Home range and habitat use of the Vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the Central Appalachian Mountains, USA

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Abstract The Virginia northern flying squirrel *Glaucomys sabrinus fuscus* is a Vulnerable sciurid that has experienced a 90% reduction of suitable high elevation boreal montane forest habitat over the last century in the central Appalachians of West Virginia and Virginia, USA. Using radiotelemetry and GIS analyses we examined the species' home range size and habitat use in the Monongahela National Forest, Kumbrabow State Forest and the MeadWestvaco Ecosystem Research Forest in West Virginia during the summers of 2000–2003. The mean home range sizes of male and female squirrels were 54.2 and 15.3 ha, respectively, based on the adaptive kernel method. Euclidean distance analysis indicated the squirrels used spruce, mixed spruce-northern hardwood, and open habitats more than was available across the landscape. Selection of spruce and mixed spruce-northern hardwood habitats indicates that forest management activities designed to restore and increase these types in the central Appalachian landscape are required to conserve and increase this Vulnerable species.

Keywords Central Appalachian Mountains, *Glaucomys sabrinus fuscus*, northern hardwoods, spruce, telemetry, USA, Virginia northern flying squirrel.

Introduction

The northern flying squirrel *Glaucomys sabrinus* is a small nocturnal sciurid found throughout northern North America. Its range is continuous throughout Canada southward into the northern USA. However, there are satellite populations in the Appalachian Mountains in the east and in the Black Hills, the Sierra Nevada Mountains and Rocky Mountains in the west. Both Appalachian subspecies have been confined to high elevation islands of suitable boreal montane habitat within the Allegheny Mountains of West Virginia and north-western Virginia and the Blue Ridge Mountains of western North Carolina, eastern Tennessee and south-eastern Virginia since the end of the last glacial period in North America (USFWS, 1990). In addition to natural isolation, exploitative logging of high elevation red spruce *Picea rubens* dominated forests followed by wildfires at the turn of the 20th century further reduced suitable habitat for *G. s. fuscus* from >200,000 ha to *c.* 20,000 in West Virginia (Stephenson, 1993).

Listed as Endangered by the United States Fish and Wildlife Service (USFWS) in 1985 and categorized as Vulnerable on the IUCN Red List (IUCN, 2004), *G. s. fuscus* continues to face additional threats to its habitat from atmospheric acid deposition, global climate change, introduced forest insect pests, second home/recreational development, surface mining and wind energy development on forest lands (USFWS, 1990; Schuler *et al.*, 2002). Much of the area that was once dominated by forests of red spruce was replaced with northern hardwood stands with a greater hard-mast producing capacity from tree species such as black cherry *Prunus serotina* and northern red oak *Quercus rubra*. This increase in hard-mast production has probably allowed the southern flying squirrel *G. volans*, a superior nest site competitor to *G. sabrinus*, to expand its local distribution to higher elevation forest communities (Weigl, 1968; Arbogast, 1996). Furthermore, *G. volans* can also asymptomatically host the parasitic nematode *Strongyloides robustus*, which is believed to be pathogenic to *G. sabrinus* (Pauli *et al.*, 2004).

Despite its threatened status and occurrence in a relict forest type with high conservation concern (Menzel, 2003), there has been little quantitative work examining *G. s. fuscus* habitat preferences and use other than limited observations from live trapping and nest box surveys (Odom *et al.*, 2001) and one radiotelemetry study (Urban, 1988). Concurrent with a renewed interest in red spruce

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forest restoration in the central Appalachian Mountains (Schuler *et al*., 2002), *G. s. fuscus* is now the focal species for a number of proposed Habitat Conservation Plans in industrial forests, large recreational areas, and wind energy developments. Accordingly, definitive relationships between the subspecies and its boreal montane forested habitat are necessary for effective forest management and for regulatory mitigation and restoration purposes. The objectives of this study were to quantitatively determine home ranges and habitat selection by *G. s. fuscus* using a GIS habitat analysis of radiotelemetry data.

