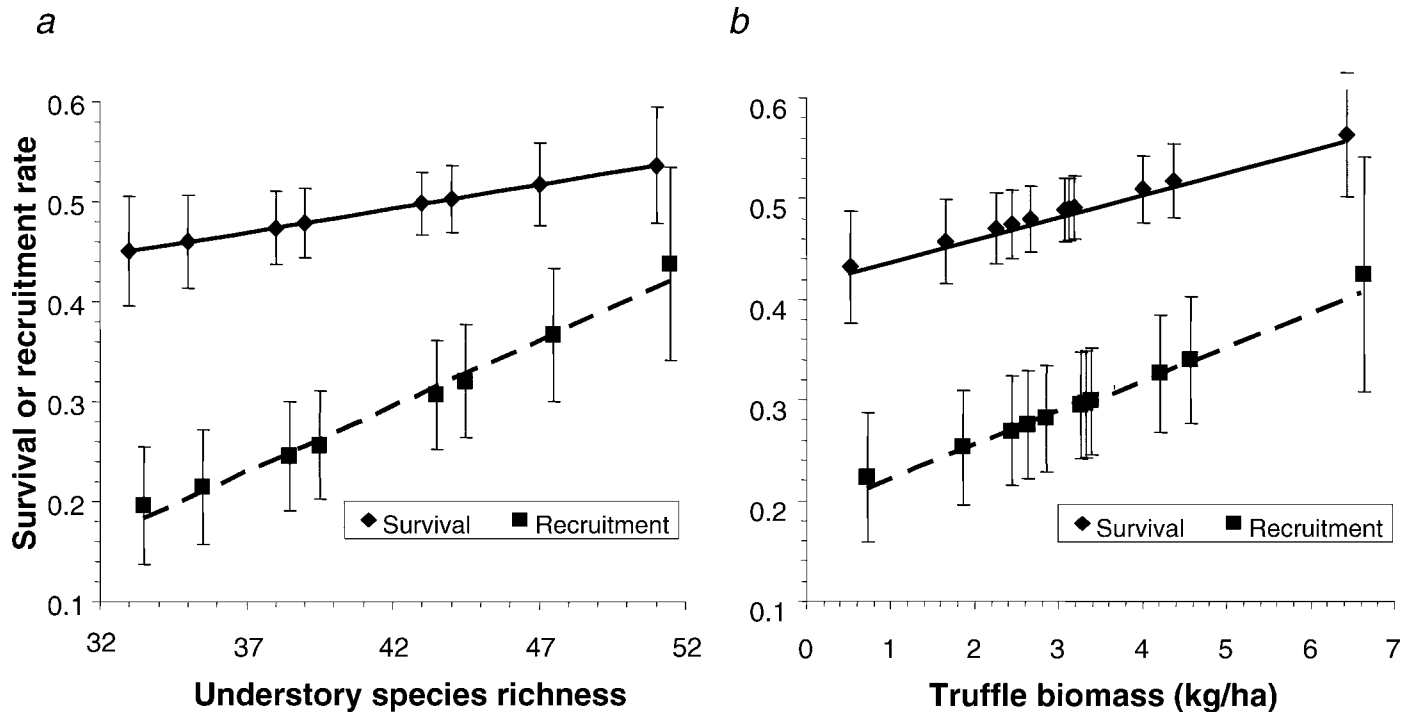


FIG. 8.—Survival and recruitment rates of populations of *Glaucomys sabrinus* relative to a) species richness of understory vegetation (Lehmkuhl et al. 2006) and b) truffle biomass (Lehmkuhl et al. 2006) in ponderosa pine and mixed conifer forests of the eastern Cascade Range, Washington.

availability of den sites, especially cavities; and diversity and abundance of mycorrhizal fungi sporocarps and other foods. Arguably, factors that limit local populations of *G. sabrinus* vary among regions and likely over time within regions, especially in portions of its range where broad-scale disturbance has dramatically altered forest habitats and landscapes (Bowman et al. 2005; Ford et al. 2004). Of the 3 hypotheses, predation appears to have the least empirical support, at least in terms of a being a pervasive ecological force limiting populations of *G. sabrinus*. Although *G. sabrinus* is important prey for several avian and mammalian predators (Carey et al. 1992; Forsman et al. 2001; Wilson and Carey 1996), and some predator populations are closely linked to squirrel population density (Fryxell et al. 1999), there are few examples of predators limiting populations of *G. sabrinus* (Carey et al. 1992).

