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THE NORTHERN FLYING SQUIRREL: BIOLOGICAL PORTRAIT OF A FOREST SPECIALIST IN POST-EUROPEAN SETTLEMENT NORTH AMERICA

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Papers in this Special Feature were presented at a symposium on the biology of *Glaucomys sabrinus* convened at the 86th Annual Meeting of the American Society of Mammalogists in June 2006. Because *G. sabrinus* is an arboreal species that relies on several attributes of older forests, it is an ideal model organism for studying impacts of broad-scale habitat loss and alteration from logging, clearing, and natural disturbances. The objective of the symposium was to integrate knowledge of mammalogists from multiple disciplines to achieve a more complete biological portrait to gain insights about how forest communities are being impacted by dramatic changes in forest composition and distribution following European settlement of North America, and to identify gaps in knowledge and information needs that can guide future research. The symposium included 5 papers that encompass a diversity of biological information, including the evolutionary origin and systematics of *Glaucomys*, the anatomy and evolution of *G. sabrinus*, its biogeography, genetic variation within and among regional populations, its ecology, functional morphology, kinetics, and issues and challenges of conservation.

Key words: anatomy, biogeography, boreal forest, conservation, ecology, evolution, *Glaucomys sabrinus*, kinetics, locomotion, symposium

The northern flying squirrel (*Glaucomys sabrinus*) has received considerable study during the last 2 decades. Much of this attention was precipitated by concerns over the risk to viability of populations of *G. sabrinus* (or species that depend on *G. sabrinus*) because of the negative impacts of land use (Carey 2000; Smith and Nichols 2003; Weigl 2007; Weigl et al. 1999). Early studies documented an acute sensitivity of *G. sabrinus* to cumulative habitat disturbance (Carey 2000; Payne et al. 1989; Weigl et al. 1999), presumably a consequence of its reputed reliance on old-growth forests (Carey 1989). In the Pacific Northwest, *G. sabrinus* apparently performs a keystone role in forest communities (Carey 2000; Maser and Maser 1988). The findings of early investigations together with the imperiled status of multiple regional populations (Weigl 2007) led to the prominence of *G. sabrinus* in land-use and conservation planning as an ecological indicator of old-forest condition or as a surrogate of biological diversity (Carey 2000).

In addition, *G. sabrinus* is a model organism for studying the Pleistocene biogeography of boreal forests in North America (Arbogast 1999, 2007). Because it is an obligate forest dweller closely tied to boreal forests (Wells-Gosling and Heaney 1984), populations of *G. sabrinus* responded to historical changes in forest distribution associated with Pleistocene glacial–interglacial cycles. Similarly, *G. sabrinus* is an ideal model species for examining the effects of forest fragmentation at an evolutionary scale (i.e., fragmented populations of the Appalachian, southern California, Black Hills, and southern Rocky Mountain regions) and on an ecological scale (i.e., post–European settlement land use). Not surprising, populations of *G. sabrinus* also are sensitive to environmental and ecological phenomena associated with global warming (Bowman et al. 2005).

A forest obligate (Smith 2007; Smith et al. 2003, 2005) that relies on large trees for its primary means of locomotion (Scheibe et al. 2006, 2007; Vernes 2001) and natal den sites (Smith 2007), it is not surprising that local populations likely were extirpated (Payne et al. 1989; Weigl et al. 1999) after the extensive forest clearing (Cole et al. 1998; Klopatek et al. 1979; Sisk 1998; White and Mladenoff 1994) and dramatic modification of landscape structure (e.g., Mladenoff et al. 1993) that followed European settlement of North America. Evolution apparently shaped *G. sabrinus* for inhabiting land-

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scapes of boreal or montane forests, but in so doing, created an organism with little tolerance for frequent catastrophic habitat disturbances.

The future of *G. sabrinus* (and boreal or montane forest communities) is uncertain in many regions of North America, because a substantial portion of boreal forests in the United States and Canada have been converted to a nonforest land cover (Alig and Butler 2004; Sisk 1998; Smith et al. 2004); all but 30% of historical forestlands are under active management or allocated for timber management. In the contiguous United States alone there has been a 30% reduction in forested land cover (from 48% to 33%) since European settlement (Klopatek et al. 1979); more recent figures indicate that about 400,000 ha of forestlands are converted for development each year (Sisk 1998). Only through a thorough understanding of its biology can we identify practical and effective means to mitigate cumulative negative impacts of forest conversion and habitat fragmentation.

The purpose of this paper is to introduce 5 Special Feature papers that were presented in a symposium on the biology of *G. sabrinus* convened at the 86th Annual Meeting of the American Society of Mammalogists in June 2006. The objective of the symposium was to integrate the knowledge of mammalogists from multiple disciplines to achieve a more comprehensive biological portrait of a disturbance-sensitive, keystone species of boreal forests from which new insights are gained about the cumulative impacts of broad-scale disturbances on small mammal communities. Equally important are the gaps in knowledge that will become apparent and guide future research.

The opening presentation by Richard Thorington and Erica Santana (Thorington and Santana 2007) offers a perspective on how evolution shaped flying squirrel anatomy, particularly the skeletal features that facilitated a transition to gliding flight. These morphological and underlying genetic changes ultimately established the limits of this organism's fundamental niche. Therefore, greater insights into the evolutionary history and functional morphology of flying squirrels may underscore anatomical or physiological constraints that, when viewed in an ecological context reveal habitat and landscape features critical for sustaining populations of *G. sabrinus* across highly modified and fragmented forestlands.

The 2nd presentation, by Brian Arbogast (Arbogast 2007), describes the evolutionary and biogeographic history of the New World flying squirrels of the genus *Glaucomys*. Arbogast (2007) details how Quaternary climatic fluctuations and corresponding changes in forest distribution likely promoted diversification within the genus, contributed to genetic structuring of populations of *G. sabrinus*, and produced isolated populations, many of which are now of conservation concern. From these results, one can infer how populations responded to major geological events and predict how *G. sabrinus* will respond to future broad-scale habitat disturbances (e.g., climate change).

John Scheibe and colleagues (Scheibe et al. 2007) discuss fundamental elements of locomotion in *G. sabrinus*. Through an assessment of locomotor performance, they quantify several postural and movement parameters that are integral to gliding and profoundly influenced by habitat. They discuss their findings in the context of forest stand structure and use these results to examine competing hypotheses regarding the evolved adaptive value of gliding (Scheibe et al. 2007).

In my paper (Smith 2007), I review this species' habitat, demography, and community relations, with a focus on populations along the upper Pacific coast. I endeavor to advance a general ecological portrait of *G. sabrinus* through a synthesis of key findings from my research in southeastern Alaska and from studies throughout the geographic range of this species; highlighting relationships, patterns, similarities, and differences, and offering possible underlying mechanisms to explain variation among forest communities. I use a preponderance of evidence to evaluate ecological factors that potentially limit populations of *G. sabrinus*. I conclude by postulating the ecological processes that appear most sensitive to broad-scale disturbance, the circumstances in which populations of *G. sabrinus* are most vulnerable, and the future research needed to test these ideas.

In the final paper, Peter Weigl (Weigl 2007) reviews the status, causes, and conservation measures of imperiled populations, with a focus on endemic taxa of the Appalachians. Because of 40+ years of experience studying *G. sabrinus* in this region, he is able to offer a unique perspective on its conservation and underlying ecology. Weigl (Weigl 2007) highlights geological events, natural disturbances, ecological associations, and land-use practices that have contributed to present day circumstances and conservation concerns, offering insights regarding the future of this species and its role in conservation and land-use planning.

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