Study Area

Our study was conducted in May–September 2000, May–August 2001, May–September 2002 and May–July 2003 in West Virginia on the MeadWestvaco Ecosystem Research Forest in south-western Randolph County, in Kumbrabow State Forest in Randolph County, and in three areas of the Monongahela National Forest (Stuart Knob, Canaan Heights and McGowen Mountain; Fig. 1). The MeadWestvaco Ecosystem Research Forest is a 3,360 ha intensively managed private forest whereas Kumbrabow State Forest and the Monongahela National Forest are 3,834 ha and 367,455 ha, respectively, of publicly owned forest subject to a variety of land use practices from moderately intensive forest management to wilderness designation. All three study sites are located in the Allegheny Mountain and Plateau physiographic province (Fenneman, 1938). Topography throughout consisted of north-east to south-west running steep ridges divided by narrow valleys at elevations of 800–1,300 m. Weather conditions are generally cool and moist with annual precipitation of 120–150 cm, much of which occurs as winter snow (Stephenson, 1993).

Within our study sites forest communities consisted of four general types: spruce *Picea* spp. dominant, mixed spruce-northern hardwood, northern hardwood-Allegheny hardwood, and mixed mesophytic with an oak *Quercus* spp. component. Occurring at the highest elevations (>1,100 m) and somewhat lower along sheltered north-facing slopes, spruce forests were dominated by red spruce, although one site, Canaan Heights, was unique because of the presence of a large, mature Norway spruce *Picea abies* plantation (>1,000 ha). At both high and mid elevations mixed spruce-northern hardwood forests contained hardwood species such as sugar maple *Acer saccharum*, red maple *Acer rubrum*, yellow birch *Betula alleghaniensis* and black cherry with a significant red spruce and eastern hemlock *Tsuga canadensis* component (>25%). Northern hardwood forests were similar but with little or no conifer component except for eastern hemlock along riparian zones. At the lowest elevations (<900 m) or along more xeric aspects at mid-elevations, mixed mesophytic forests also contained the aforementioned hardwood species in addition to northern red oak, black birch *Betula lenta*, yellow poplar *Liriodendron tulipifera*, Fraser's magnolia *Magnolia fraseri*, cucumber magnolia *Magnolia acuminata* and American basswood *Tilia americana*. Open habitats such as recent even-aged timber harvests (<5 years), maintained roads, skidder trails and recreational trails also occurred throughout.

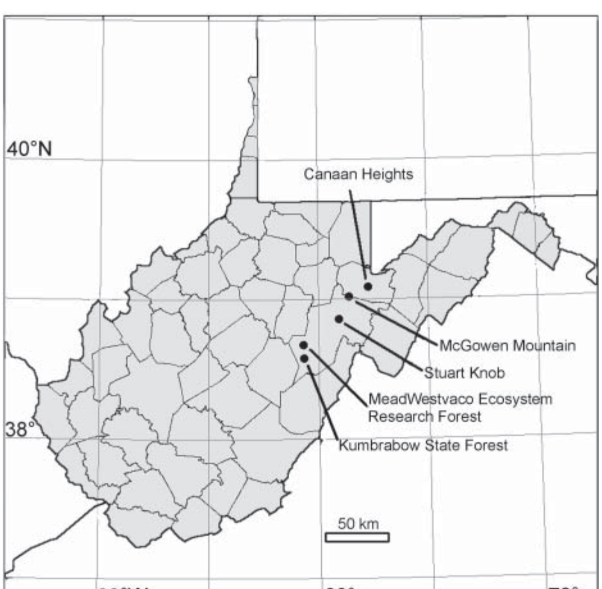

Fig. 1 Locations of the five study sites in West Virginia, United States.