As for cavities, most of the empirical support for dens as a limiting factor is indirect evidence—positive correlations between squirrel population density and large trees or large snags (Carey 1995; Gomez et al. 2005; Holloway 2006; Lehmkuhl et al. 2006; Smith et al. 2004). One experimental study suggested that nest boxes increase the carrying capacity of 2nd-growth forests (Witt 1991). However, more recent manipulative experiments indicate that populations of *G. sabrinus* probably are not generally limited by cavities (Carey 2002; Ransome and Sullivan 2004). Furthermore, a review of several studies across the range of *G. sabrinus* reveals that cavities are widely used, but drays and witches' broom also comprise a substantial proportion of nests (Fig. 3a). Still, there appear to be circumstances in which, either because of disturbance or other factors influencing ecological commu-

nities, the availability of cavities might become limiting. Examination of distributional and behavioral data from the southern Appalachians suggests that populations of *G. sabrinus* are excluded from hardwood forests as a result of direct competition with *G. volans* for cavities (Muul 1968; Weigl 1978; Weigl et al. 1999). Similarly, *G. sabrinus* in southeastern Alaska use external nests more often and are at lower population densities in sympatry with *T. hudsonicus* than on islands where red squirrels are absent (Fig. 3b; W. Smith and S. Pyare, in litt.). Ransome and Sullivan (2004) reported that in populations limited by food, more females used nest boxes in stands with supplemental food than in stands supplemented only with nest boxes. Their explanation was that the additional food likely increased the number of reproductive females, which rely on cavities for natal dens. A similar pattern was reported for populations of *G. sabrinus* in southeastern Alaska, where density of reproductive females, population growth rates, and overall population density varied directly with large tree and snag availability (Smith et al. 2004; Smith and Person 2007).

Several lines of indirect evidence support availability of food resources as the primary factor limiting populations *G. sabrinus* across its range (Ransome and Sullivan 1997, 2004; but see Carey 2002). Not only is population density correlated with truffle abundance (Fig. 2), but survival is positively correlated with biomass of forage lichen (Lehmkuhl et al. 2006) and survival and recruitment are directly related both to truffle abundance and to understory species richness (Fig. 8), a measure of food availability (Lehmkuhl et al. 2006). Furthermore, many habitat features that explain population

density or capture probability (e.g., decayed logs) are correlates of truffle abundance (Amaranthus et al. 1994; Carey et al. 1999, 2002; Smith et al. 2000). In fact, the lower habitat suitability of many 2nd-growth forests (Carey 1989, 1991; Carey et al. 1992; Ransome and Sullivan 1997) is likely related to the effects of clear-cut logging (Smith et al. 2002) or active management of 2nd-growth stands (Meyer et al. 2005c) on the abundance and diversity of fungal communities. In addition, truffle abundance and distribution influence movements of females (Gomez et al. 2005; Wilson et al., in press) and how individuals use space (Meyer and North 2005; Meyer et al. 2005a). Indeed, *G. sabrinus* tracks the location and timing of truffle sporocarps (Pyare and Longland 2002). Moreover, the size and location of core areas coincide with the availability of food resources (Gerrow 1996; Holloway 2006; Meyer et al. 2005a), and the magnitude of difference (10-fold) between core nest area and home-range size illustrates the significance of food resources in determining area requirements (Wilson et al., in press).

The experimental evidence in support of food limiting populations of *G. sabrinus* is sparse and ambiguous. Ransome and Sullivan (1997) reported population densities in food-supplemented stands that were twice as high as in untreated stands. Somewhat surprising, however, was the absence of a treatment effect on reproduction, adult body mass, recruitment, or adult survival. Perhaps season (summer compared to winter), or amount or type (natural compared to unfamiliar) of food was inappropriate to stimulate a measurable response among individuals (Ransome and Sullivan 1997). Alternatively, the marked increase in food resources attracted individuals residing outside the treated area, and thus the increase in population density was due to immigration rather than reproduction. Comparably high densities of *G. sabrinus* can be sustained in poorer quality (not necessarily food-limited) habitats through immigration (Lehmkuhl et al. 2006; Smith and Nichols 2003; Smith and Person 2007).

In a similar, more recent study, Ransome and Sullivan (2004) observed that the abundance, body mass, and recruitment of *G. sabrinus* did not differ between treated stands and controls. However, food supplementation markedly reduced trappability, which likely confounded efforts to detect a change in abundance. Nonetheless, survival was lower in controls than in stands that received additional food. Also, more females used nest boxes in treated stands than in controls, suggesting that more females became reproductive when food was supplemented.

The preponderance of evidence (albeit correlative) suggests that individual behavior and population demography are closely linked to food resources. However, factors limiting populations of *G. sabrinus* are complex and likely vary according to specific circumstances (Carey 2002). Indeed, there clearly are circumstances in which the availability of suitable natal dens can limit reproduction (Smith and Nichols 2003; Smith and Person 2007) or habitat distribution (Weigl 2007; Weigl et al. 1999). Thus, conservation strategies or restoration efforts that consider the full suite of ecological factors limiting fitness likely will be more robust in achieving a desirable outcome.

CONCLUSIONS

Despite significant loss and alteration of forests after European settlement, *G. sabrinus* occurs throughout most of its historical range in North America. Land use, fire, and climate shifts threaten the future of fragmented populations in the Appalachians. Northward expansion of *G. volans* in conjunction with climate warming has expanded the zone of sympatry with *G. sabrinus*, consequences of which remain uncertain. There remain portions of the range of *G. sabrinus*, such as in southern California, where little is known about its status and ecology.

