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THE NORTHERN FLYING SQUIRREL (*GLAUCOMYS SABRINUS*): A CONSERVATION CHALLENGE

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The northern flying squirrel (*Glaucomys sabrinus*) has an extensive range in North America, inhabiting boreal, coniferous, and mixed forests of the northern United States and Canada and the slopes of the mountains of the east and west. Most undisturbed northern populations are apparently thriving, but those in the southern mountains are considered disjunct relicts occupying declining remnants of suitable habitat. It is clear that range contraction in the past has been associated with climate and vegetation change in the Pleistocene and the large-scale timber harvests of the early 20th century and that today a significant threat comes from forest practices and development. However, the major problem in dealing with conservation of this species is understanding its complex ecological position in its regional communities and the subtle as well as obvious influences of human activities. Thus, to preserve this species over its extensive range one will have to consider its various roles as a biological opportunist, an important prey item, a disperser of mycorrhizae, a potential victim of biological warfare, and a small, secretive glider especially vulnerable to anthropogenic and possible climatic changes in the size, arrangement, and quality of its home forests.

Key words: conservation, *Glaucomys*, heterothermy, northern flying squirrel, *Strongyloides*, truffles

The ability to develop an effective conservation strategy for a vulnerable species presupposes that one knows enough about the animal's biology and the potential threats in its environment to create a meaningful protection plan. In the case of the northern flying squirrel (*Glaucomys sabrinus*), both the acquisition of adequate data and their interpretation have been a challenge. Although concern for this species over much of its range in North America has stimulated a great number of studies over the past 20 years after a long period of limited interest, the listing of some populations as endangered fueled an intense search for that ''magic'' factor or formula that might explain its biology, guarantee its survival, and eliminate its interference with the human exploitation of its home forests. We still have much to learn. As a participant in a symposium held at the annual meeting of the American Society of Mammalogists in June 2006, I was asked to address the broad problem of flying squirrel conservation. Although this topic may be approached in a number of ways, I have chosen to attempt to provide an overview—with pertinent background and examples—of 2 interacting components of this conservation issue: the particular or salient ecological factors potentially critical to species survival; and those human activities, past and present, contributing to the species' vulnerability. I am looking for common denominators—factors important to varying degrees over the wide range and diverse habitats occupied by this species as well as special, regional threats, and I wish to raise questions about current ideas and assumptions. I maintain that in the field of northern flying squirrel conservation there may be no simple solutions but instead, within some common denominator of basic biology, an array of problems and possible management strategies dictated by regional variation in squirrel ecology and in the kinds of human influences.

With some chagrin I have recently realized that I started my studies of flying squirrels as a graduate student 43 years ago. Thus, I have decided to approach the topic partially from a personal point of view, stressing my own experiences as well as findings documented in the literature and derived from discussions with other researchers. Although my studies have included many other vertebrates over the years, I have been repeatedly drawn back to flying squirrel investigations as interesting questions and concerns have arisen. Along with a few other workers, I have become a ''marked man,'' because, over the past 25 years, inquiries have poured in from federal and state agencies, conservancies, consulting firms, and various business concerns. Everyone wants definitive information on flying squirrels in order to preserve rare or endangered squirrel populations, to find a rationale to protect threats to parks and especially significant forests, or to provide justifications for logging, road building, or development in or near the species' habitat. I would argue that the predicament of the northern

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flying squirrel is often too complicated and subtle for the pat answers these people request. Thus, I hope I can be forgiven for using my own experiences in the southern Appalachians as a starting point for a broad but not a definitive discussion of the species, linking these findings to much of the other North American research.

Background

The northern flying squirrel is not uniformly threatened over its wide range across the boreal forests of North America and the montane and mixed forests of the south-trending mountains of the east and west (Wells-Gosling and Heaney 1984). Except in areas under heavy settlement and large-scale clear-cutting, this species is holding its own rather well in much of the northern part of its range. Its vulnerability is most pronounced in the mountain areas at the southern margins of its range—the southern Appalachians, Sierra Nevada, and Rocky Mountains.

It is quite clear from historical studies of climate and vegetation that the species has experienced a number of range contractions in the past (Arbogast 1999, 2007; Arbogast et al. 2005; Weigl 1968). During times of glacial advance in the Pleistocene, boreal forests repeatedly extended as broad southern peninsulas along the eastern and western mountains and even down the Mississippi Valley (Davis 1976; Delcourt and Delcourt 1981, 1987). One can assume, based on a few fossil records, that the northern flying squirrel then occupied a much larger southern range. The retreat of the glaciers starting 18,000 years ago would have confined squirrels to narrower strips of land and isolated massifs along the Appalachians and western mountains, but much of its remaining habitat was probably quite adequate. Then, in the late 19th and early 20th century the catastrophic clear-cut logging of Appalachian forests took place. Huge areas were denuded and burned over a short period of time—a process repeated in the west somewhat later (Loeb et al. 2000). From what we can surmise from species' habitat requirements this was a critical time of range contraction, disjunction, and probably population extinction in the mountains. However, it is unlikely that the public or even the biologists of the time were at all aware of the plight of the flying squirrels. Many of the subspecies considered endangered or rare today were unknown. Hall (see Hall and Kelson 1959) described *Glaucomys sabrinus lucifugus* of Utah in 1934, Miller (1936) described *G. s. fuscus* of West Virginia in 1936, and Handley (1953) described *G. s. coloratus* of North Carolina and Tennessee in 1953. Although some populations from the west were described in the 1890s, many subspecies remained undiscovered until well into the 20th century (Hall and Kelson 1959; Howell 1918).

