AREA OCCUPANCY AND DETECTION PROBABILITIES OF THE VIRGINIA NORTHERN FLYING SQUIRREL (*GLAUCOMYS SABRINUS FUSCUS*) USING NEST-BOX SURVEYS

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Abstract.—Concomitant with the delisting of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in 2008, the U.S. Fish and Wildlife Service mandated a 10-year post-delisting monitoring effort to ensure that subspecies population and distribution stability will persist following a changed regulatory status. Although criticized for the inability to generate detailed population parameters, most distribution and demographic data for the Virginia northern flying squirrel have come from long-term nest-box monitoring. Because live-trapping efforts to generate mark-recapture census data largely have failed due to low trap susceptibility, post-delisting monitoring will continue to rely on nest-box surveys. However, managers will need a better understanding of actual Virginia northern flying squirrel occupancy and detection probabilities to fully use these data. Using the program PRESENCE, we analyzed 16 variants of the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ (initial occupancy, local colonization, extinction, and detection) model with habitats ranked by probability of occurrence as a covariate for 72 nest-box lines surveyed for variable periods from 1985-2008. We defined overall presence as at least one capture per nest-box line per year of either sex or age class and persistence as the capture of either a female or juvenile per nest-box line per year. We observed an average of 4.48 ± 0.64 and 3.56 ± 0.48 years per nest-box line with a capture for overall presence and persistence, respectively. Our most parsimonious model for all Virginia northern flying squirrels was the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ model, where ψ (occupancy) = 0.87 and ρ (detection) = 0.65. For persistence, our most parsimonious model was the $\psi(\text{Hab}),\gamma(.),\varepsilon(.),\rho(.)$ model, where habitat probability influenced occupancy with ψ = 0.95 for high-ranking habitat, 0.80 for medium-ranking habitat, and 0.50 for low-ranking habitat and ρ = 0.65. Contrary to our expectations, detection was not a function of habitat ranking in our best-approximating models for either category. However, competing models where detection was a function of habitat ranking did receive empirical support. Simulations using these parameters suggest that ≥20 nest-box lines surveyed continually over 5+ years will provide relatively robust occupancy data sufficient to meet the needs of the post-delisting monitoring effort for the Virginia northern flying squirrel.

INTRODUCTION

The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) is a disjunct northern flying squirrel subspecies that occurs in the Allegheny Mountains portion of the central Appalachians in east-central and extreme northwestern Virginia south of the species' continuous distribution on the North American continent (Wells-Gosling and Heaney 1984). Along with the endangered Carolina northern flying squirrel (*G. s. coloratus*), which occurs in the Blue Ridge Mountains portion of the southern Appalachians, the Virginia northern flying squirrel is an arboreal, cavity-nesting, and hypogeal fungal-feeding specialist largely restricted to red spruce (*Picea rubens*) and red spruce-northern hardwood forest communities at higher elevations (>900 m) (Ford et al. 2004). The Virginia northern flying squirrel was listed as endangered by the U.S. Fish and Wildlife Service in 1985 (U.S. Fish and Wildlife Service

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1990). Factors for listing included severely altered habitat from exploitative logging of the red spruce forests at the turn of the 20th century (Stephenson and Clovis 1983), coupled with few collection records; a poorly known natural history; and ongoing perceived threats from surface mining, forest management, recreational development, and atmospheric acid deposition (Stihler et al. 1995, Schuler et al. 2002). Widespread nest-box and live-trapping surveys by state, federal, university, and industry consultants from the time of listing through the present have greatly expanded the known distribution of the Virginia northern flying squirrel within eight counties in West Virginia and one county in Virginia (Stihler et al. 1995, Reynolds et al. 1999). The current known distribution closely matches that of the approximate distribution of extant red spruce or red spruce-northern hardwood forests in the region (Menzel et al. 2006a). From these survey efforts, considerable data on reproductive characteristics, such as breeding chronology and juvenile maturation, and food habits have been quantified (Reynolds et al. 1999, Mitchell 2001). Use of radio-telemetry has allowed researchers to investigate and quantify important ecological components of the Virginia northern flying squirrel: den tree use and preference (Menzel et al. 2004) and home range and foraging habitat selection (Urban 1988, Menzel et al. 2006b, Ford et al. 2007a). In turn, predictive habitat models for assessing the likelihood of Virginia northern flying squirrel presence or absence across the Allegheny Mountains have been created with these data and capture records (Odom et al. 2001, Menzel et al. 2006a).