An emerging ecological portrait of *G. sabrinus* differs from what was depicted from early studies in western North America. Although *G. sabrinus* often attains its highest population densities in pristine forest communities, it does not necessarily depend on old-growth forests to persist in forested landscapes. Rather, it flourishes in a wide variety of forest types and apparently can satisfy its life-history needs in deciduous forests and younger forests, depending on local conditions. However, further study is needed to determine whether younger forests can sustain viable populations. The extent to which local populations of *G. sabrinus* depend on select old-forest attributes likely is determined as much by the ecological community as by its autecological requirements. Direct evidence comes from populations of *G. sabrinus* in similar habitat, but vastly different ecological communities; forest structure and productivity appear similar, but habitat relations, population density, and demography differ and likely reflect interspecific interactions (predation and competition) that often are unique to local communities.

Habitat correlates of population density and microsite use also explain the spatial distribution of food resources, which likely limit populations of *G. sabrinus* through effects on home-range size, space use, reproduction by females, adult survival, and recruitment. Availability of suitable cavities limits the density of breeding females, which can limit populations in habitats where suitable den trees are less abundant (e.g., young growth). Much of the perception that *G. sabrinus* has a specialized diet stems from early studies in the Pacific Northwest where *G. sabrinus* relies heavily on truffles. However, evidence from portions of the range of this species indicates that it has the potential to be opportunistic, capable of eating a wide variety of food items with its local diet varying according to the diversity of ecological communities. In some portions of its range, *G. sabrinus* experiences less competition because of a depauperate indigenous vertebrate fauna or reduces competition by selecting habitats where it has exclusive use of select food resources. In highly diverse communities of arboreal rodents, *G. sabrinus* apparently has coevolved a specialized diet and mutualistic relationship that contributes directly to the availability of its future food resources. In summary, it appears the ecology of *G. sabrinus* is as varied as the forest communities in which it occurs.

However, the degree to which *G. sabrinus* can adapt to new circumstances is unclear; the wide variety of habitats, food, and other resources it can use suggest a relatively broad

fundamental niche. Although regional differences in body size and morphology (and their potential effects on thermoregulation or other biological functions) are not trivial, there is no evidence to suggest that ecological variability across its range corresponds with genetic-based differences in environmental tolerances, physiology, or other biological attributes. An alternative explanation is that populations of *G. sabrinus* exhibiting varying degrees of specialization or sensitivity to perturbation represent examples where the fundamental niche of *G. sabrinus* has been modified by unique ecological circumstances of local forest communities.

As its forest habitats continue to be altered through disturbance or climatic shifts, the fate of local populations of *G. sabrinus* depends on its ability to sustain breeding populations in younger forests or forests that are undergoing shifts in plant and vertebrate species composition. The empirical evidence suggests that *G. sabrinus* likely has the ecological plasticity to adapt to changing conditions, but further study is needed, especially in regions where changes are occurring most rapidly. Indeed, further study is needed to identify regions of rapid transition. Limited empirical evidence (Bowman et al. 2005; Payne et al. 1989) indicates that priority be given to studying populations along the fringe of its geographic distribution, especially where knowledge is scarce (e.g., southern Sierra Nevada). Nevertheless, *G. sabrinus* cannot live in all forest habitats. In addition to the resources highlighted in this paper, there are essential elements of forest habitat that I did not consider, such as structural features of the overstory and midstory that facilitate gliding (see Scheibe et al. 2007). Because food resources frequently are clumped and ephemeral, relatively dense canopies, large tall trees, and open midstories are needed for individuals to move through their home range efficiently and safely (Scheibe et al. 2006; Vernes 2001). Furthermore, if climate change increases ambient temperatures and reduces precipitation, forest habitats in those regions (e.g., southern Sierra Nevada) likely will become less suitable and the presence of streams and mesic–wet microsites will become increasingly essential.

However, the most significant challenge is maintaining functional connectivity across landscapes. Many populations are fragmented and an increasing number of populations are becoming fragmented or more isolated throughout its range. Moreover, the relative importance of functional connectivity in sustaining viable and well-distributed populations of *G. sabrinus* increases as forests become increasingly altered, habitat suitability diminishes, and the uncertainty of persistence increases. Given the expected variability in population dynamics and the influence of demographic variability on intrinsic population growth rate, the presence of comparably high densities of breeding individuals does not ensure sustainability. Moreover, there is substantial uncertainty about the ability of *G. sabrinus* to disperse across managed habitats and the rate of dispersal required to sustain viable metapopulations of flying squirrels in fragmented landscapes. For this reason, I recommend that future studies of *G. sabrinus* focus on assessing metapopulation viability in fragmented landscapes, using demographic and genetic data from populations across an

array of landscape configurations (i.e., size, composition, and spatial arrangement of habitat patches) to determine which landscapes have a high probability of sustaining populations of *G. sabrinus*.