Starting in the early 1980s the northern flying squirrel became the object of intensive research, but much of this work concentrated on the more abundant and widely distributed northwestern forms, whereas the rare, relict, often inaccessible populations of the mountain ridges to the south received only limited attention in spite of the listing of some subspecies as endangered in 1985 (Weigl et al. 1999). Fortunately, recent studies have provided much more background information, and the pace of research has accelerated. However, we still have much to learn about the peculiarities of the ecology of this species and both the obvious and subtle effects of human activity. And that is why conservation of this species is such a challenge.

Northern Flying Squirrel Ecology

General

In the simplest terms one can describe the northern flying squirrel as a small, nocturnal, nonhibernating, gliding tree squirrel that occupies boreal conifer and mixed forests and uses both tree cavities and dreys for nesting (Smith 2007; Wells-Gosling and Heaney 1984). Contrary to suggestions that this squirrel is a narrow, boreal specialist, the northern flying squirrel is best described as a behaviorally plastic opportunist, capable of adjusting its biology to wide range of conditions. For example, it is quite capable of occupying deciduous and lower-elevation woodlands of the east and west, not just the spruce, fir, and other conifer forests usually cited in the literature (B. S. Arbogast, pers. comm.; Weigl et al. 2002; Weigl and Osgood 1974). Faced with cold temperatures, turbulent weather, and short periods of food limitation, the squirrel can become heterothermic, dropping its body temperature several degrees without becoming torpid (Bowen 1992). This enables it to wait out short intervals of bad weather and make the most of its body energy reserves. Unlike most squirrels, it does not depend on seeds and nuts, even when these are available (Brink 1965; Brink and Dean 1966; Hall 1991; Mitchell 2001; Thysell et al. 1997), but, although occasionally using mast, generally subsists on fungi, lichens, buds, berries, staminate cones, and animal material, none of which it appears to store. Even its reproductive biology is rather flexible. Although the squirrel commonly produces a litter in early spring, in some areas energy availability and condition of females lead either to reproductive failure or delay, with litters being observed late into the summer and even into October or December (Raphael 1984; Weigl et al. 1999; Witt 1991, 1992). Thus, compared to the smaller southern flying squirrel (*G. volans*) and most other North American tree squirrels, *G. sabrinus* possesses some unusual ecological characteristics, in keeping with the diversity of environmental conditions it must survive.

What salient features of the ecology of the northern flying squirrel need to be considered in developing conservation measures? Our knowledge of the species is still quite fragmentary, because relatively few long-term studies have been conducted (Carey et al. 1999; Cotton and Parker 2000a, 2000b; Fryxell et al. 1998; Lehmkuhl et al. 2006; Ransome and Sullivan 2002; Smith and Person 2007; Weigl et al. 1999). Most studies have been of short duration, confined to warmer months, or limited to surveys. Long-term, year-round investigations are rare. In addition, once some populations were listed as endangered in 1985 in the Appalachians and others were deemed vulnerable because of habitat modifications in the west, researchers avidly attempted to acquire and interpret new data in a quest for unitary and perhaps overly simple strategies to preserve these squirrels. Because the extensive literature on the genetics, biogeography, and ecology have been largely reviewed by Arbogast (2007) and Smith (2007) in this issue, I will concentrate on aspects of the squirrel's biology that appear essential to conservation of the species and then raise questions about the current state of our knowledge and interpretations. Some of my comments will be based on the literature, some on personal experiences.

Habitat

In reviewing the voluminous literature on the habitats utilized by northern flying squirrels, one cannot help but be impressed by certain common features as well as some regional variations that perhaps reinforce this perceived "common denominator" (Waters and Zabel 1995; see Smith 2007). Northern flying squirrels generally occupy boreal or north temperate conifer, mixed conifer–hardwood, and northern hardwood forests, as found in the northern United States and Canada, at various elevations of mountain regions, and in some narrow valleys subject to cold air drainage. These habitats support old-growth forest, communities with old-growth elements, or younger woodlands usually contiguous with such forest. Such areas are usually cool and moist, have cold winters, and possess a well-developed canopy, substantial ground cover, quantities of wet, dead, and downed wood, and often organic substrates. These conditions favor an abundance of snags, cavities, witches brooms, trees festooned with lichens and moss, and a diverse array of buds, berries, seeds, and fungi. In drier sites in the west, squirrels appear to select riparian areas where these cooler and wetter conditions prevail, and where there is easy access to drinking water (Meyer et al. 2005, 2007). In fact, Carey (1989, 1995) observed differences in population densities in Washington and Oregon that might be associated with moisture conditions in various forest types. Although one can point out variations in this "typical" habitat description, it is clear that the northern flying squirrel is versatile enough to prosper in a wide range of forest types as long as the above conditions occur in enough favorable patches and enough habitat is left undisturbed.

