



Home range use and survival of southern flying squirrels in fragmented forest landscapes

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We studied home range use, spatial activity patterns, and annual survival of southern flying squirrels (SFS; *Glaucomys volans*) across fragmented landscapes of west-central Illinois. We calculated seasonal home range sizes and annual survival from 67 animals (36 males, 31 females) captured during 2014–2016. Home range and core area sizes were similar ($P \geq 0.46$) among males and females across summer (April–September) and winter (October–March) seasons. Average distance between consecutive animal locations did not vary by sex, season, or year. Similarly, cumulative distance between consecutive locations did not vary by sex, season, or year and ranged from 1,189 to 1,661 m between summer and winter seasons. Mean annual composite home range and core area sizes were 10.39 and 1.25 ha, respectively; estimated home ranges (10.3 ha) of females are the largest documented for this species. We documented 8 deaths, all attributed to predation, the majority (63%) of which occurred during winter; annual survival was 71%. Our results underscore effects of habitat productivity on seasonal home range dynamics and space use patterns of SFS in fragmented landscapes. SFS may compensate for reduced availability of overstory mast-producing trees that characterize unproductive habitats and low-density populations by exhibiting similar movement patterns and use of available habitat by both sexes throughout the year. Winter communal nesting appears to be influenced by availability of cavity trees, thereby confirming the importance of standing snags in contributing essential habitat to flying squirrel populations in fragmented forests.

Key words: adaptive kernel, core area, fragmentation, *Glaucomys volans*, home range, Illinois, southern flying squirrel, survival

Habitat fragmentation and its consequences are a principal cause of endangerment of natural populations and a key issue in conservation biology (Soulé 1986; Lawler et al. 2002; Kerr and Cihlar 2004; Macdonald and Service 2007). Major ecosystems have been fragmented through anthropogenic disturbances, and fragmentation of forested ecosystems over the past 200 years has been extensive (Lomolino and Perault 2001; Desrochers et al. 2003; Taulman and Smith 2004; Koprowski 2005; Smith and Person 2007). Changes in home range size and spatial overlap with other individuals are important individual responses to fragmented landscapes (Ims et al. 1993; Andreassen et al. 1998). Though potential effects of habitat fragmentation on spatial requirements of animals are varied, they may include decreased overlap between individual home ranges as a consequence of small population size, or home range expansion to incorporate adequate resources for survival (Ims et al. 1993).

Recent investigations of mammalian landscape ecology have included a variety of gliding mammals, including flying squirrels (Hanski et al. 2000; Selonen et al. 2001; Desrochers et al. 2003; Taulman and Smith 2004; Pyare et al. 2010), squirrel gliders (*Petaurus norfolcensis*—Sharpe and Goldingay 2007), and mahogany gliders (*P. gracilis*—Jackson 2000). Home ranges of flying squirrels (*Glaucomys* and *Pteromys*) in fragmented habitat typically are larger (Hanski et al. 2000; Selonen and Hanski 2003; Menzel et al. 2006) than those reported for individuals inhabiting contiguous forests (Desrochers et al. 2003; Smith 2007). Additionally, habitat fragmentation can create a matrix of early successional habitats that reduce or isolate flying squirrel populations (Carey 2000; Ford et al. 2004; Smith 2007; Pyare et al. 2010), and in turn lead to lower population densities or local extirpations (Hanski et al. 2000; Smith and Person 2007; Pyare et al. 2010). Flying squirrels are especially sensitive to forest fragmentation due to their reliance on trees

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for locomotion, refugia, and primary food sources (Taulman and Smith 2004).

Habitat productivity also may contribute to differences in resource requirements and space use between male and female flying squirrels. For example, home range use by females should be eclectic and dependent on food and nest resources, whereas home ranges of males should be more dependent on the spatial distribution of females (Ostfeld 1990; Fridell and Litvaitis 1991; Hanski et al. 2000). Home range sizes for males and their overlap with home ranges of females typically increase during summer (i.e., mating season) for many mammals other than flying squirrels, and are thus directly influenced by the spatial distribution and abundance of females (Ims 1987; Clutton-Brock 1989). During winter, resource acquisition is often the principal factor influencing home range sizes of male and female non-gliding mammals (Erlinge and Sandell 1986; Dahle and Swenson 2003), and particularly for gliding mammals (e.g., southern flying squirrels, *Glaucomys volans*; SFS) that reflect plasticity in sexual dimorphism across their geographic range (Madden 1974; Robins et al. 2000; Taulman and Smith 2004). Thus, male and female SFS should maintain similar home range sizes (assuming the 2 sexes overlap nearly completely in diet and do not differ significantly in body size) during winter.