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LITERATURE CITED

- AMARANTHUS, M. P., D. S. PARRISH, AND D. A. PERRY. 1994. Decaying logs as moisture reservoirs after drought and wildfire. Pp. 191–194 in Stewardship of soil, air, and water resources: proceedings of Watershed 89 (E. Alexander, ed.). United States Department of Agriculture, Forest Service, Juneau, Alaska.
- ARBOGAST, B. S. 1999. Mitochondrial DNA phylogeography of the New World flying squirrels (*Glaucomys*): implications for Pleistocene biogeography. *Journal of Mammalogy* 80:142–155.
- ARBOGAST, B. S. 2007. A brief history of the New World flying squirrels: phylogeny, biogeography, and conservation genetics. *Journal of Mammalogy* 88:840–849.
- BAKKER, V. J., AND K. HASTINGS. 2002. Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. *Canadian Journal of Zoology* 80:1623–1633.
- BAYNE, E. M., AND K. A. HOBSON. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. *Canadian Journal of Zoology* 76:62–69.
- BOWMAN, J., G. L. HOLLOWAY, J. R. MALCOLM, K. R. MIDDEL, AND P. J. WILSON. 2005. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Canadian Journal of Zoology* 83:1486–1494.
- BULL, E. L. 2000. Seasonal and sexual differences in American marten diet in northeastern Oregon. *Northwest Science* 74:186–191.
- CALDWELL, I. R., K. VERNES, AND F. BÄRLOCHER. 2005. The northern flying squirrel (*Glaucomys sabrinus*) as a vector for inoculation of red spruce (*Picea rubens*) seedlings with ectomycorrhizal fungi. *Sydowia* 57:166–178.
- CAREY, A. B. 1989. Wildlife associated with old-growth forests in the Pacific Northwest. *Natural Areas Journal* 9:151–162.
- CAREY, A. B. 1991. The biology of arboreal rodents in Douglas-fir forests. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR 276:1–46.
- CAREY, A. B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. *Ecological Applications* 5:648–661.
- CAREY, A. B. 1996. Interactions of Northwest forest canopies and arboreal mammals. *Northwest Science* 60(Special Issue):72–78.
- CAREY, A. B. 2000. Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. Pp. 45–66 in *Biology of gliding mammals* (R. L. Goldingay and J. S. Scheibe, eds.). Filander Verlag, Fürth, Germany.
- 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. 2002. Response of northern flying squirrels to supplementary dens. *Wildlife Society Bulletin* 30:547–556.

- CAREY, A. B., W. COLGAN III, J. M. TRAPPE, AND R. MOLINA. 2002. Effects of forest management on truffle abundance and squirrel diet. *Northwest Science* 76:148–157.
- CAREY, A. B., S. P. HORTON, AND B. L. BISWELL. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223–250.
- CAREY, A. B., J. KERSHNER, B. BISWELL, AND L. DOMINGUEZ DE TOLEDO. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildlife Monographs* 142:1–71.
- CAREY, A. B., AND H. R. SANDERSON. 1981. Routing to accelerate tree-cavity formation. *Wildlife Society Bulletin* 9:14–21.
- CAREY, A. B., T. M. WILSON, C. C. MAGUIRE, AND B. L. BISWELL. 1997. Dens of northern flying squirrels in the Pacific Northwest. *Journal of Wildlife Management* 61:684–699.
- CAZARES, E., D. L. LUOMA, M. P. AMARANTHUS, C. L. CHAMBERS, AND J. F. LEHMKUHL. 1999. Interaction of fungal sporocarp production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade Range. *Northwest Science* 73:64–76.
- CLARKSON, D. A., AND L. S. MILLS. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. *Northwest Science* 68:259–265.
- COLE, K. L., STEARNS, M. B. DAVIS, F. STEARNS, G. GUNTENSPERGER, AND K. WALKER. 1998. Chapter 6: historical landcover changes in the Great Lakes region. Pp. 43–50 in *Perspectives on the land use history of North America: a context for understanding our changing environment*. United States Department of Interior, Geological Survey, Biological Sciences Report USGS/BRD/BSR-1998-0003.
- COLGAN, W., III, A. B. CAREY, AND J. M. TRAPPE. 1997. A reliable method of analyzing diaries of mycophagous small mammals. *Northwestern Naturalist* 78:65–69.
- COLGAN, W., III, A. B. CAREY, J. M. TRAPPE, R. MOLINA, AND D. THYSELL. 1999. Diversity and productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir forest. *Canadian Journal of Forest Research* 29:1259–1268.