Although *G. sabrinus* may be a habitat opportunist and readily uses a diversity of potentially suitable forests, habitat is a major conservation problem, exacerbated by various controversial approaches to forest management. The ongoing harvest of old-growth forest, its replacement with plantations or regenerating stands, and the increasing fragmentation of much of the remaining habitat has alarmed some biologists concerned about this and other rare animal species (see Smith 2007). When rare species are declared endangered, as in the case of the northern flying squirrel, then economic forces exert tremendous pressure on researchers to develop definitive management plans that will protect the rare organisms, but also allow a return to timber harvest and development. Such is the case in Alaska (Smith and Person 2007) where the size, quality, and connectedness of planned reserves is an issue, in the Pacific Northwest where the debate over the importance of old growth versus successional forests to rare species has raged for years (Carey 1989, 1995; Lehmkuhl et al. 2006; Waters and Zabel 1995; Witt 1992; but see Ransome and Sullivan 1997, 2002, 2004; Rosenberg and Anthony 1992), and in the Sierra Nevada where thinning, fire, and harvesting may limit the size and quality of squirrel habitat (Meyer et al. 2005; Meyer and North 2005). Another example comes from the Appalachians where the currently endangered subspecies *G. s. fuscus* of West Virginia is a candidate for delisting. In the Appalachians northern flying squirrels are commonly found in older forests of spruce (*Picea rubens*), fir (*Abies fraseri*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), especially in the ecotones between conifers and hardwoods. However, throughout the east from Nova Scotia, Canada (Lavers 2004), to southern North Carolina (Weigl et al. 2002) the species is known to occupy hardwood habitats without spruce and fir. An array of studies have documented the squirrel's habitat diversity (Ford et al. 2004; Menzel et al. 2006; Payne et al. 1989; Stihler et al. 1987; United States Department of the Interior, Fish and Wildlife Service 2006; Urban 1988) pointing out the importance of hardwood and mixed forest habitats. *G. sabrinus* of West Virginia is more abundant and its populations more continuous than in most parts of the east. Many of the squirrels are caught in forests in which spruce is present, and this tree species supports one of the fungal genera (*Elaphomyces*) eaten by the squirrel (Loeb et al. 2000). Therefore, the United States Fish and Wildlife Service has decided that if forests containing spruce are protected in the national forests, the flying squirrel's preservation is insured, and it can be delisted, not to the "threatened" level but taken off the critical list entirely. The problems with this approach are many. First, it is not clear if there is any direct causality between the presence of flying squirrels and spruce. Both animal and plant may be responding independently to the same boreal conditions. Squirrels may nest in spruces occasionally and use them as one of many food sources, but there is no proof of any obligate relationship. Second, in more than 40 years of trapping and nestbox checking in various Appalachian habitats, I almost never captured animals in extensive, pure conifer stands, although telemetry revealed that they sporadically used them. Third, such a course of action fails to sufficiently protect the northern hardwood areas often used by *G. sabrinus*. Finally, the quality and connectedness of the proposed spruce-containing reserves, now and in the future, need careful study, especially in a region where timber harvest is an important part of the local economy. My main point is that economic pressures may at times influence how ecological information is interpreted resulting in overly simplistic solutions to a conservation and political issue.

Foods

One of the especially significant aspects of northern flying squirrel ecology and conservation is the direct link between the squirrel, its diet, and the perpetuation of its forest habitats. Years ago, McKeever (1960) noted high levels of fungi in the guts of California animals, and in 1965 I discovered that North Carolina squirrels were consuming large quantities of fungi and the staminate cones of fir (Weigl 1968). Subsequently, research in the Pacific Northwest documented the dependence of northern flying squirrels on the fruiting bodies of hypogeous, mycorrhizal fungi (truffles—Carey et al. 2002; Fogel and Trappe 1978; Lehmkuhl et al. 2004; Maser and Maser 1998; Maser et al. 1978, 1985, 1986; Meyer and North 2005; North et al. 1997; Pyare and Longland 2001b). The hyphae of these underground fungi form associations with tree roots, greatly increasing their surface area for the absorption of water and minerals at a small energy cost to the tree. Many tree species grow poorly or not at all without mycorrhizae. But spore dispersal to new seedlings and older trees is a problem for an underground fungus. Based on our study of the northern flying squirrel and another truffle eater, the fox squirrel (*Sciurus niger*—Weigl et al. 1989), and the work of Zabel and Waters (1997) and Pyare and Longland (2001a), the following scenario has taken shape. The truffle produces a fruiting body that gives off a chemical signal on ripening; this causes a squirrel to avidly excavate and devour the fungus (Secrest 1990). However, although the squirrel obtains energy and certain minerals (e.g., sodium and phosphorous) from these truffles, it is unable to digest the fungal spores, which are then dropped over the landscape for days or weeks afterward (Gamroth 1988). The resulting inoculation of young trees and spread of the fungus may thus have a marked impact on the perpetuation of the forest habitat on which the squirrel depends. Although *G. sabrinus* is not the only mycophagist in its home forest, it is one of the most mobile and spends much time on the ground during foraging (Bird and McCleneghan 2005; Loeb et al. 2000; Mitchell 2001; Zabel and Waters 1997). In any case, because of these food habits and their positive effect on the trees of its habitats, conservation of this species assumes a greater dimension and significance. In fact, many of the habitat models for *G. sabrinus* are now implicitly based on recognition of this squirrel, tree, and fungus symbiosis (Ford et al. 2004; Menzel et al. 2006; Odom et al. 2001; see Smith 2007).