SFS are nocturnal, arboreal, gliding rodents found in a wide variety of hardwood and pine-hardwood forest types throughout the central and eastern United States (Bendel and Gates 1987; Taulman 1999). A fundamental conservation issue pertaining to this species has been to what extent habitat fragmentation affects variation in home range size and fine-scale habitat use (Bendel and Gates 1987; Taulman et al. 1998; Holloway and Malcolm 2007; Steinhoff et al. 2012). Previous studies suggested that several structural attributes of overstory hardwood trees seem essential to SFS life history needs, especially locomotion (Scheibe et al. 2006, 2007), den site selection (Bendel and Gates 1987; Steinhoff et al. 2012), and reproduction (Taulman et al. 1998).

Previous evaluations of SFS survival using radiotelemetry are limited to 2 studies in Arkansas, in which seasonal survival estimates ranged from 0.12 to 0.64 (Taulman et al. 1998; Taulman and Smith 2004). However, SFS populations in the southern and midwestern United States experience considerable differences in climate and habitat. Additional estimates of survival of SFS may provide a better understanding of the generality of previously reported estimates.

Because SFS are active year-round, nest communally during winter months (Muul 1974; Stapp et al. 1991; Layne and Raymond 1994), and exhibit sexual differences in territoriality (males are non-territorial and females are territorial during summer—Madden 1974), they are model organisms to evaluate hypotheses about seasonal variation in space use. Our objectives were to 1) evaluate summer and winter home range use and spatial activity patterns of SFS, and 2) estimate annual survival rates of SFS in west-central Illinois. Changes in space use by SFS may be associated with seasonal changes in social behavior and reproductive activities, thus we hypothesized that

home range size and movements of males would increase during the summer season, but those of females would vary little between seasons. We also hypothesized that overlap among core areas of males and females would be similar during winter, and that home range sizes would be larger in our fragmented habitat than those associated with more contiguous (and presumably higher quality) habitats. Evaluation of these hypotheses may contribute to a greater understanding of the spatial requirements of SFS, and provide insight into viable conservation strategies for this species.

MATERIALS AND METHODS

Study areas.—We conducted our study at the Alice L. Kibbe Field Station (40°21'36"N, -91°25'48"W), a 0.9-km² area surrounded by 4 km² of land owned by the Illinois Department of Natural Resources within Hancock County of west-central Illinois. Our study site was bordered to the north and west by the Mississippi River and predominantly by agricultural land to the south and east. Functionally, our study site represented an isolated patch of relatively contiguous hardwood forests surrounded by a matrix of unsuitable habitat dominated by row crop agriculture. Consequently, we assumed that the local population of SFS was a closed population. Elevation ranged from 145 to 213 m above sea level (Walker 2001). Additionally, summer and winter temperatures average 22.9°C and -3.4°C, respectively, while total mean annual precipitation and seasonal snowfall across Hancock County are 97.7 and 62.5 cm, respectively (Walker 2001). Landscape characteristics ranged from sandbars, islands, intermittent creeks, limestone cliffs, hill prairies, floodplain forests along the Mississippi River shoreline, and mature second growth oak woodlands (Schwegman et al. 1973). Dominant trees at xeric sites included white oak (*Quercus alba*), post oak (*Q. stellata*), black oak (*Q. velutina*), and mockernut hickory (*Carya tomentosa*), whereas mesic sites were dominated by northern red oak (*Q. rubra*), shagbark hickory (*C. ovata*), bitternut hickory (*C. cordiformis*), white ash (*Fraxinus americana*), sugar maple (*Acer saccharum*), basswood (*Tilia americana*), American elm (*Ulmus americana*), and wild black cherry (*Prunus serotina*). Hard mast-producing trees constituted 15% of the trees in the study area (11% oaks, 4% hickories). Dominant understory vegetation in open oak woodland communities included pointed-leaved tick trefoil (*Desmodium glutinosum*), elmleaf goldenrod (*Solidago ulmifolia*), white snakeroot (*Ageratina altissima*), clustered black snakeroot (*Sanicula odorata*), nodding fescue (*Festuca subverticillata*), Pennsylvania sedge (*Carex pensylvanica*), ironwood (*Ostrya virginiana*), and roughleaf dogwood (*Cornus drummondii*).