With more than 1,200 unique individuals handled since the late 1980s (Ford et al. 2007b) and with the realization that its habitat associations, requirements, and full geographic distribution were known (Ford et al. 2007a), the U.S. Fish and Wildlife Service moved to completely delist the Virginia northern flying squirrel in 2008 following the completion of a multi-factor status review (U.S. Department of the Interior 2008). From a regulatory perspective in West Virginia, the change in legal status at the federal level and the absence of state endangered-species statutes means that private land managers are not required to consider the Virginia northern flying squirrel in their management activities. However, the subspecies is still listed as state-endangered in Virginia; on federal ownership, primarily national forest lands in both states, the Virginia northern flying squirrel is a U.S. Forest Service Regions 8 and 9 "Sensitive Species" that still requires consideration such that agency actions do not adversely affect viability (U.S. Fish and Wildlife Service 2007). Additionally, the U.S. Fish and Wildlife Service's post-delisting monitoring plan specifically charges that state and federal agencies in the Allegheny Mountains continue Virginia northern flying squirrel surveys to assess the subspecies' recovery status—increasing, stable, or declining—over the next decade (U.S. Fish and Wildlife Service 2007).

Low live-trap susceptibility of the Virginia northern flying squirrel (Menzel et al. 2006b) has made it difficult for managers to assess population parameters such as density estimates among habitat types as are generated for other wildlife species. Although similarly plagued with a relatively low capture success, data taken from annual or biennial surveys of established nest-box lines with 15-25 boxes scattered over an approximately 275,000 ha area (Odom et al. 2001) have been the most reliable for naïve estimates of presence or absence and persistence and occupancy (Stihler et al. 1995, Reynolds et al. 1999). Numerous nest-box lines have been established, maintained, and surveyed since the mid-1980s in West Virginia and Virginia. However, whether or not nest-boxes can provide relatively unbiased and robust measures of Virginia northern flying squirrel occupancy sufficient to meet post-delisting monitoring requirements is unknown. Similarly, recognizing that the predicted probability of Virginia northern flying squirrel occurrence varies by habitat quality (Menzel et al. 2006a), we do not know whether detection probability is constant or variable by habitat as is routinely observed for other wildlife (Royle et al. 2005). Using the program PRESENCE, we used the aforementioned historic Virginia northern flying squirrel nest-box data from West Virginia to examine occupancy and detection probability measures to provide survey guidance for post-delisting monitoring.

METHODS

Detailed descriptions of the high-elevation red spruce and red spruce-northern hardwood habitats occupied by the Virginia northern flying squirrel in the Allegheny Mountains of eastern West Virginia and northwest Virginia are provided by Ford and others (2004, 2007a) and Menzel and others (2006b). We summarized nest-box survey data from records maintained by the West Virginia Division of Natural Resources to generate annual presence or absence values for each survey line for each year a line was visited between 1985 and 2008. Nest-boxes (33.3 x 12.1 x 12.5 cm with a 4.8 cm opening) typically were constructed using white cedar (*Thuja* sp.) or cypress (*Taxodium* spp.) and hung > 3 m on trees (Terry 2004). Nest-box lines, each consisting of 15-25 nest boxes typically arranged along a linear transect, occurred from approximately 800 m to 1,500 m in elevation, although most occurred at elevations >1,000 m (Odom et al. 2001, Menzel et al. 2006a). Although some nest-box lines were located on state-owned lands or private properties, most data were from those nest-box lines located on the Monongahela National Forest. Nest-boxes usually were surveyed once a year, most often in late spring to early summer, though some surveys occurred in summer or fall. Individual nest-box lines were surveyed an average of 9.34 ± 1.35 years. We limited our analyses to those nest-box lines that had been located with geographic positioning systems or were mapped previously (Odom et al. 2001). Within a geographic information system (GIS) (ArcMap 9.1, Environmental Systems Research Institute, Redlands, CA), we assigned each nest-box line a ranking of high, medium, or low according to a simple, yet relatively robust, Virginia northern flying squirrel habitat probability-of-occurrence model developed for the area (Menzel et al. 2006a). For nest-box lines that crossed habitat type polygons within the GIS, we visually assessed lines and made an assignment based on the habitat ranking into which the majority of boxes within an individual line fell, along with our expert assessment of adjacent habitat type.