Given the above account of the use of hypogeous fungi, it is important to link these and other foods to certain environmental factors. Truffles are the fruiting bodies of mycorrhizal fungi and appear to be most abundant in association with larger and older living trees, especially in moist, organic soils. The time course of fungal inoculation, growth, and maturation of sporocarps may vary in different forests, but old-growth conditions may be optimal. Epigeous fungi and lichens, which also are important foods, depend on abundance of dead wood and extensive tree surface areas, respectively, and, once again, cool, wet conditions. Although lichens and animal material such as insects and carrion may help support squirrels in the winter when most other foods are unavailable, some researchers also have found evidence for winter truffle use in habitats with frozen ground. Hackett and Pagels (2003) and Smith (2007) have data on the use of underground nests, but no one has reported underground foraging in winter. The other plant materials making up the squirrels diet—staminate cones, berries, beechnuts, and some seeds—are reflective of a preference for boreal habitats and old-growth conditions but also are indicative of an opportunistic species that is not limited to truffles and that might utilize additional foods.

Demographic Considerations

In spite of the spectacular increase in northern flying squirrel studies, we have surprisingly little information on the species' life history and population biology. Most studies have been dedicated to particular questions such as home range, relative density, foods, and habitat associations. Longer-term studies (e.g., Carey et al. 1999; Fryxell et al. 1998; Smith et al. 2004, 2005; Smith and Nichols 2003; Weigl et al. 1999) have begun to fill in some gaps in our knowledge, but we know very little about most population parameters and long-term temporal and spatial trends.

Smith and Person 2007 have recently reviewed much of the demography of the species and raised questions about the distribution and stability of populations. The picture of *G. sabrinus* that is developing is of a relatively long-lived (4–7 years) species with a low reproductive rate for a small mammal. In the western part of the range of *G. sabrinus*, flying squirrels appear to be more abundant than in the east and more continuous in their distribution within the old-growth forests that they commonly occupy. However, most workers report lower densities in managed or successional stands. In the east, populations often occur in distinct patches, often kilometers away from other groups in spite of what seems to be suitable intervening habitat (Weigl et al. 1999, 2002). Also in the east, population size appears to be highly variable. In some years, squirrels will be abundant in an area; in other years the populations are low or nonexistent. Have the animals died out or moved? No answer is available, but population fluctuations have been noted by other researchers (Fryxell et al. 1998). In spite of the meager data from recaptures, it is clear that at least some of the squirrels missing in intervening sampling sessions show up again months or years later (Weigl et al. 1999).

Examination of telemetry data from throughout North America suggests that home-range size is associated with habitat quality and food resources (Smith 2007). Home ranges from 2 to 60 ha have been reported. Our own work and that of others have revealed that squirrels have relatively small core home ranges (3–15 ha) that vary somewhat with sex and season, but that many individuals will display bouts of extensive linear travel, in some cases more than a kilometer, that involve both outward movement and return (Menzel et al. 2006; Weigl et al. 1999). There is some evidence that this long-distance travel is associated with a search for foods and possibly mates (Weigl et al. 1999). Such forays may affect home-range estimates if data are taken at wide time intervals. The important question here relates to the use of space by the species. If populations in a locality can fluctuate widely in numbers, have a distinctly patchy distribution in fairly uniform forest, and consist of individuals that can cover spectacular distances, it is possible that northern flying squirrels may use and thus require much larger expanses of suitable habitat than is commonly acknowledged if they are going to survive in many parts of their range. Both habitat size and connectedness assume great significance under these conditions.

Smith and Person 2007 have recently provided an intriguing example of space use that may partially relate to the preceding discussion. Working in Alaska in undisturbed habitat, they investigated populations in prime old-growth forest and adjacent groups in a wet, mixed muskeg and forest landscape. Examination of the demographic data suggested that there was a dynamic source–sink situation governing these populations. The muskeg areas were not maintaining viable squirrel populations in a steady state, but were the beneficiary of constant migration of animals from the better forest habitats. To what extent high mobility, source–sink conditions, and metapopulation distributions of squirrels are a common phenomenon is unknown, but this may be worth investigating in areas with old-growth forest adjacent to human-modified habitats. The squirrel populations reported from cutover and regenerating areas may be more variable because they are not self-perpetuating. Certainly the status of populations in West Virginia, the Sierra Nevada, and parts of the Pacific Northwest should be evaluated with this possibility in mind.