Methods

We captured *G. s. fuscus* in nest-boxes and Tomahawk 201 live traps (14 * 14 * 41 cm; Tomahawk Live Trap Co., Tomahawk, USA). Traps were placed on the ground or attached to tree boles and baited with a mixture of peanut butter, rolled oats and molasses. We set traps in the evening (19.00) and checked them in the morning (06.00) to minimize captures of non-target diurnal species. We placed polyfiber in each to reduce exposure during cold periods. Upon capture we recorded sex, mass, hind foot length, age and reproductive condition. We determined age by examining mass and pelage (Witt, 1992) with *G. s. fuscus* characterized as adults if mass was >75 g (Wells-Gosling & Heaney, 1984). For recapture identification we attached uniquely numbered ear tags (No. 1005-1, National Band & Tag Co., Newport, USA) to all squirrels captured. We differentiated between *G. sabrinus* and *G. volans* by examining hind foot length and colouration of fur on the ventral side. *G. sabrinus* had hind foot measurements >34 mm and lead-coloured ventral fur (Wells-Gosling & Heaney, 1984). We attached SM1-BR radio collars (4.0–5.0 g; AVM Instruments Company, Ltd., Livermore, USA) to 15 adult *G. s. fuscus*. To reduce stress on the animal and to ensure proper fitting of the radio collar we anaesthetized squirrels with Halothane (Halocarbon Laboratories, River Edge, USA). Prior to release we monitored squirrels to ensure recovery and released them at their capture site. Our methods for anaesthesia and tagging were approved by the West Virginia University Animal Care and Use Committee (permit # 9912-01).

We used Wildlife Materials TR4-2000S receivers (Carbondale, USA) and 3-element Yagi antennas to track radio-collared squirrels at night; tracking began at sundown (20.00) continuing until animal movement ceased, which typically occurred between 24.00 and 02.00. We obtained telemetry locations using standard 2-station triangulation techniques taken simultaneously to minimize temporal error from animal movement (Springer, 1979; Schmutz & White, 1990). Telemetry stations were selected so that the bearings would be as close to a 90° angle as possible while maintaining a >50 m distance between stations and radio-collared squirrels (White, 1985). To decrease possible autocorrelation among telemetry locations and based on expected home range size and travel speed of squirrels, we took bearings at 18 minute or greater intervals (Swihart & Slade, 1985; White & Garrott, 1990). We determined UTM coordinates of telemetry stations using a Global Positioning System. Following White & Garrott (1990) we estimated the average telemetry bearing error by determining the difference between bearings taken on transmitters hidden in the field and the true bearings from the telemetry station to the location of the transmitter. We calculated the average error polygon as the average size of the polygon created by the error arcs of two bearings taken on a transmitter from two telemetry stations (Hurst & Lacki, 1999). Error testing was conducted at multiple locations for all individuals involved in the telemetry portion of the project.

We entered UTM coordinates of telemetry stations and triangulation bearings into the software *LOCATE* (J.G. Kie, USDA Forest Service, Fresno, USA) to obtain UTM coordinates of animal locations. To create home range estimates we entered individual squirrel location UTM coordinates into the Animal Movement Analysis Extension (Hooge & Eichenlaub, 1997) in *ArcView* (Environmental Systems Research Institute, Redlands, USA). We only calculated home ranges for individuals with >30 telemetry locations (Seaman *et al*., 1999). We used the adaptive kernel method to determine squirrel home ranges at 95% use distributions as well as the minimum convex polygon (MCP) method for comparison with previous studies. We tested for differences in home range size between males and females using a *Z*-test (SAS Institute, 1990).

We used Euclidean distance based analysis (DA) to conduct habitat use analysis (Conner & Plowman, 2001). The DA approach was chosen because of its ability to incorporate edge and fragmented habitats into habitat use analysis (Conner *et al*., 2002). Additionally, the use of DA reduces the effect of telemetry and Type 1 errors commonly associated with other habitat analysis methods such as compositional analysis (Bingham & Brennan, 2004). We defined the lateral extent of the study area as the distance between the centre of all squirrel home ranges and the telemetry point located the greatest distance from the centre of each study site. Within this area we used *ArcView* to calculate the Euclidean distances between squirrel locations and the nearest representative of each habitat type. We paired each telemetry location with a randomly located point within the study site, and we calculated a Euclidean distance from each telemetry and random location to each habitat type in the study area. Based on these Euclidean distances we created a vector of ratios using the distances of telemetry and random locations. We used a MANOVA to determine if the ratios differed from 1.0, and this indicated that use of the habitat by the squirrels we tracked was not random. We therefore used a paired *t*-test to determine which habitat types were used disproportionally based on their abundance in the study area. Lastly, we used a series of pairwise *t*-tests to evaluate the relative rankings (or order of preference) of each habitat type in the study area. We performed all statistical analyses using *SAS* (SAS Institute, 1990), with significance determined at $P \leq 0.05$. We pooled habitat use data over sex and year after we found no significant differences ($P > 0.1$) in the proportion of habitat type used between years and sex using two-way ANOVA on ranked data (Sokal & Rohlf, 1987).