Capture, handling, and monitoring of flying squirrels.—We captured flying squirrels using nest boxes ($n = 50$ —Taulman et al. 1998) during fall (September–November) 2014 and 2015 (1,200 total trap-nights); nest boxes were mounted 3–4 m above ground on randomly selected trees during July 2014. Additionally, we used Sherman traps (7.62 × 9.53 × 30.48 cm; H. B. Sherman Co., Tallahassee, Florida) baited with a mixture

of peanut butter, oats, and bacon grease (Weigl and Osgood 1974); 30 traps were placed 3–6 m above ground every 15–20 m along each of 12 450-m transects during summer (May–August) 2015 (4,604 trap-nights). We conducted trapping efforts simultaneously on 2 transects for 5 days, after which time we redeployed traps to 2 new transects where trapping had not been conducted previously until all transects ($n = 12$) were trapped. We repeated this trapping schedule until all transects were re-trapped a second time. We aligned the trapping transects with the permanently mounted nest boxes and to maximize the probability of detecting SFS presence across the study area. We checked nest boxes weekly between 1000 and 1400 h to maximize probability of occupancy by individuals. We checked all Sherman traps daily between 0600 and 0900 h to minimize time in traps and potential loss of body mass (Kaufman and Kaufman 1994; Powell and Proulx 2003). We closed Sherman traps during daylight hours (0900 to 1700 h) and adverse environmental conditions (e.g., ambient temperatures $\leq 16^\circ\text{C}$ or $\geq 32^\circ\text{C}$, thunderstorms) to minimize stress or capture-related mortality events on flying squirrels or non-target species. We reopened Sherman traps during late afternoon (1800–2000 h). Because our trapping effort (12 total transects) yielded complete coverage of suitable SFS habitat across the study site, our sample of collared animals was representative of the local SFS population.

After capture, we anesthetized adult flying squirrels in a sealed container using 3 ml of isoflurane injected into a cotton ball soaked in mineral oil (Steinhoff et al. 2012). We fitted adult (≥ 55 g—Sollberger 1943) animals with radiocollars (collar weight = 4.2 g, $\leq 7\%$ total body mass; 165 MHz, model M1540; Advanced Telemetry Systems, Isanti, Minnesota) and recorded body mass, sex, age (juvenile or adult), and reproductive condition of all captured individuals (Wells-Gosling 1985; Taulman et al. 1998). We considered males with scrotal testes and females with enlarged, perforated vaginas reproductively active or sexually receptive, respectively (Taulman et al. 1998). Additionally, we fitted all squirrels with 2 metal ear tags (Number 1; National Band and Tag Company, Newport, Kentucky) prior to release.

We used handheld directional antennas (Telonics, Inc., Mesa, Arizona) to monitor survival and movement status of radiocollared squirrels 2–3 times per week from October 2014 through April 2016, after which field work was terminated. We located individuals using the homing technique (White and Garrott 1990) at random times between 0.5 h after sunset and 0.5 h before sunrise. All individuals were radiotracked to nest tree locations or until animals were visually detected; locations of individuals were recorded as Universal Transverse Mercator coordinates using a handheld global positioning system (Garmin International Inc., Olathe, Kansas) when signal strength and directionality indicated that transmitters were positioned directly above researchers. Consequently, we did not estimate triangulation error or error polygon size for telemetry locations. Most (~80%) radiocollared individuals were not disturbed (e.g., did not flee) during radiotelemetry sessions, as evidenced by animals climbing higher in trees, waiting until

approaching researchers moved further away, or appearing to ignore approaching researchers (Selonen and Hanski 2003). When mortalities occurred, we examined squirrel remains and attempted to determine cause of death (Conner 2001). Based on field evidence collected at transmitter locations (i.e., ground disturbance, blood, canine, or talon marks on transmitters, presence of squirrel remains in owl pellets—Conner 2001; Prince et al. 2014), we categorized mortality events as predation (mammalian or avian), natural causes (other than predation), or capture-related (deaths that occurred within 7 days post-release or otherwise related to capture and handling, e.g., as a consequence of fitting with collars). Our trapping and handling methods followed guidelines of the American Society of Mammalogists for the care and use of animals (Sikes et al. 2016) and were approved by the Institutional Animal Care and Use Committee at Western Illinois University (approval number 15-01).