Other Species of Animals

The fate of northern flying squirrels may be closely linked to the presence of other animal species—predators, competitors, and parasites—that are in turn often of particular concern to wildlife biologists and conservationists.

Predators.—Smith (2007), Carey et al. (1992), and Weigl et al. (1999) have described some of the potential predators of the flying squirrel, but 2 in particular may be of interest in different parts of the range. Over the past 20 years it has become clear that the northern spotted owl (*Strix occidentalis*), an endangered and much celebrated species of western forests, is especially dependent on the northern flying squirrel as a prey item (Carey et al. 1992). The owl seems to thrive in extensive old-growth forests or in habitats with old-growth elements where the squirrels are most abundant (Carey 1995; Carey et al. 1999). The size and condition of the habitat ideal for supporting both the flying squirrel and the owl have been the focus of ferocious debate (Carey et al. 1992; Ransome and Sullivan 2002; Rosenberg and Anthony 1992). Old-growth forests in the west are becoming smaller in size and increasingly fragmented, but often are viewed as the economic salvation for a timber industry that is worried about an endangered species restricting the exploitation of remaining tracts. For the squirrel the issue of habitat quality, size, and connectedness is of great importance and has been the focus of several studies. Conservation of squirrel and owl thus seems inextricably linked, but doubtless shall remain a source of intense political and economic controversy.

In the eastern United States another rare animal is periodically associated with the issue of protection of *G. sabrinus*. Every few years, wildlife biologists consider the reintroduction of the fisher (*Martes pennanti*) to the southern Appalachians; this species was known to exist in the region in the recent past. In most areas fishers can probably coexist with northern flying squirrels without problems. But in small habitat islands of the southern Appalachians with few squirrels and limited alternate prey items, a predator such as the fisher might kill off these relict populations. Although there have been no introductions of fishers in areas with isolated flying squirrel populations, this idea resurfaces frequently (R. Powell, pers. comm.) and will require the careful attention of wildlife agencies in the region.

Competitors.—Smith et al. (2004, 2007) have suggested that the biology of *G. sabrinus* in the Pacific Northwest may be different from that in Alaska and the east because of the abundance of other small mammals in western forests. This diversity of sympatric rodents might then produce a greater degree of den-site and food specialization in response to direct and diffuse completion. In reality, we have little information on resource competition between northern flying squirrels and other mammals. Although red squirrels (*Tamiasciurus hudsonicus*) and Douglas squirrels (*T. douglasii*) are often mentioned as possible competitors, there is not much evidence of any severe interaction. Flying squirrels may pilfer food from red squirrel middens and the 2 species may both use cavities for nesting sites and fungi for food, but the very different overall diets of these squirrels and their nocturnal–diurnal activity separation may minimize interactions, especially in good habitat. In many years of trapping both species, I was always surprised to find that the best years for capturing northern flying squirrels also were the best for red squirrels.

The southern flying squirrel (*G. volans*) often has been considered a major competitor (Weigl 1968, 1978). Both species are nocturnal gliders that use tree cavities for dens and both may consume fungi, insects, and plant parts. Although experimental studies suggested that *G. volans* was the more active and aggressive in interactions, especially around nests (Weigl 1978), habitat preferences, diets, and climatic tolerances of the 2 species (Bowen 1992; Bowman et al. 2005) suggest only limited competition. In fact, except in the north, the 2 species usually show limited and unstable sympatry. Thus, except for the diffuse interactions suggested by Smith et al. (2005) in the west, and a few instances of resource overlap, there is little evidence that competition per se is a significant factor in the conservation of the northern flying squirrel.