Results

We captured 20 (14 female, 6 male) *G. s. fuscus* during 7,926 trap nights and numerous, repeated nest-box checks. Of these, we fitted 15 adults with radio collars and obtained a total of 1,018 telemetry locations. Twelve of the squirrels tracked had ≥ 30 locations and could therefore be used for home range analysis. Male *G. s. fuscus* had significantly ($Z = 1.90$, $P = 0.029$) larger home ranges than females. The 95% confidence interval adaptive kernel home range of male *G. s. fuscus* averaged $54.2 \pm$ SE 18.4 ha and the MCP home range $59.8 \pm$ SE 23.5 ha. Females averaged $15.3 \pm$ SE 7.1 ha with the adaptive kernel method and $15.9 \pm$ SE 8.7 ha with the MCP method. After testing all personnel who assisted with telemetry we calculated our telemetry bearing error to be 2° and our error polygon to be 0.16 ha.

The average distance between a *G. s. fuscus* location and the nearest spruce, mixed spruce-northern hardwood, northern hardwood, mixed mesophytic and open habitat was 1,095.0, 446.4, 571.9, 5,588.1 and 622.4 m, respectively. The average distance between randomly selected locations and the nearest spruce, mixed spruce-northern hardwood, northern hardwood, mixed mesophytic and open habitat was 2,513.3, 1,085.7, 1,235.6, 4,574.1 and 634.1 m, respectively. A comparison of these distances indicates that the squirrel locations were not sex specific and that squirrels we tracked did not move randomly across the study area ($F_{5,7} = 75.47$, $P < 0.0001$). For example, the squirrels we tracked occurred significantly closer to spruce ($t_{11} = -3.36$, $P = 0.0063$), mixed spruce-northern hardwoods ($t_{11} = -17.87$, $P < 0.0001$), and open habitats ($t_{11} = -3.69$, $P = 0.0035$) than expected based on the relative availability of these habitat types in the study area. A comparison of the distance between actual and randomly selected locations and northern hardwoods and mixed mesophytic habitats indicates that the squirrels we tracked neither selected nor avoided these habitat types ($t_{11} = 0.21$, $P = 0.8358$, and $t_{11} = 1.30$, $P = 0.2198$, respectively).

Pairwise comparisons of the distances between each habitat type and squirrel locations indicates that the squirrels we tracked occurred significantly closer to spruce than mixed mesophytic forests (Table 1). They also occurred significantly closer to mixed spruce-northern hardwood forests than northern hardwood, mixed mesophytic and open habitats (Table 1). Lastly, the squirrels occurred significantly closer to open habitats than mixed mesophytic forests (Table 1). A ranking of the habitats based on each habitat's use shows that, proportionally, mixed spruce-northern hardwood forests were used the most followed, in order of preference, by spruce, open habitats, northern hardwoods, and mixed mesophytic forests.