- CÔTÉ, M., AND J. FERRON. 2001. Short-term use of different residual forest structures by three sciurid species in a clear-cut boreal landscape. *Canadian Journal of Forest Research* 31:1805–1815.
- COTTON, C. L., AND K. L. PARKER. 2000a. Winter activity patterns of northern flying squirrels in sub-boreal forests. *Canadian Journal of Zoology* 78:1896–1901.
- COTTON, C. L., AND K. L. PARKER. 2000b. Winter habitat and nest trees used by northern flying squirrels in sub-boreal forests. *Journal of Mammalogy* 81:1071–1086.
- COWAN, I. McT. 1936. Nesting habits of the flying squirrel, *Glaucomys sabrinus*. *Journal of Mammalogy* 17:58–60.
- CURRAH, R. S., E. A. SMRECIU, T. LEHESVIRTA, M. NIEMI, AND K. W. LARSEN. 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. *Canadian Journal of Botany* 78:1514–1520.
- DALE, V. H., et al. 2001. Climate change and forest disturbances. *BioScience* 51:723–734.
- DAVIS, W. 1963. Reproductive ecology of the northern flying squirrel in Saskatchewan. M.S. thesis, University of Saskatchewan, Saskatoon, Canada.
- DESROCHERS, A., I. HANSKI, AND V. SELONEN. 2003. Siberian flying squirrel responses to high- and low-contrast forest edges. *Landscape Ecology* 18:543–552.
- FLANNIGAN, M. D., Y. BERGERON, O. ENGELMARK, AND B. M. WOTTON. 1998. Future wildfire in circumboreal forests in relation to global warming. *Journal of Vegetation Science* 9:469–476.
- FOGEL, R. M. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas fir stand. *Canadian Journal of Botany* 54:1152–1162.
- FORD, W. M., S. L. STEPHENSON, J. M. MENZEL, D. R. BLACK, AND J. W. EDWARDS. 2004. Habitat characteristics of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. *American Midland Naturalist* 152:430–438.
- FORSMAN, E. D., ET AL. 2001. Spatial and temporal variation in diets of spotted owls in Washington. *Journal of Raptor Research* 35:141–150.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs* 87:1–64.
- FRELICH, L. E. 1995. Old forest in the lake states today and before European settlement. *Natural Areas Journal* 15:157–167.
- FRYXELL, J. M., J. B. FALLS, E. A. FALLS, AND R. J. BROOKS. 1998. Long-term dynamics of small-mammal populations in Ontario. *Ecology* 79:213–225.
- FRYXELL, J. M., J. B. FALLS, E. A. FALLS, R. J. BROOKS, L. DIX, AND M. A. STRICKLAND. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. *Ecology* 80:1311–1321.
- GERROW, J. S. 1996. Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. M.S. thesis, Acadia University, Wolfville, Nova Scotia, Canada.
- GOMEZ, D. M., R. G. ANTHONY, AND J. P. HAYES. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. *Journal of Wildlife Management* 69:1670–1682.
- GOMEZ, D. M., R. G. ANTHONY, AND J. M. TRAPPE. 2003. The influence of thinning on production of hypogeous fungus sporocarps in Douglas-fir forests in the northern Oregon Coast Range. *Northwest Science* 77:308–319.
- HACKETT, H. M., AND J. F. PAGELS. 2003. Nest site characteristics of the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*) in southwest Virginia. *American Midland Naturalist* 150:321–331.
- HALL, D. S. 1991. Diet of the northern flying squirrel at Sagehen Creek, California. *Journal of Mammalogy* 72:615–617.
- HALL, E. R. 1981. *The mammals of North America*. Wiley Interscience, New York.
- HAMANN, A., AND T. WANG. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87:2773–2786.
- HENNON, P. E., AND C. G. SHAW III. 1997. What is killing these long-lived, defensive trees? *Journal of Forestry* 95:4–10.
- HOKKANEN, H., T. TÖRMÄLÄ, AND H. VUORINEN. 1982. Decline of the flying squirrel (*Pteromys volans* L.) populations in Finland. *Biological Conservation* 23:273–284.
- HOLLOWAY, G. 2006. Flying squirrel (*Glaucomys sabrinus* and *G. volans*) habitat use and ecology in landscapes managed with partial harvesting silviculture in central Ontario. Ph.D. dissertation, University of Toronto, Toronto, Ontario, Canada.
- HOLLOWAY, G., AND J. R. MALCOLM. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. *Journal of Wildlife Management* 70:1735–1745.
- HOLLOWAY, G., AND J. R. MALCOLM. 2007. Nest trees used by northern and southern flying squirrels in central Ontario. *Journal of Mammalogy* 88:226–233.