From capture records, we created two datasets. First, we created a presence or absence dataset for overall Virginia northern flying squirrel captures regardless of actual number of individuals encountered, sex, or age class to examine overall detection and occupancy. Secondly, to examine detection and occupancy from a persistence perspective, we created a dataset whereby presence was assigned only if an individual nest-box line produced either a female or juvenile capture during the annual survey (adult males excluded). We considered any Virginia northern flying squirrel <75 g as a juvenile (Wells-Gosling and Heaney 1984) and decided that individuals captured in spring would represent local production rather than immigration. In this dataset, the presence of an adult male without the additional capture of an adult or juvenile female or juvenile male on a nest-box line was considered an absence. Using program PRESENCE (McKenzie et al. 2005, Hines and McKenzie 2008) and habitat probability rankings (high = 2, medium = 1, and low = 0) (Menzel et al. 2006a) as a covariate, we calculated detection probabilities and occupancy values for all 16 combinations of the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ (initial occupancy, local colonization, extinction, and detection) model for both datasets. Although not expressly interested in local colonization and extinction, we used this "open" model because of the survey duration at many of the nest-box lines.

We used Akaike's Information Criterion (AIC) corrected for small sample size to rank models (Burnham and Anderson 2002). We drew our primary inference from the best-approximating model for each dataset. We considered those models within two units ΔAIC_c as competing models with the most empirical support. We discarded all models for which the program PRESENCE failed to find convergence. To assess efficacious post-delisting monitoring designs using nest-boxes, i.e., number of lines and number of years monitored, we input the detection probabilities and occupancy values from our best-approximating models into the program PRESENCE simulation function. Using runs of 1,000 iterations each, we simulated occupancy standard errors for combinations of 5, 10, 15, 20, and 25 nest-box lines and survey durations of 3, 5, 7, 10, and 15 years.

RESULTS

We were able to analyze nest-box survey data from 72 individual nest-box survey lines that met our selection criteria. Survey effort and Virginia northern flying squirrel captures varied by habitat type, but most (88.9 percent) nest-box lines occurred in either high-ranking or medium-ranking habitat (Table 1). Effort varied by individual nest-box line with surveys occurring from only 2 successive years to as many as 24 successive years (Table 1). For all Virginia northern flying squirrels, the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ model without habitat ranking as a covariate for any parameter was the highest weighted (Table 2) with $\psi = 0.87 \pm 0.28$ (SE) and $\rho = 0.65 \pm 0.10$. The ψ(Hab),γ(.),ε(.),ρ(.) model had almost equal empirical support relative to model weighting (Table 2). For this model, increasing habitat ranking positively influenced occupancy. For our persistence models, the best-approximating model was the ψ(Hab),γ(.),ε(.),ρ(.) model (Table 2). Increasing habitat ranking positively influenced occupancy with $\psi = 0.95 \pm 0.17$ for high-ranking habitat, $\psi = 0.80 \pm 0.29$ for medium-ranking habitat, and $\psi = 0.50 \pm 0.00$ for low-ranking habitat and $\rho = 0.65 \pm 0.10$. For the remaining models that showed some empirical support but were not within 2 units of ΔAIC_c in both datasets, the habitat-ranking covariate positively influenced detection probability and habitat ranking and had an inverse relationship to colonization. Simulations using $\psi = 0.87$ and $\rho = 0.65$ over a range of years and nest-box lines suggested that ≥20 nest-box lines surveyed annually for 5+ years should provide suitable estimates of precision in occupancy estimates for Virginia northern flying squirrels for post-delisting monitoring purposes as set forth by the U.S. Fish and Wildlife Service (Fig. 1).

Table 1.—Summary of mean (± SE) years of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) monitoring and percent captures using nest-box survey lines in West Virginia, 1985-2008, by habitat ranking of probability of occurrence (see text).