Discussion

Home ranges of the *G. s. fuscus* we observed were larger than those previously reported for any subspecies of *G. sabrinus* (Table 2). Within the central and southern Appalachians, Weigl *et al*. (2002) found mean home range of *G. s. coloratus* to be 7.5 ha in the Unicoi Mountains of North Carolina and Tennessee, whereas the three *G. s. fuscus* tracked by Urban (1988) had a mean home range 5.2 ha during the summer and fall near our Stuart Knob study area in the Monongahela National Forest in West Virginia. Firstly, the differences between the home ranges we report and that of others may be in part due to use of the minimum convex polygon estimator, which is dependent on number of sampling locations and bearings collected (Seaman *et al*., 1999). Secondly, study duration may also have influenced the home range size reported as we tracked individuals over an average of 12 weeks each, longer than in other studies (Urban, 1988; Witt, 1992; Weigl *et al*., 1999). Lastly, we used simultaneous triangulation to determine location rather than physically following squirrels and inducing behavioural reactions that bias movements (Witt, 1992). Simultaneous triangulation also prevents any temporal lag between bearings collected by observers.

The large home ranges of *G. s. fuscus* observed in our study may be a result of the patchy distribution and degraded condition of suitable forest habitat in the region. Due to both natural processes and past logging and burning most high elevation spruce and mixed spruce-northern hardwood stands in the region are highly disjunct. Because many of the extant spruce and mixed spruce-northern hardwood patches are generally insufficient in size or quality to sustain a population of *G. sabrinus*, individuals may utilize several patches or stands to meet their ecological requirements for food and den resources. This will have inflated the calculated home ranges.

G. s. fuscus primarily selected spruce and mixed spruce-northern hardwood forest types. Both Appalachian subspecies of *G. sabrinus* are associated with red spruce-dominated forests (Urban, 1988; Payne *et al*., 1989; Weigl *et al*., 1999; Hackett & Pagels, 2003). Payne *et al*. (1989) reported that overstorey red spruce was present at all capture sites examined in the Appalachians. Loeb *et al*. (2000) hypothesized that the link between *G. sabrinus* and

Table 1 Ranking matrix of Virginia northern flying squirrel habitat use in West Virginia, 2000–2003. Numbers are *t* statistics (P values) associated with pairwise comparisons of corrected distances to habitat.

	Spruce	Mixed spruce-northern hardwood	Northern hardwood	Mixed mesophytic	Open habitats
Spruce		1.76 (0.11)	−1.29 (0.23)	−6.79 (0.001)	−1.69 (0.12)
Mixed spruce-northern hardwood	−1.76 (0.11)		−2.14 (0.05)	−7.63 (0.001)	−4.33 (0.001)
Northern hardwood	1.29 (0.23)	2.14 (0.05)		−0.12 (0.90)	0.94 (0.37)
Mixed mesophytic	6.79 (0.001)	7.63 (0.001)	0.12 (0.90)		5.91 (0.001)
Open habitats	1.69 (0.12)	4.33 (0.001)	−0.94 (0.37)	−5.91 (0.001)	

Table 2 Comparison of northern flying squirrel home range estimates from previous research in the central and southern Appalachians and the Pacific north-west.

			Male home range (ha)		Female home range (ha)	
Source	Location	Season	AKM[1]	MCP[2]	AKM[1]	MCP[2]
This study	West Virginia	Summer-Fall	54.2 (n = 4)	59.8 (n = 4)	15.3 (n = 8)	15.9 (n = 8)
Weigl *et al*. (2002)	North Carolina	Winter		23.9 (n = 4)		4.3 (n = 2)
	North Carolina	Summer		11.0 (n = 2)		4.0 (n = 2)
Martin & Anthony (1999)	Oregon	Summer-Fall	5.8 (n = 20)		4.1 (n = 19)	
Weigl *et al*. (1999)	North Carolina	Summer		3.4 (n = 3)		10.5 (n = 2)
	North Carolina	Winter		16.9 (n = 3)		3.4 (n = 2)
Witt (1992)	Oregon	Fall		3.7 (n = 4)[3]		
Urban (1988)	West Virginia	Summer-Fall		5.2 (n = 3)		
Weigl & Osgood (1974)	North Carolina	Summer				5.9 (n = 3)[4]
	Pennsylvania	Summer				8.7 (n = 3)[4]

[1]Adaptive kernel method.
[2]Minimum convex polygon method.
[3]Study did not differentiate between male and female home ranges.
[4]Study delineated home ranges by estimating range of transmitter signal.