Habitat measurements.—From October 2014 to April 2016, we sampled overstory characteristics of SFS habitat at diurnal nest tree locations situated within core areas of radiocollared individuals. Within 300-m² (9.8-m radius) circular plots centered on diurnal nest trees, we quantified the abundance of large (≥ 35 -cm diameter-at-breast-height [DBH]—Auchmoody et al. 1993; Steinhoff et al. 2012) living trees and standing dead trees (i.e., snags), as well as snag decay class (0–5—Steinhoff et al. 2012). Overstory trees were recorded by genus (e.g., *Quercus* spp., *Carya* spp.) and considered an index to hard mast production. We considered snags an index of cavity abundance (Fridell and Litvaitis 1991); abundance of cavities in snags is typically greater than in living trees (Healy et al. 1989).

Data analysis.—We limited our home range analyses to animals with ≥ 30 locations per season to control for potential effects of sampling intensity on home range size (Boulanger and White 1990; Seaman and Powell 1996; Linders et al. 2004). We used area-observation curves to determine whether home range size was asymptotic with number of locations for each radiocollared individual. Our analysis revealed no change in interfix distances with increasing numbers of locations (i.e., slope of the regression line was zero). We determined duration of seasons (winter: October through March; summer: April through September—Mumford and Whitaker 1982; Raymond and Layne 1988) from data on reproductive condition and emergence of offspring (Raymond and Layne 1988).

We used the Home Range Tools (HRT) Analysis Extension in ArcView (Rodgers and Carr 1998) to calculate summer and winter adaptive kernel estimates of 95% home ranges and 50% core areas (Kie et al. 1996; Seaman et al. 1999). We generated home range estimates using an ad hoc smoothing parameter by choosing the smallest increment of the reference bandwidth (h_{ref}) that resulted in a contiguous 95% kernel home range (i.e., $h_{ad hoc} = 0.9 \times h_{ref}$, $0.8 \times h_{ref}$, etc.—Kie 2013). Kernel estimators are nonparametric and thus are not dependent on assumptions concerning underlying probability distributions (Seaman et al. 1999). We calculated seasonal home ranges for flying squirrels within a season using the same criteria defined above. We calculated composite (i.e., all seasons combined) home ranges

using a minimum of 30 locations for each radiocollared squirrel. To avoid potential bias in the number of locations collected between individuals and seasons, we attempted to distribute telemetry location efforts evenly between individuals across summer and winter seasons.

We determined seasonal core area overlap among squirrels by recording the number of instances where a squirrel's 50% core area was overlapped by other male or female squirrels (Pasch and Koprowski 2006). Because we limited our relocation of animals to 2–3 times per week, we were unable to calculate daily or cumulative distances traveled by SFS. However, we calculated interfix and cumulative distances between successive locations to serve as indices of daily and total distances traveled (Pasch and Koprowski 2006). We calculated interfix distance between successive squirrel locations using the interfix times and distances option in ArcView (Rodgers and Carr 1998). We calculated cumulative distance between successive locations by summing each successive interfix distance for each individual by season. To minimize potential confounding effects of time between subsequent animal locations and variation in total numbers of locations, we standardized interfix distances across study animals and locations by dividing interfix distance by number of days between subsequent locations. Similarly, we standardized cumulative distance between successive locations for all radiocollared SFS by randomly selecting 30 locations (i.e., minimum number of locations obtained for 98% of study animals) and calculating total distance between locations by season. To achieve temporal independence between successive telemetry locations of an individual SFS, we obtained a single location on each collared squirrel during the entire nightly activity period following the recommendation of Swihart and Slade (1985).