- LEADBITTER, P., D. EULER, AND B. J. NAYLOR. 2002. Comparison of historical and current forest cover in selected areas of the Great Lakes St. Lawrence Forest of central Ontario. *Forestry Chronicle* 78:522–529.
- LEHMKUHL, J. F., L. E. GOULD, E. CÁZARES, AND D. R. HOSFORD. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. *Forest Ecology and Management* 200:49–65.
- LEHMKUHL, J. F., K. D. KISTLER, J. S. BEGLEY, AND J. BOULANGER. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. *Ecological Applications* 16:584–600.
- LEWIS, S. B. 2001. Breeding season diet of northern goshawks in southeast Alaska with a comparison of techniques used to examine raptor diet. M.S. thesis, Boise State University, Boise, Idaho.
- LOEB, S. C., F. H. TANTER, AND E. CÁZARES. 2000. Habitat associations of hypogeous fungi in the southern Appalachians: implications for the northern flying squirrel (*Glaucomys sabrinus coloratus*). *American Midland Naturalist* 144:286–296.
- LOMOLINO, M. V., AND D. R. PERRAULT. 2001. Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. *Global Ecology and Biogeography* 10:113–132.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. *Monographs in Population Biology* 1:1–203.
- MARTIN, K. J., AND R. G. ANTHONY. 1999. Movements of northern flying squirrels in different-aged forest stands of western Oregon. *Journal of Wildlife Management* 63:291–297.
- MASER, C., R. ANDERSON, AND E. L. BULL. 1981. Aggregation and sex segregation in northern flying squirrels in northeastern Oregon, an observation. *Murrelet* 62:54–55.
- MASER, C., AND Z. MASER. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. *Great Basin Naturalist* 48:358–369.
- MASER, C., Z. MASER, J. W. WITT, AND G. HUNT. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. *Canadian Journal of Zoology* 64:2086–2089.
- MASER, Z., C. MASER, AND J. M. TRAPPE. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. *Canadian Journal of Zoology* 63:1084–1088.
- MCDONALD, L. 1995. Relationship between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. Pp. 227–231 in *Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta* (J. B. Stelfox, ed.). Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, Alberta, Canada, and Canadian Forest Service (project 0001A), Edmonton, Canada.
- McKEEVER, S. 1960. Food of the northern flying squirrel in northeastern California. *Journal of Mammalogy* 41:270–271.
- MENZEL, J. M., J. W. EDWARDS, W. M. FORD, J. W. EDWARDS, AND M. A. MENZEL. 2004. Nest tree use by the endangered Virginia northern flying squirrel in the central Appalachian Mountains. *American Midland Naturalist* 151:355–368.
- MENZEL, J. M., W. M. FORD, J. W. EDWARDS, AND L. J. CEPERLEY. 2006a. A habitat model for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. United States Department of Agriculture, Forest Service Research Paper NE-729:1–14.
- MENZEL, J. M., W. M. FORD, J. W. EDWARDS, AND T. M. TERRY. 2006b. Home range and habitat use of the vulnerable Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains, USA. *Oryx* 40:1–7.
- MEYER, M. D., D. A. KELT, AND M. P. NORTH. 2005a. Nest trees of northern flying squirrels in the Sierra Nevada. *Journal of Mammalogy* 86:275–280.
- MEYER, M. D., D. A. KELT, AND M. P. NORTH. 2007. Microhabitat associations of northern flying squirrels in burned and thinned forest stands of the Sierra Nevada. *American Midland Naturalist* 157:202–211.
- MEYER, M. D., AND M. P. NORTH. 2005. Truffle abundance in riparian and upland mixed-conifer forest of California's southern Sierra Nevada. *Canadian Journal of Botany* 83:1015–1020.
- MEYER, M. D., M. P. NORTH, AND D. A. KELT. 2005b. Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. *Canadian Journal of Zoology* 83:1581–1589.
- MEYER, M. D., M. P. NORTH, AND D. A. KELT. 2005c. Short-term effects of fire and thinning on truffle abundance and consumption by *Neotamias speciosus* in the Sierra Nevada of California. *Canadian Journal of Forest Research* 35:1061–1070.
- MITCHELL, D. 2001. Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). *American Midland Naturalist* 146:439–443.
- MOWREY, R. A., AND J. C. ZASADA. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. Pp. 351–356 in *Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held in Juneau, Alaska, April 12–15, 1982* (W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, eds.). American Institute of Fishery Research Biologists, Morehead City, North Carolina.
- MUNTON, T. E., K. D. JOHNSON, G. N. STEGER, AND G. P. EBERLEIN. 1998. Diets of California spotted owls in the Sierra National Forest. Pp. 99–105 in *Proceedings of a symposium on the Kings River Sustainable Forest Ecosystem Project: progress and current status* (J. Verner, ed.). United States Department of Agriculture, Forest Service General Technical Report PSW-GTR-183:1–154.
- MUUL, I. 1968. Behavioral and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. *Miscellaneous Publications, Museum of Zoology, University of Michigan, Miscellaneous Publications* 134:1–66.
- NORTH, M., J. TRAPPE, AND J. FRANKLIN. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. *Ecology* 78:1543–1554.
- NOWACKI, G. J., AND M. G. KRAMER. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-421:1–25.
- ODOM, R. H., W. M. FORD, J. W. EDWARDS, C. W. STIHLER, AND J. M. MENZEL. 2001. Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia. *Biological Conservation* 99:245–252.
- PAGELS, J. F., R. P. ECKERLIN, J. R. BAKER, AND M. L. FIES. 1990. New records of the distribution and the intestinal parasites of the endangered northern flying squirrel, *Glaucomys sabrinus* (Mammalia: Sciuridae), in Virginia. *Brimleyana* 16:73–78.
- PAULI, J. N., S. A. DUBAY, E. M. ANDERSON, AND S. J. TAFT. 2004. *Strongyloides robustus* and the northern sympatric populations of northern (*Glaucomys sabrinus*) and southern (*G. volans*) flying squirrels. *Journal of Wildlife Diseases* 40:579–582.
- PAYNE, J. L., D. R. YOUNG, AND J. F. PAGELS. 1989. Plant community characteristics associated with the endangered northern flying squirrel, *Glaucomys sabrinus*, in the southern Appalachians. *American Midland Naturalist* 121:285–292.