Parasites.—A particularly intricate relationship between squirrel ecology and conservation grew out of some unusual discoveries in the southern Appalachians. In the 1960s I had set out to study the interaction of *G. sabrinus* and *G. volans* in the Appalachians as a model system for evaluating aspects of competition theory (Weigl 1968). Northern flying squirrels were exceedingly rare, but after several months of trapping I eventually captured enough for the experimental parts of my study. Colonies of both species were then housed in large outdoor aviaries in North Carolina. The 1st spring saw the demise of almost all of the *G. sabrinus* except those kept in the laboratory, whereas the *G. volans* seemed to thrive in an adjacent cage. With the help of 2 veterinarians and a former zoo pathologist, I narrowed down the cause of this massive die-off to an infection by the nematode *Strongyloides robustus*. *S. robustus* has a life cycle like that of the famous hookworms (*Necator* and *Ancylostoma*): embryonated eggs released with animal feces hatch and develop into infective larvae in the substrate; these penetrate the skin of a host, are carried to the lungs where they break through to the lumen, are swallowed, and finally lodge in the intestine doing marked physical and nutritional damage (Weigl 1968; Weigl et al. 1999). The parasite is most common in warmer climates where it has been reported to cause marked pathology in wild species (Davidson 1975). Once the cause of the affliction of the captive *G. sabrinus* was determined, other wild populations of squirrels were checked. All of the captive *G. volans* in my colony were parasitized (and were probably the source of the infection in the *G. sabrinus*), but had suffered no ill effects. In fact, all populations of *G. volans* studied in subsequent years carried this parasite. On the other hand, *S. robustus* could not be found in any of the *G. sabrinus* captured on the Appalachian peaks during the remaining years of the study. In the 1980s the federal listing of the Appalachian subspecies *G. s. coloratus* prompted a new 5-year study of the northern flying squirrel over a wide area of the North Carolina and Tennessee mountains. *G. volans* now also appeared intermittently in some of the capture sites of *G. sabrinus*, although there was never any stable sympatry of the 2 species (Weigl et al. 1999). *G. sabrinus* now supported varying intensities of parasite infection, and in the summer months there appeared to be some correlation between parasite loads and the condition of the animals (Weigl et al. 1999). We eventually cultured the parasite through its life cycle in the laboratory and determined its cold sensitivity (Wetzel and Weigl 1994) and its ability to be transferred by contact with contaminated nest material or soil substrates. Based on all the data to-date and some additional studies by Pauli et al. (2004) and Sparks (2005), I would suggest the following scenario. The cold, high-elevation or northern forests occupied by *G. sabrinus* only intermittently can support *S. robustus* because of the sensitivity of the infective larvae to cold. When *G. sabrinus* moves down into the more climatically moderate forests at lower elevations or when infected *G. volans* invade the upper slopes during the summer months along paths of human-modified habitat, the 2 species come into contact, especially by using the same tree cavities or feeding areas (Hackett and Pagels 2003), and *S. robustus* is then transferred. Even if the northern flying squirrels are not killed by the parasite, its effects may be sufficiently debilitating to put the species at a disadvantage. It is interesting that only in the colder parts of the range of *G. volans*—the Great Lakes area, northern New England, Ontario, and Nova Scotia—does one get reports of some degree of sympatry of the 2 flying squirrel species (J. Bowman, pers. comm.; Lavers 2004; Pauli et al. 2004). Why then doesn't *G. volans* take over the high-elevation refuges or northern habitats of *G. sabrinus*? The answer probably lies in sensitivity to cold of *G. volans*, its dependence on stored nuts and seeds for winter survival (Bowman et al. 2005; Doby 1984), and the virtual absence of these resources in most habitats of *G. sabrinus*. In summary, *G. volans* may possess a kind of biological weapon that at least in the southern and central part of its range, can prevent the persistence and spread of *G. sabrinus* (Barbehenn 1969; Haldane 1949; Hatcher et al. 2006; Price et al. 1988; P. D. Weigl, in litt.). It has been argued recently that the loss of genetic heterogeneity in the increasingly isolated, high-elevation populations of *G. sabrinus* of the east may make the species even more susceptible to parasite and other infections (Sparks 2005). What will happen if warming climatic conditions favor invasion of higher peaks and northern habitats by *G. volans* is thus an open question in considerations of species persistence.

Genetics

In many parts of the range of the northern flying squirrel, one can reasonably argue that the species is an island inhabitant, subject to most of the constraints that afflict other such populations (Brown 1971, 1978; MacArthur and Wilson 1967). Whether occupying real islands off the coast of Alaska; widely scattered habitats of the San Jacintos, Sierra Nevada, Rocky Mountains, and perhaps the Black Hills; or the upper elevations of the southern Appalachians, the species often occurs in small, disjunct populations, relicts of broader ranges in the late Pleistocene. The genetics of these populations have received intensive study over the last 10 years (Arbogast 1999, 2007; Arbogast et al. 2005; Bidlack and Cook 2001; Browne et al. 1999; Sparks 2005; Wartell 2005; A. Wartell, in litt.). Genetic structuring, private alleles, and loss of heterozygosity have been detected in many populations, most likely as a result of reduced population size, isolation, inbreeding, bottlenecks, and other drift effects. Although inbreeding tolerance and the replacement of alleles in time by mutation (Sparks 2005) might alleviate the plight of some groups, the loss of genetic diversity is usually seen as a potential threat, especially in changing environments. The persistence of reasonably large and interconnected populations thus appears to be critical to the species survival, and that means sufficiently large habitat reserves and the maintenance of forested corridors. Such a conservation solution might work if the environmental status quo can be maintained. However, in the face of continued forest destruction, drought cycles, El Niño effects, and the still largely unknown impacts of global climate change, the reduction of available habitat and of corridors could well spell the regional demise of this species from both a loss of genetic variability and the loss of viable places to live.