We used known fate models with the logit link function in Program MARK (White and Burnham 1999) to estimate annual survival of SFS, which accommodated staggered entry and exit times of marked squirrels during our analysis interval (Kaplan and Meier 1958; Pollock et al. 1989). We right-censored individuals from analyses if radiocollars were prematurely shed, deaths were capture-related, or when radiocollars stopped transmitting. We assumed collars were shed prematurely when we found the transmitter with no clear sign of mortality. Because survival data were limited to a single year and mortality events limited, covariate modeling was not conducted. Nevertheless, we constructed a survival model in which survival was constant (S_{constant}) between years and across sexes.

Prior to home range and movement analyses, we screened all dependent and independent variables for collinearity using Pearson's correlation coefficient; we excluded collinear ($|r| > 0.5$) variables from analyses (Jacques et al. 2017). Additionally, we used residual plots, quantile plots, and a Shapiro–Wilk test (Shapiro and Wilk 1965) to evaluate assumptions of normality. To assure normality and homoscedasticity (Ramsey and Schafer 2002), we log-transformed our response variables (i.e., home range size, overlap characteristics, number of mast trees, number of snags). We used t -tests to determine differences in snag decay classes (light [0–1], moderate [2–3],

and advanced [4–5]—Steinhoff et al. 2012) between sex, season, and year. We pooled data for modeling if no differences ($P > 0.05$) were detected between snag decay classes. We used multivariate analysis of variance (MANOVA) with all possible 2- and 3-way interactions and main effects to evaluate potential effects of sex, season, and year on differences in space use and habitat parameters (i.e., home range size and overlap, numbers of mast trees and snags). We used analysis of variance (ANOVA) with 2- and 3-way interactions to evaluate the influence of sex, season, and year on differences in core area habitat characteristics and movements by SFS. Additionally, we used 1-way ANOVA to test for intersexual differences in body mass. We generated Type III sums of squares in ANOVA models to account for our use of cross-classification designs with unbalanced data (SAS Institute Inc. 2008). We conducted statistical analyses using Program R (R Core Team 2015).

RESULTS

Home ranges and seasonal movements.—We collected 3,550 locations from 62 flying squirrels from 11 October 2014 to 26 April 2016. Mean body mass at capture was similar ($F_{1,65} = 1.60$, $P = 0.21$) for male ($\bar{x} = 67.25$ g, $SE = 1.19$, $n = 36$) and female ($\bar{x} = 69.45$ g, $SE = 1.28$, $n = 31$) flying squirrels. We calculated seasonal home ranges ($n = 66$; 32 male, 34 female) using at least 30 fixes ($\bar{x} = 48.4$, $SE = 2.3$, range = 89). Our analyses revealed no significant 2- or 3-way interactions between sexes, years, and seasons on 95% or 50% home range size or overlap characteristics (Tables 1 and 2), thus we report results only for main effects. We documented no differences in 95% home range size between seasons ($F_{1,52} = 0.88$, $P = 0.35$), sexes ($F_{1,52} = 0.005$, $P = 0.95$), or years ($F_{1,52} = 0.60$, $P = 0.44$). Similarly, mean 50% home range size did not vary by season ($F_{1,50} = 0.40$, $P = 0.53$), sex ($F_{1,50} = 0.67$, $P = 0.42$), or year ($F_{1,50} = 0.02$, $P = 0.89$). Mean annual composite home range and core area sizes were 10.39 ha ($SE = 1.25$, $n = 56$) and 1.25 ha ($SE = 0.15$, $n = 56$), respectively. Estimated home ranges of females are the largest documented for this species (Table 3).

Average distance between consecutive fixes (i.e., locations) did not vary by sex ($F_{1,53} = 0.09$, $P = 0.76$), season ($F_{1,53} = 0.16$,

Table 1.—Multivariate analysis of variance estimating effects of year, season, and sex on variation in 95% home range size and overlap characteristics of southern flying squirrels (*Glaucomys volans*) in west-central Illinois, October 2014 to May 2016.