- PULLIAM, R. H. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- PYARE, S., AND W. S. LONGLAND. 2001a. Mechanisms of truffle detection by northern flying squirrels. *Canadian Journal of Zoology* 79:1007–1015.
- PYARE, S., AND W. S. LONGLAND. 2001b. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. *Journal of Mammalogy* 82:681–689.
- PYARE, S., AND W. S. LONGLAND. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. *Canadian Journal of Forest Research* 32:1016–1024.
- PYARE, S., W. P. SMITH, J. V. NICHOLS, AND J. A. COOK. 2002. Dietary uniqueness of northern flying squirrels in southeast Alaska. *Canadian Field-Naturalist* 116:97–102.
- RANSOME, D. B., P. M. F. LINDGREN, D. S. SULLIVAN, AND T. P. SULLIVAN. 2004. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest. I. Population dynamics of northern flying squirrels and red squirrels. *Forest Ecology and Management* 202:355–367.
- RANSOME, D. B., AND T. P. SULLIVAN. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. *Journal of Mammalogy* 78:538–549.
- RANSOME, D. B., AND T. P. SULLIVAN. 2002. Short-term population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in commercially thinned and unthinned stands of coastal coniferous forest. *Canadian Journal of Forestry Research* 32:2043–2050.
- RANSOME, D. B., AND T. P. SULLIVAN. 2003. Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forests. *Canadian Journal of Forest Resources* 33:587–596.
- RANSOME, D. B., AND T. P. SULLIVAN. 2004. Effects of food and dense site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. *Journal of Mammalogy* 85:206–215.
- REUNANEN, P., M. MÖNKÖNEN, AND A. NIKULA. 2000. Managing boreal forest landscapes for flying squirrels. *Conservation Biology* 14:218–226.
- REYNOLDS, R. T., AND E. C. MESLOW. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. *Auk* 101:761–779.
- REYNOLDS, R. J., J. F. PAGELS, AND M. L. FIES. 1999. Demography of northern flying squirrels in Virginia. *Proceedings Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 53:340–349.
- ROSENBERG, D. K., AND R. G. ANTHONY. 1992. Characteristics of northern flying squirrel populations in young, second- and old-growth forests in western Oregon. *Canadian Journal of Zoology* 70:161–166.
- ROSENBERG, D. K., K. A. SWINDLE, AND R. G. ANTHONY. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology* 81:1715–1725.
- ROSENBERG, D. D., J. R. WATERS, K. J. MARTIN, R. G. ANTHONY, AND C. J. ZABEL. 1996. The northern flying squirrel in the Pacific Northwest: implications for management of the greater Fundy Ecosystem. Pp. 23–29 in *Conserving species dependent on older forests: a population viability workshop*, Fundy National Park, New Brunswick, Canada 26–28 October 1993 (S. P. Flemming, ed.). Parks Canada, Alma, New Brunswick, Canada.
- ROSENRETER, R., G. D. HAYWARD, AND M. WICKLOW-HOWARD. 1997. Northern flying squirrel seasonal food habits in the interior conifer forests of central Idaho. *Northwest Science* 71:97–102.
- SCHEIBE, J. S., K. PASKINS, S. FERDOUS, AND D. BIRDSILL. 2007. Kinematics and functional morphology of leaping, landing, and branch use in *Glaucomys sabrinus*. *Journal of Mammalogy* 88:850–861.
- SCHEIBE, J. S., W. P. SMITH, J. BASHAM, AND D. MAGNESS. 2006. Cost of transport in the northern flying squirrel, *Glaucomys sabrinus*. *Acta Theriologica* 51:169–178.
- SCHULER, T. M., W. M. FORD, AND R. J. COLLINS. 2002. Successional dynamics and restoration implications of a montane coniferous forest in the central Appalachians, USA. *Natural Areas Journal* 22:88–98.
- SELONEN, V., AND I. K. HANSKI. 2003. Movements of the flying squirrel *Pteromys volans* in corridors and in matrix habitat. *Ecography* 26:641–651.
- SELONEN, V., AND I. K. HANSKI. 2004. Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests. *Behavioral Ecology* 15:564–571.
- SELONEN, V., AND I. K. HANSKI. 2006. Habitat exploration and use in dispersing juvenile flying squirrels. *Journal of Animal Ecology* 75:1440–1449.
- SMITH, J. E., R. MOLINA, M. M. P. HUSO, AND M. J. LARSEN. 2000. Occurrence of *Piloderma fallax* in young, rotation age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, U.S.A. *Canadian Journal of Botany* 78:995–1001.
- SMITH, J. E., ET AL. 2002. Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, U.S.A. *Canadian Journal of Botany* 80:186–204.
- SMITH, W. P. 2005. Evolutionary diversity and ecology of endemic small mammals of southeastern Alaska with implications for land management planning. *Landscape and Urban Planning* 72:135–155.
- SMITH, W. P., R. G. ANTHONY, J. R. WATERS, N. L. DODD, AND C. J. ZABEL. 2003. Ecology and conservation of arboreal rodents of the Pacific Northwest. Pp. 157–206 in *Mammal community dynamics in western coniferous forests: management and conservation* (C. J. Zabel and R. G. Anthony, eds.). Cambridge University Press, Cambridge, United Kingdom.
- SMITH, W. P., S. M. GENDE, AND J. V. NICHOLS. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rain forest of southeastern Alaska. *Journal of Mammalogy* 85:663–674.
- SMITH, W. P., AND J. V. NICHOLS. 2003. Demography of the Prince of Wales flying squirrel: an endemic of southeastern Alaska temperate rain forest. *Journal of Mammalogy* 84:1044–1058.
- SMITH, W. P., J. V. NICHOLS, AND S. M. GENDE. 2005. The northern flying squirrel as a management indicator species of north temperate rainforest: test of a hypothesis. *Ecological Applications* 15:689–700.
- SMITH, W. P., AND D. K. PERSON. 2007. Persistence of northern flying squirrel populations in temperate rain forest fragments of southeast Alaska. *Biological Conservation* 137:626–636.
- SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forestry Research* 12:18–28.
- STAPP, P. 1992. Energetic influences on the life history of *Glaucomys volans*. *Journal of Mammalogy* 73:914–920.