spruce was due to the greater association of hypogeal fungi important in the diet of *G. sabrinus*. Also similar to others, our results indicate that pure stands of either red or Norway spruce are not exclusively used by *G. s. fuscus*, as they also frequently used northern hardwood habitats at our study sites. Several of the individuals we tracked denned during the day in northern hardwood patches and foraged during the evening in spruce or mixed spruce-northern hardwood patches. Weigl (1968) noted that *G. s. coloratus* were commonly captured in the ecotone between spruce and northern hardwood, and some populations of that subspecies occur in northern hardwood forests lacking any spruce component (Weigl *et al*., 2002).

In the southern Appalachians *G. s. coloratus* are not commonly associated with high elevation hardwood stands that contain significant amounts of northern red oak (Weigl & Boynton, 1992; Loeb *et al*., 2000; Odom & McNab, 2000). For the squirrels we tracked the avoidance of mixed mesophytic stands with a northern red oak component was a significant trend. Oak forests at higher elevations may provide a high-energy and cacheable food supply in the form of acorns that allows *G. volans* a competitive advantage over *G. sabrinus* (Weigl, 1968; Weigl & Boyton, 1992). Although primarily a function of travel between foraging habitats and the reflection of the high degree of forest patch fragmentation and edge, we recorded more locations within open habitats such as forest roads and newly harvested forest stands than mixed mesophytic forests with an oak component.

Forest site quality issues beyond the presence of northern red oak also could be a potential factor in habitat selection and use, as Menzel *et al*. (2004) found that *G. s. fuscus* most often selected yellow birch as cavity dens and red and Norway spruce for drey nests over other tree species. Perhaps the more xeric conditions found in mixed mesophytic stands with northern red oak lack necessary habitat components such as suitable den sites or hypogeal fungi abundance. Although our knowledge of older forest microhabitat variables such as abundant downed woody debris and complex multi-aged forest stand structure is limited in the central Appalachians (Hackett & Pagels, 2003; Ford *et al*., 2004), these are habitat components identified as important for other *G. sabrinus* subspecies (Carey, 2000).

Our findings indicate that *G. s. fuscus* in West Virginia primarily use spruce, mixed spruce-northern hardwood and open habitats. This generalist approach to habitat selection has made it possible for *G. s. fuscus* to persist in and around relict spruce and mixed spruce-northern hardwood patches despite the past natural habitat changes and the more catastrophic anthropogenic forest disturbances in the last century. The restoration of native red spruce and the promotion of older forest structural attributes in current spruce and mixed spruce-northern hardwood forests should be the primary objective for managing *G. s. fuscus*. Deterioration and reduction of these habitats are the main factors threatening this subspecies and therefore efforts to reverse these occurrences would be prudent (McLaughlin *et al*., 1987; Schuler *et al*., 2002). A forest management strategy in northern hardwood stands that combines retention of large overstorey tree species valued as dens with selective thinning to release suppressed spruce in the understorey could result in conditions more favourable for *G. sabrinus* (Carey, 2000; Schuler *et al*. 2002). Moreover, such efforts would not only protect and enhance *G. s. fuscus* habitat, but could also benefit other high elevation species of conservation concern such as the saw-whet owl *Aegolius acadicus*, snowshoe hare *Lepus americanus*, northern goshawk *Accipiter gentilis* and the fisher *Martes pennanti*.

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Jennifer Menzel has studied the ecology and conservation of the Virginia northern flying squirrel since 1999, including habitat use, denning, and GIS applications for the species' conservation. Her other research includes the ecology of bats and other small mammals in the eastern USA.

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John Edwards' research interests include wildlife-habitat relationships and interactions of wildlife with forestry. He has worked extensively with tree squirrels in the eastern USA, and with the red-cockaded woodpecker, white-tailed deer, black bear and bats in the Appalachians.

Tamara Terry's research interests include the ecology of the Virginia northern flying squirrel in sub-optimal and ecotone habitats, as well as GIS applications for the species' conservation. She has also worked with white-tailed deer in the southern USA.