	Wilks' λ^a	F -value	Num $d.f.^b$	Den $d.f.^c$	P
Sex	0.961	0.971	2	48	0.386
Season	0.945	1.399	2	48	0.257
Year	0.807	5.745	2	48	0.006
Sex \times season	0.994	0.142	2	48	0.868
Sex \times year	0.964	0.905	2	48	0.411
Season \times year	0.943	1.446	2	48	0.246
Sex \times season \times year	0.965	0.887	2	48	0.423

^aWilks' lambda test statistic.

^bNumerator degrees of freedom.

^cDenominator degrees of freedom.

$P = 0.69$), or year ($F_{1,53} = 0.19, P = 0.67$). Mean distance between successive locations ranged from 39 to 46 m between winter and summer seasons (Table 3). Similarly, cumulative distance between consecutive locations did not vary by sex ($F_{1,53} = 0.45, P = 0.51$), season ($F_{1,53} = 0.22, P = 0.64$), or year ($F_{1,53} = 0.13, P = 0.72$), and ranged from 1,189 to 1,661 m between winter and summer seasons (Table 4). Disturbance events for approximately 20% of radiocollared animals occurred and were characterized by individuals moving away from approaching researchers, though in all cases animals moved ≤ 18 m before climbing higher in trees and waiting until researchers moved further away. In addition, interfix distances and home range size did not differ between disturbed and undisturbed individuals. Thus, our efforts to locate animals likely had minimal effects on telemetry data used in home range analyses. Overlap of 50% core areas for all individuals averaged $17.6\% \pm 0.02 SE$ (95% CI = 0.14–0.21). Percent overlap of core areas varied ($F_{1,50} = 5.12, P = 0.03, R^2 = 0.12$) by sex; core areas of females were overlapped more by those of males ($\bar{x} = 21.9\%$, 95% CI = 0.17–0.27) than by those of other females ($\bar{x} = 13.2\%$, 95% CI = 0.10–0.16). We documented no differences in percent core area overlap between seasons ($F_{1,50} = 0.11, P = 0.73$) or year ($F_{1,50} = 1.06, P = 0.31$).

Habitat measurements.—From October 2014 to April 2016, we evaluated overstory tree characteristics within core areas by

Table 2.—Multivariate analysis of variance estimating effects of year, season, and sex on variation in 50% home range size and overlap characteristics of southern flying squirrels (*Glaucomys volans*) in west-central Illinois, October 2014 to May 2016.

	Wilks' λ^a	F-value	Num d.f. ^b	Den d.f. ^c	P
Sex	0.833	4.828	2	48	0.012
Season	0.944	0.138	2	48	0.871
Year	0.972	0.703	2	48	0.500
Sex \times season	0.969	0.779	2	48	0.465
Sex \times year	0.948	1.309	2	48	0.280
Season \times year	0.991	0.226	2	48	0.799
Sex \times season \times year	0.977	0.576	2	48	0.566

^aWilks' lambda test statistic.

^bNumerator degrees of freedom.

^cDenominator degrees of freedom.

Table 3.—Mean home range size (ha) based on 95% and 50% kernel density estimates and SE by sex (males, females) and season for radiocollared southern flying squirrels (*Glaucomys volans*) in west-central Illinois, October 2014 to May 2016.

Season ^a	Males			Females			Sexes combined		
	n	Home range	SE	n	Home range	SE	n	Home range	SE
95 SHR	8	9.20	2.35	12	8.32	2.01	20	8.76	1.50
95 WHR	24	10.98	2.29	22	11.06	2.50	46	11.02	1.67
95 CHR	29	10.49	1.76	27	10.28	1.87	56	10.39	1.25
50 SHR	8	1.24	0.37	12	1.17	0.30	20	1.21	0.30
50 WHR	24	1.11	0.22	22	1.44	0.33	46	1.32	0.19
50 CHR	29	1.15	0.19	27	1.36	0.25	56	1.25	0.15

^a95 SHR = 95% home range during the summer season (April–September); 95 WHR = 95% home range during the winter season (October–March); 95 CHR = 95% annual composite home range; 50 SHR = 50% core area during the summer season; 50 WHR = 50% core area during the winter season; 50 CHR = 50% annual composite core area.