- STAPP, P., P. J. PEKINS, AND W. M. MAUTZ. 1991. Winter energy expenditure and the distribution of southern flying squirrels. *Canadian Journal of Zoology* 69:2548–2555.
- STIHLER, C. W., K. B. KNIGHT, AND V. K. URBAN. 1987. The northern flying squirrel in West Virginia. Pp. 176–183 in *Proceedings of the Third Southeast Nongame and Endangered Species Symposium* (R. R. Odum, K. A. Riddleberger, and J. C. Dozier, eds.). Georgia Department of Natural Resources, Atlanta, Georgia.
- TAYLOR, P. D., L. FAHRIG, K. HENEIN, AND G. MERRIAM. 1993. Landscape connectivity is a vital element of landscape structure. *Oikos* 68:571–573.
- THYSELL, D. R., L. J. VILLA, AND A. B. CAREY. 1997. Observations of northern flying squirrels feeding behavior: use of non-truffle items. *Northwestern Naturalist* 78:87–92.
- VERNER, J., R. J. GUTIÉRREZ, AND G. I. GOULD, JR. 1992. The California spotted owl: general biology and ecological relations. Pp. 55–77 in *The California spotted owl: a technical assessment of its current status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, eds.). United States Department of Agriculture, Forest Service General Technical Report PSW-GTR-133:1–85.
- VERNES, K. 2001. Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forests of eastern Canada. *Journal of Mammalogy* 82:1026–1033.
- VERNES, K., S. BLOIS, AND F. BÄRLOCHER. 2004. Seasonal and yearly changes in consumption of hypogeous fungi by northern flying squirrels and red squirrels in old-growth forest, New Brunswick. *Canadian Journal of Zoology* 82:110–117.
- VERTS, B. J., AND L. N. CARRAWAY. 1998. *Land mammals of Oregon*. University of California Press, Berkeley.
- VILLA, L. J., A. B. CAREY, T. M. WILSON, AND K. E. GLOS. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-444:1–59.
- WATERS, J. R., K. S. MCKELVEY, D. L. LUOMA, AND C. J. ZABEL. 1997. Truffle production in old-growth and mature fir stands in northeastern California. *Forest Ecology and Management* 96:155–166.
- WATERS, J. R., K. S. MCKELVEY, C. J. ZABEL, AND D. LUOMA. 2000. Northern flying squirrel mycophagy and truffle production in fir forests in northeastern California. United States Department of Agriculture, Forest Service General Technical Report PSW-GTR-178:1–113.
- WATERS, J. R., AND C. J. ZABEL. 1995. Northern flying squirrel densities in fir forests of northeastern California. *Journal of Wildlife Management* 59:858–866.
- WEIGL, P. D. 1978. Resource overlap, interspecific interactions, and the distribution of the flying squirrels *Glaucomys volans* and *G. sabrinus*. *American Midland Naturalist* 100:83–96.
- WEIGL, P. D. 2007. The northern flying squirrel (*Glaucomys sabrinus*). A conservation challenge. *Journal of Mammalogy* 88:897–907.
- WEIGL, P. D., T. W. KNOWLES, AND A. C. BOYNTON. 1999. The distribution and ecology of the northern flying squirrel, *Glaucomys sabrinus coloratus*, in the southern Appalachians. North Carolina Wildlife Resources Commission, Nongame and Endangered Wildlife Program, Raleigh.
- WEIGL, P. D., AND D. W. OSGOOD. 1974. Study of the northern flying squirrel, *Glaucomys sabrinus*, by temperature telemetry. *American Midland Naturalist* 92:482–486.
- WELLS-GOSLING, N., AND L. R. HEANEY. 1984. *Glaucomys sabrinus*. *Mammalian Species* 229:1–8.
- WILSON, J. A., D. A. KELT, AND D. VAN VUREN. In press. Home range and activity of northern flying squirrels (*Glaucomys sabrinus*) in the Sierra Nevada. *Southwestern Naturalist*.
- WILSON, T. M. 2003. Sex and the single squirrel: a genetic view of forest management in the Pacific Northwest. *Pacific Northwest Science Findings* 51:1–6.
- WILSON, T. M., AND A. B. CAREY. 1996. Observation of weasels in second-growth Douglas-fir forests in the Puget Trough, Washington. *Northwestern Naturalist* 77:35–39.
- WITT, J. W. 1991. Increasing the carrying capacity of second-growth stands for flying squirrels with the use of nest boxes. P. 529 in *Wildlife and vegetation of unmanaged Douglas-fir forests* (L. F. Ruggiero, K. B. Aubry, A. B. Carey, and H. Huff, technical coordinators). United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-285.
- WITT, J. W. 1992. Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon. *Journal of Mammalogy* 73:921–929.
- ZABEL, C. J., AND J. R. WATERS. 1997. Food preferences of captive northern flying squirrels from the Lassen National Forest in northeastern California. *Northwest Science* 71:103–107.

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