The Impact of Human Activity

Habitat Size and Quality

So far I have emphasized some of the complexities of northern flying squirrel ecology and its implications for species conservation. However, it is clear that the really major threats to these squirrel's persistence come from human activities, especially in areas of small disjunct populations such as those on islands or at the southern extension of the range. Clearcutting, development, or anything that destroys extensive tracts of habitat will have obvious harmful effects. The size of the remaining forest habitat and its condition then becomes critical to survival. One has only to fly over parts of the Rocky Mountains, Sierra Nevada, and Cascades or along the Appalachians to appreciate the scope of forest destruction and roadway construction in national and privately owned forests. And landscape modification is not the only concern. Successional and regenerating communities require considerable time to develop into habitats of sufficient quality to support flying squirrels. Using demographic models, Smith and

Person (2007) have questioned the adequacy of the size of planned reserves in Alaska; Carey and others (Carey 1995; Carey et al. 1999) have provided evidence that the 2nd-growth landscapes of the Pacific Northwest do not always have the same capacity as old growth for supporting flying squirrels. In the Sierra Nevada, thinning and controlled burning may have adverse impacts on the canopy and organic material on the ground, respectively. Finally, some 2nd-growth stands may well appear to support healthy densities of squirrels, but, in reality, are population sinks for migrants from neighboring old-growth habitats and thus may not permanently maintain viable populations (Smith and Person 2007). Only long-term studies can provide the conclusive data on the suitability of these special or successional areas. The small disjunct squirrel populations of the central and southern Appalachians appear particularly vulnerable to any further modification or reduction of their habitats.

Given the above problem of loss of quality habitat, one needs to recognize 2 major forces that can aggravate this threat. One is economic and political—the demand for forest products and recreation venues, for local and regional employment, and for tax revenues and investment returns. These factors are of overwhelming significance, but are beyond the scope of this paper. The other force—climate change—is more intangible. A warming climate could cause the retreat of some tree species and communities to higher latitudes and cause the substantial reduction or elimination of boreal communities on mountains. Change in the composition and the position of communities might be especially dire in areas already modified by other human influences. Thus, the persistence of northern flying squirrels in the already-disturbed forests of West Virginia could be more tenuous than many have thought during a period of global warming. In addition to modifying community composition and distribution, climate change may have another major impact. A recent paper by Westerling et al. (2006) has documented a link between progressive climate warming and changes in the phenology, desiccation, and fire frequency in western forests. Thus, climatic warming may not only cause modifications of forest distributions, but also their complete annihilation by fire. It is likely that the desiccation observed by Westerling et al. (2006) would also have a marked impact on the moisture-requiring staple foods (fungi and lichens) of flying squirrels.

Habitat Connectedness

Along with habitat size and quality, habitat connectedness assumes an important role in species preservation. The extent of unsuitable terrain between high-quality habitat and the absence of wooded corridors could be major factors in regional survival. Frequently, the greater the reduction of contiguous forest, the wider the barriers to dispersal. Such fragmentation of flying squirrel distributions could destroy the viability of metapopulation-structured groups of squirrels, and the resulting small isolates then would be susceptible to the genetic problems mentioned earlier.

The impact of barriers on movements of flying squirrels needs further study, especially the effects of the proliferation of roadways through quality habitats. One example of barrier effects comes from the southern Appalachians. A 3-year study of an extravagant economic development scheme in the North Carolina–Tennessee mountains called the Cherohala Skyway revealed such unexpected impacts (Weigl et al. 2002). Clearly, a 2-lane scenic road removes a quantity of habitat, but, of greater significance, it also can act as a barrier to dispersal to different parts of the forest. Although *G. sabrinus* is an able glider and is known to cover distances along the ground, it is unable to cross wide, exposed roadways, especially the kind of blast-and-fill rights-of-way commonly cut into the sides of mountains. In 2 years of telemetry and trapping, no squirrel was observed to have crossed the Cherohala Skyway. The resulting range fragmentation may doom this southernmost population. In addition to barrier formation, there are 2 more-subtle impacts from a roadway. One impact was detected in the winter when snow permitted the identification of mammals moving on or along the roadway. It was obvious that various predators—bobcats, coyotes, and foxes—used the roadway as patrol routes when hunting and might easily catch any small mammals on the road. Hawks and owls also hunted over the road. Thus, one can easily see that such a right-of-way is both a physical barrier and a site of increased mortality. Another effect of roadways or similar corridors is the modification of adjacent vegetation or other habitat conditions in ways that favor the invasion of potential predators, competitors, or pathogens. In the case of *G. sabrinus*, strips of oak, cherry, and other hardwood species in disturbed areas along roadways provide foods for *G. volans* and favor its invasion of high-elevation habitats, and the transfer of *Strongyloides* to *G. sabrinus*. Thus, linear disturbances of a certain width and severity are a potential source of species fragmentation and possibly increased deleterious species interactions. The impact of roads, systems of ski trails, ridge-top wind farms, recreational vistas, and other types of habitat subdivision need careful evaluation in the future—much more then they have received to-date.