tracking 55 SFS to 111 diurnal nest tree locations. Our analyses revealed no significant 2- or 3-way interactions between sex, year, and season on overstory mast tree or snag densities within core areas (Table 5), thus we report results only for main effects. Within core areas, mean density of snags per plot was higher ($F_{1,107} = 13.72, P < 0.001, R^2 = 0.17$) during summer ($\bar{x} = 2.90, SE = 0.32, n = 41$) than winter ($\bar{x} = 2.12, SE = 0.23, n = 68$), and did not differ by sex ($F_{1,107} = 0.034, P = 0.85$) or year ($F_{1,107} = 0.82, P = 0.37$). Similarly, mean density of mast trees within core areas was higher ($F_{1,107} = 9.14, P = 0.003, R^2 = 0.18$) in winter ($\bar{x} = 2.84, SE = 0.26, n = 69$) than in summer ($\bar{x} = 1.74, SE = 0.42, n = 42$), but did not differ by sex ($P = 0.15$) or year ($P = 0.07$). Within core areas, mean density of snags in more advanced stages of decay was higher ($F_{1,107} = 4.58, P = 0.03, R^2 = 0.12$) in summer ($\bar{x} = 3.41, SE = 0.47, n = 42$) than in winter ($\bar{x} = 2.73, SE = 0.39, n = 69$), and did not differ by sex ($P = 0.32$) or year ($P = 0.42$).

Flying squirrel survival and cause-specific mortalities.—We captured and radiocollared 67 adult flying squirrels (25 in 2014, 42 in 2015), of which 36 (54%) were males and 31 (46%) were females. We right-censored 29 individuals from our survival analysis due to premature collar loss ($n = 24$) and transmitter failure ($n = 5$) within 8 weeks post-capture. Additionally, 4 deaths of SFS were attributed to capture-related mortalities and thus removed from survival analyses. We documented 8 deaths of squirrels (2 males, 6 females) and these all were attributed to predators. Five of the 8 deaths occurred during winter. Naïve annual survival was 0.77 (26/34 individuals). The estimated annual survival rate using model $S_{\text{[constant]}}$ was 0.71 (95% CI = 0.46–0.82). We documented nonlinear patterns of collar loss by season; most (83%) instances of premature collar loss occurred during winter (Fig. 1).

DISCUSSION

Home ranges and seasonal movements.—We evaluated annual home range use and movements of SFS in a fragmented Midwestern landscape. We predicted that home range size would be larger than in more contiguous habitats and that males and females would show similar seasonal patterns of core area overlap. Both predictions were supported. However, our prediction that home range size and seasonal movements would vary

Table 4.—Mean and total interfix distances between successive locations for male and female southern flying squirrels (*Glaucomys volans*) during summer and winter seasons in west-central Illinois, October 2014 to May 2016.

Sex - season	Average interfix distance (m) ^a			Cumulative interfix distance (m) ^b		
	<i>n</i>	\bar{x}	<i>SE</i>	<i>n</i>	\bar{x}	<i>SE</i>
Male - summer	8	46.48	12.59	8	1,661.21	423.23
Male - winter	21	39.10	6.37	21	1,188.58	239.52
Female - summer	8	43.21	6.12	8	1,481.49	250.55
Female - winter	20	41.93	7.54	20	1,276.24	152.61

^aAverage distances between radiotelemetry fixes.

^bCumulative (total) distances was calculated by summing all interfix distances between radiotelemetry fixes.

Table 5.—Multivariate analysis of variance estimating effects of year, season, and sex on variation in density of overstory mast trees and snags within core areas of southern flying squirrels (*Glaucomys volans*) in west-central Illinois, October 2014 to May 2016.

	Wilks' λ^a	<i>F</i> -value	Num <i>d.f.</i> ^b	Den <i>d.f.</i> ^c	<i>P</i>
Sex	0.978	1.161	2	102	0.317
Season	0.794	13.195	2	102	< 0.001
Year	0.964	1.921	2	102	0.152
Sex × season	0.997	0.157	2	102	0.855
Sex × year	0.960	2.116	2	102	0.126
Season × year	0.983	0.904	2	102	0.408
Sex × season × year	0.966	1.801	2	102	0.170

^aWilks' lambda test statistic.

^bNumerator degrees of freedom.

^cDenominator degrees of freedom.