Quality	*n*	Year range	Mean years surveyed	Percent years with capture	Percent years with females/juveniles
All	72	2 - 24	9.34 ± 1.35	44.47	41.13
Low	8	2 - 19	8.75 ± 0.86	41.19	33.89
Medium	29	2 - 24	8.44 ± 1.57	47.26	41.68
High	35	2 - 23	10.22 ± 1.06	42.84	42.23

Table 2.—Akaike's Information Criterion ranking of best-approximating ψ(.),γ(.),ε(.),ρ(.) (initial occupancy, local colonization, extinction, and detection) models and competing models with empirical support for Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) presence or absence data using nest-box survey lines in West Virginia, 1985-2008. Habitat ranking of probability of occurrence was used as a model covariate (see text). Models that failed to converge were not included in assessment.

Model	K	AIC_c	ΔAIC_c	AIC_{wt}
All squirrels				
ψ(.),γ(.),ε(.),ρ(.)	5	923.05	0.00	0.44
ψ(Hab[a]),γ(.),ε(.),ρ(.)	7	923.72	0.67	0.32
ψ(.),γ(Hab),ε(.),ρ(.)	7	925.91	2.86	0.11
ψ(Hab),γ(.),ε(.),ρ(Hab)	9	926.30	3.25	0.09
ψ(.),γ(Hab),ε(.),ρ(Hab)	9	927.69	4.64	0.04
Female or juvenile squirrels				
ψ(Hab),γ(.),ε(.),ρ(.)	7	923.72	0.00	0.68
ψ(.),γ(Hab),ε(.),ρ(.)	7	925.91	2.19	0.23
ψ(.),γ(Hab),ε(.),ρ(Hab)	9	927.69	3.97	0.09

[a]habitat ranking of probability of occurrence (high, medium, or low)

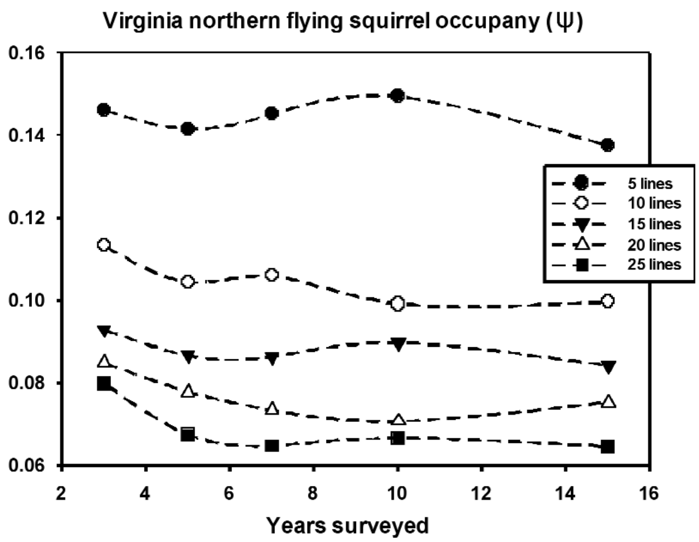

Figure 1.—Simulated standard errors for Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) occupancy values over combinations of increasing survey effort (box-lines) and increasing survey time (years). Monitoring efforts using ≥20 nest-box lines surveyed for 5+ years satisfy requirements of the U.S. Fish and Wildlife Service post-delisting monitoring plan.

DISCUSSION

The positive link between habitat ranking and occupancy in the best-approximating model for persistence (females and juveniles) and the strongly supported competing model for all Virginia northern flying squirrels confirms the utility of recent predictive habitat modeling efforts at stand levels (Ford et al. 2004) and landscape levels (Menzel et al. 2006a). Anecdotal evidence and current opinion among managers and researchers working with the Virginia northern flying squirrel have suggested that detection probability might be lower; that is, individuals might be less likely to be detected when present in good habitat conditions where an abundance of natural den sites exist or conditions are suitable for drey-nest formation in red spruce. Similarly, it is possible that detection probability was biased upward in lesser-quality habitat or younger stands, where dens could be less abundant and nest-boxes were functioning as a supplement to a limiting factor. Our best-approximating models and those with the strongest empirical support do not support this assertion. Rather, detection probability was constant among high-, medium-, and low-ranking habitat designations in the Allegheny Mountains. For the models with some empirical support that were not within two units of ΔAIC_c in both datasets, colonization probabilities inverse to habitat ranking could be indicative of greater year-to-year population stability and higher overall population densities per unit area.