Pathogens, Pests, Pollutants, and People

Another anthropogenic factor threatening northern flying squirrels is the introduction of plant pathogens, insect pests, and industrial contaminants into squirrel habitats. In the southern Appalachians, the high-elevation conifer forests have been decimated by an adelgid insect (*Adelges piceae*) that kills Fraser fir (*Abies fraseri*), a valuable timber and Christmas tree species and a source of food and habitat for northern flying squirrels (Amman 1966; Amman and Speers 1965). The staminate cones of fir and spruce are important foods for flying squirrels in the spring when they are eaten in vast quantities. Interestingly, both field and experimental studies suggest that the essential oils from these foods suppress gut parasites such as *Strongyloides* (Weigl et al. 1999). The loss of Fraser fir then would remove a source of food (truffles, staminate cones, and possibly seed), den sites, and a possible natural medicine. In any case the adelgid killing firs, a new adelgid now destroying hemlocks, the impact of pine bark beetles in some parts of the west, and the effect of acid precipitation on vegetation and soils all represent potential threats to flying squirrels.

The last intrusion mentioned in the heading of this section of the text—people—usually goes unmentioned. One of the major effects of building of roads through prime habitat is the provision of access to lands for private and commercial development. The state or federal government builds a road, and nearby landowners demand the right to connect in order to develop their forest property. During an era of explosive interest in living in natural environments or in 2nd-home ownership, the demand for newly accessible forest land is intense and is often fueled by the economic aspirations of neighboring municipalities. A short trip on the Blue Ridge Parkway in the Appalachians reveals the result of this process. The end result is the loss and fragmentation of habitat and possibly a loss of flying squirrels. Thus, the inclusion of people as a factor along with pathogens, pests, and pollutants may indeed be appropriate.

Summary

In the past 25 years the northern flying squirrel has come under increasing scrutiny as new studies have been initiated, papers published, and various agencies alerted to its status and ecological significance. Because of physical, logistical, and economic difficulties associated with long-term research in remote and often rugged areas, our knowledge of this species is still fragmentary, especially in the southern Rocky Mountains, parts of the Sierra Nevada, the Black Hills, and the northeastern United States. Enough is known now to form a picture of the species' ecology and those aspects of its biology that may affect its preservation. In 2 cases, the northern flying squirrel makes a positive contribution to the forests it occupies. Throughout its range its use and dispersal of mycorrhizal fungi—both hypogeous and epigeous—make it an integral part of a squirrel–fungus–tree mutualism that may well help maintain the very forests needed for its survival. In the northwestern United States and western Canada, the flying squirrel is a critical food item for the endangered spotted owl. Thus, if its habitat is protected and the squirrel is permitted to flourish, the owl has a greater probability of survival.

In spite of the fact that the northern flying squirrel is something of an ecological opportunist, versatile enough to occupy several forest types, consume a number of foods, and reproduce when conditions permit, certain of its characteristics potentially increase its vulnerability. Its dependence on fungi and lichens during much of the year confine it to a certain array of old-growth, boreal forests with cool, moist climates and abundant dead wood and organic soils. The phenology of fungi, particularly the locality and timing of sporocarp production, may require the exploitation of a multitude of widely spaced, ephemeral patches and thus the use at times of extensive home ranges or reliance on long-distance travel. In short, the area needed to support these animals may be larger than our short-term telemetry studies have indicated. And although its diet and tolerance of cold conditions facilitate survival in habitats with severe climates, the low caloric density of much of its diet may be a factor in its relatively low metabolic and reproductive rates (McNab 1986).

The influence of others animals in the environment of the northern flying squirrel needs further study. In no part of its undisturbed range does it seem adversely affected by predators or competitors. Perhaps only in human-modified areas do these markedly assume importance. In the southern and central parts of the eastern United States the possibility that the nematode *S. robustus*, carried by the southern flying squirrel, harms the northern species is unresolved. However, the obvious ability of northern flying squirrels to occupy lowland, deciduous habitats in the absence of the smaller species, their confinement to high elevations when *G. volans* is present, and the instability of populations in contact zones argue for some kind of interaction. In Ontario, Nova Scotia, and northern Pennsylvania, the 2 species have been found in the same nest boxes (J. Bowman, pers. comm.; A. Lauers, pers. comm.; M. Steele, pers. comm.), but these are areas that are climatically unfavorable for the parasite. Thus, in part of the range of the northern flying squirrel a parasite-mediated interaction may be operating. Clearly more research on this topic is needed.

Although there is abundant evidence of the effect of small population size and isolation on the genetic diversity of northern flying squirrel populations, there is at present no evidence of a direct link between loss of genetic diversity and survival. The isolation of populations may occur naturally because of climatic responses of forest communities, but, more likely today, it is caused—or least aggravated—by human activity. We may never know when genetic impoverishment is a major or just a contributing factor to a population's disappearance.

All of the above ecological aspects of the biology of the northern flying squirrel may have varying effects on the perpetuation of populations in different parts of the range. When one adds the human component, the probability of survival can change spectacularly. Human influences on habitat size, quality, and connectedness are most likely the main threats to the species throughout its range. These critical factors in turn are the products not only of direct habitat destruction and modification, but indirect effects such introduced pathogens, pests, and contaminants and the slow, inexorable pressure of climate change. Survival of the species *G. sabrinus* is certainly critically dependent on an understanding of the species' ecology, but, even more important, an awareness of the impact of human activity on this ecology throughout its range.

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