Managers in other systems with other wildlife species have recognized that artificial structures such as nest-boxes can help overcome habitat inadequacies, such as an obvious lack of snags and cavities in younger or intensively managed forests (Lindenmayer et al. 2009). In the Pacific Northwest, Carey (2002) reported that the proportion of breeding female northern flying squirrels increased with the addition of supplemental nest-boxes although actual population productivity remained constant. In the Allegheny Mountains, however, Menzel and others (2004) demonstrated that natural den use and availability and den-switching were high across a wide variety of red spruce and red spruce-northern hardwood stands that also contained nest-box survey lines in most instances. In turn, we believe the results of our modeling along with the findings of Menzel and others (2004) relative to denning ecology would suggest that detection probabilities are unbiased across habitat conditions. Therefore occupancy measures probably are accurate reflections of Virginia northern flying squirrel presence or absence.

Nonetheless, we are aware of two caveats in our data that might contribute bias to our occupancy and detection probability measures. First, as has been observed generally with Sciurids and other cavity-dependent species monitored with nest-box surveys, captures tend to be low after the initial placement of nest-boxes before they become "weathered" (Carey 2002, Shuttleworth 2004, Lindenmayer et al. 2009). Accordingly, a small number of sites with only 2 years of recorded survey effort and hence, new nest-boxes, may have been misclassified as unoccupied. Secondly, a small proportion of sites occasionally were surveyed twice a year (C. Stihler, West Virginia Division of Natural Resources, unpubl. data), inflating detection probabilities slightly. Future detection probability and occupancy analyses should include a cumulative covariate of time since nest-box placement site/sampling.

Using our post-hoc examination of presence or absence data from Virginia northern flying squirrel nest-box survey lines, we believe this survey technique successfully can meet the post-delisting monitoring requirements over the next decade. Although nest-box lines as configured in our study would not provide detailed relative abundance or density estimates to allow a full understanding of Virginia northern flying squirrel habitat relationships, i.e., productivity by habitat condition, data from these nest-box lines would still be sufficient to assess persistence or changes in occupancy over the Allegheny Mountain landscape. Indeed, measures of occupancy and incidental collection of sex, age, and condition of captured individuals may be the only readily or practically obtainable data to assess population status for Virginia northern flying squirrels – a situation similar to many other cryptic wildlife species that are difficult to observe and/or capture and re-capture (Weller 2008). Monitoring the southern flying squirrel (*Glaucomys volans*) in Ohio, Althoff and Althoff (2001) concluded that occupancy measures derived from nest-box captures are a suitable surrogate for understanding habitat trends if measured over a long enough period and with enough sampling effort. Our simulation efforts would indicate that approximately 20 nest-box survey lines monitored for >5 years would provide a satisfactory level of precision to assess changes or the lack thereof in occupancy for the Virginia northern flying squirrel. Ongoing survey efforts range-wide by West Virginia Division of Natural Resources combined with additional surveys on the Monongahela National Forest, Canaan Valley National Wildlife Refuge, and Kumbrabow State Forest should easily exceed the 20 nest-box survey-line threshold (S. Jones, U.S. Forest Service, pers. comm.). Additionally, these surveys will occur across a wide gradient of Virginia northern flying squirrel habitat conditions.

From an economic and efficiency standpoint, much of the costs of monitoring using nest-boxes are the initial investment of constructing boxes and the time required to place nest-boxes in the forest. Depending on travel-time and nest-box survey-line location, our experience would suggest that two individuals can check two to three lines in a day. On the other hand, live-trapping requires significant effort, often requiring multiple visits to a single site over 3-7 consecutive days, thus making multiple individual site visits logistically difficult unless within very close proximity. Though less of an issue now that the Virginia northern flying squirrel has been de-listed, trap mortality from exposure, capture myopathy, or predation is a concern when working with northern flying squirrels (Rosenberg and Anthony 1993). Moreover, if live-trapping produces capture rates too low to generate usable mark-recapture or even minimum-number-known-alive types of data, then arguments against the selection of nest-box survey lines for monitoring Virginia northern flying squirrels are unpersuasive at best.

Although much remains unknown about the Virginia northern flying squirrel subspecies in particular and the species in general, an important aspect of future work should be to examine the relationships between persistence and/or more detailed demographics with habitat that have spatially explicit linkages (Smith 2007). For the Siberian flying squirrel (*Pteromys volans*) in Finland, Hurme and others (2008) observed that habitat patch occupancy was temporally dynamic and linked to habitat patch quality, size, and proximity or connectivity to other patches within the landscape matrix. Smith and Person (2007) hypothesized that Alaska northern flying squirrel populations might not be viable within optimal, but small, spatially isolated habitat patches or with reduced "rescue" immigration from nearby large, high-quality habitat patches. Relative to large conifer-dominated landscapes such as in Alaska or other parts of the northern flying squirrel's range, red spruce and red spruce-northern hardwood forests in the central and southern Appalachians are substantially fragmented and degraded from past anthropogenic disturbance (Stephenson and Clovis 1983, Weigl 2007). Therefore, the incorporation of additional habitat parameters beyond the recognition of simple habitat ranking, such as better measures of forest structure and the presence of folistic epipedons at the stand level, in ongoing and future nest-box monitoring would seem prudent. Such data could be an invaluable contribution for the design and implementation of red spruce forest enhancement and restoration efforts in the Allegheny Mountains in the coming years (Rentch et al. 2007).

ACKNOWLEDGMENTS

The U.S. Forest Service Northern Research Station and the West Virginia Division of Natural Resources provided the funding for this study. We thank S. Jones, J. Wallace, and J. Rodrigue for their help in assembling and editing these long-term data, as well as the countless personnel from the U.S. Forest Service, Monongahela National Forest, West Virginia Division of Natural Resources, West Virginia Division of Forestry, West Virginia University, Snowshoe Resort, and MeadWestvaco Corporation that surveyed nest-box lines since 1985 through the present. This manuscript was improved greatly by the comments of J. Rentch and two anonymous reviewers.

LITERATURE CITED

Althoff, D.P.; Althoff, P.S. 2001. **Monitoring southern flying squirrel populations with nest boxes.** Ohio Journal of Science. 101: 2-11.

Burnham, K.P.; Anderson, D.R. 2002. **Model selection and multi-model inference: a practical information-theoretic approach.** New York: Springer. 488 p.

Carey, A.B. 2002. **Response of northern flying squirrels to supplementary dens.** Wildlife Society Bulletin. 30: 547-556.

Ford, W.M.; Mertz, K.N.; Menzel, J.M.; Sturm, K.K. 2007a. **Winter home range and habitat use of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*).** Res. Pap. NRS-4. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 12 p.

Ford, W.M.; Rodrigue, J.L.; Chapman, B.R. 2007b. **Northern flying squirrel.** In: Trani-Griep, M.; Ford, W.M.; Chapman, B.R., eds. Land manager's guide to mammals of the South. Durham, NC: The Nature Conservancy, Southeastern Region: Atlanta, GA; U.S. Department of Agriculture, Forest Service, Southern Region: 389-394.

Ford, W. M.; Stephenson, S.L.; Menzel, J.M.; Black, D.R.; Edwards, J.W. 2004. **Habitat characteristics of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Central Appalachians.** American Midland Naturalist. 152: 430-438.

Hines, J.E.: McKenzie, D.I. 2008. **PRESENCE version 2.0**. Available: http://www.mbr-pwrc.usgs.gov/software/presence.html. Accessed November 1, 2008.

Hurme, E.; Monkkonen, M; Reunanen, P.; Nikula, A.; Nivala, V. 2008. **Temporal patch occupancy dynamics of the Siberian flying squirrel in a boreal forest landscape**. Ecography. 31 :469-476.

Lindenmayer, D.B.; Welsh, A.; Donnelly, C.; Crane, M.; Michael, D.; MacGregor, C.; McBurney, L.; Montague-Drake, R.; Gibbons, P. 2009. **Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition.** Biological Conservation. 142: 33-42.

McKenzie, D.I.; Nichols, J.D.; Royle, J.A.; Pollock, K.H.; Bailey, L.L.; Hines, J.E. 2005. **Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.** San Diego, CA: Elsevier Publishing. 344 p.

Menzel, J.M.; Ford, W.M.; Edwards, J.W.; Ceperley. 2006a. **A habitat model for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains**. Res. Pap. NE-729. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 10 p.

Menzel, J.M.; Ford, W.M.; Edwards, J.W.; Menzel, M.A. 2004. **Nest tree use by the endangered Virginia northern flying squirrel with recommendations for habitat restoration.** American Midland Naturalist. 151: 355-368.

Menzel, J.M.; Ford, W.M.; Edwards, J.W.; Terry, T.M. 2006b. **Home range and habitat use of the vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the Central Appalachian Mountains.** Oryx. 40: 204-210.

Mitchell, D. 2001. **Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*).** American Midland Naturalist. 146: 439-445.

Odom, R.H.; Ford, W.M.; Edwards, J.W.; Stihler, C.W.; Menzel, J.M. 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.

Rentch, J.S.; Schuler, T.M.; Ford, W.M.; Nowacki, G.J. 2007. **Red spruce stand dynamics, simulations and restoration opportunities in the central Appalachians.** Restoration Ecology. 15: 440-452.

Reynolds, R.J.; Pagels, J.F.; Fies, M.L. 1999. **Demography of northern flying squirrels in Virginia.** Proceedings of the Southeastern Association of Fish and Wildlife Agencies. 53: 340-349.

Rosenberg, D.K.; Anthony, R.G. 1993. **Differences in trapping mortality of northern flying squirrels.** Canadian Journal of Zoology. 71: 660-663.

Royle, J.A.; Nicols, J.D.; Kery, M. 2005. **Modeling occurrence and abundance of species when detection is imperfect.** Oikos. 100: 353-359.

Schuler, T.M.; Ford, W.M.; Collins, R.J. 2002. **Successional dynamics and restoration implications of a montane coniferous forest in the central Appalachians.** Natural Areas Journal. 22: 88-98.

Shuttleworth, C.M. 2004. **A study of nest box use by a low density red squirrel (*Sciurus vulgaris*) population within a commercial conifer plantation.** Quarterly Journal of Forestry. 98: 113-119.

Smith, W.P. 2007. **Ecology of *Glaucomys sabrinus:* habitat, demography and community relations.** Journal of Mammalogy. 88: 862-881.

Smith, W.P.; Person, D.K. 2007. **Estimated persistence of northern flying squirrel populations in temperate rain forest fragments of Southeast Alaska.** Biological Conservation. 137: 626-636.

Stephenson, S.L.; Clovis, J.F. 1983. **Spruce forests of the Allegheny Mountains in central West Virginia.** Castanea. 48: 1-12.

Stihler, C.W.; Wallace, J.L.; Michael, E.D.; Pawelczyk, H. 1995. **Range of (*Glaucomys sabrinus fuscus*), a federally endangered subspecies of the northern flying squirrel in West Virginia.** Proceedings of the West Virginia Academy of Science. 67:13-20.

Terry, T.M. 2004. ***Glaucomys sabrinus fuscus* habitat and nest box use in West Virginia with management recommendations for Kumbrabow State Forest.** Morgantown, WV; West Virginia University. 83 p. M.S. thesis.

Urban, V. 1988. **Home range, habitat utilization and activity of the endangered northern flying squirrel.** Morgantown, WV: West Virginia University. 54 p. M.S. thesis.

U.S. Department of the Interior. 2008. **Final rule removing the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) from the Federal list of endangered and threatened wildlife.** Federal Register 73 (166): 50226-50247.

U.S. Fish and Wildlife Service. 1990. **Appalachian northern flying squirrel (*Glaucomys sabrinus fuscus* and *Glaucomys sabrinus coloratus*) recovery plan.** Newton Corner, MA: U.S. Department of the Interior, Fish and Wildlife Service. 53 p.

U.S. Fish and Wildlife Service. 2007. **Post-delisting monitoring plan for the West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*).** Hadley, MA: U.S. Department of the Interior, Fish and Wildlife Service. 73 p.

Weigl, P.D. 2007. **The northern flying squirrel *Glaucomys sabrinus:* a conservation challenge.** Journal of Mammalogy. 88: 897-907.

Weller, T.J. 2008. **Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: bats in the Pacific Northwest.** Biological Conservation. 141: 2279-2289.

Wells-Gosling, N.; Heaney, L.R. 1984. ***Glaucomys sabrinus.*** Mammalian Species. 229: 1-8.