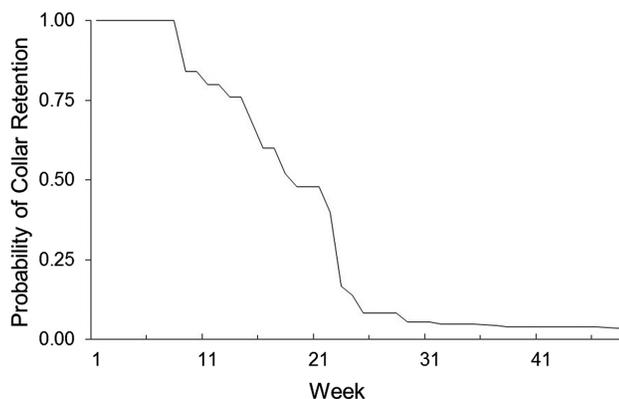


Fig. 1.—Probability of radiocollar retention to 48 weeks post-capture (October through September) for southern flying squirrels (*Glaucomys volans*) in west-central Illinois, 2014–2016. We used the Kaplan–Meier estimator to estimate the probability of radiocollar retention (Kaplan and Meier 1958) across winter (October through March; weeks 1–23) and summer (April through September; weeks 24–48) seasons.

by sex was not supported. Home range sizes in this study were generally larger than those reported for southern and eastern SFS populations, where estimated home ranges varied from 2.3 to 5.3 ha (Gilmore and Gates 1985; Bendel and Gates 1987). However, Fridell and Litvaitis (1991) reported home ranges

in New Hampshire that were 1.5 to 2 times larger than those from the southern United States. Their result may be related to the distribution of mast-producing trees along the northern distributional limit of SFS. Geographic variation in home range size has been attributed to regional differences in abundance of mast-producing trees (Fridell and Litvaitis 1991), which constituted only 15% of the trees in our study area. Home range estimates for SFS in this study are comparable to those provided by Fridell and Litvaitis (1991), and the largest yet reported for female SFS (10.3 ha).

Unlike most previous studies, we observed no differences in seasonal home range size or movements between the sexes, despite intersexual variation in patterns of overlap within core areas. Our inability to detect seasonal differences in percent core area overlap may have been a consequence of reduced statistical power due to limited numbers of male squirrels available during the summer season. Nevertheless, home ranges of females were overlapped more by those of males ($24.1\% \pm 0.05$) than those of other females ($14.1\% \pm 0.05$) during summer and similarly by both sexes during winter. However, home ranges of males were overlapped more by those of other males during the winter ($21.1\% \pm 0.04$) than summer ($12.5\% \pm 0.06$) and concomitant seasonal movements of males were not greater than those of females as predicted. Numerous studies across the ranges of northern and SFS have established relationships between density and optimal habitat features, including large-diameter trees (Taulman et al. 1998; Smith et al. 2004; Gomez et al. 2005), large snags (Taulman et al. 1998; Carey et al. 1999; Smith et al. 2004; Holloway and Malcolm 2006), and measures of food abundance (Waters and Zabel 1995; Taulman et al. 1998; Gomez et al. 2005; Lehmkühl et al. 2006). Possibly, low habitat productivity and animal density affect home range dynamics across Midwestern landscapes in opposing and complex ways. Increased overlap of core areas of females by those of males during the summer season may reflect limited spatial distribution of females and a propensity for males to maximize mating opportunities (Fridell and Litvaitis 1991). In contrast, low spatial overlap by female–female neighbors may reflect territorial behavior and resource defense during parturition and rearing of young during summer (Madden 1974).

The distribution of food resources and potential den sites had apparent effects on habitat use by SFS, most notably the disproportionate use of sites with a greater abundance of snag trees in advanced stages of decay during summer and increasing food resources during the winter. Several factors may explain these differences. First, variation in sex-specific spatial activity patterns (movements, core area overlap) have been associated with annual population fluctuations and low population densities (Fridell and Litvaitis 1991; Layne and Raymond 1994). Based on animal capture data, our naïve density of SFS was 0.30 animals/ha. This density estimate was on the lower end of observed densities (0.15–7.4 animals/ha) for SFS (Sonenshine et al. 1979; Gilmore and Gates 1985; Taulman et al. 1998), within the range of observed densities for northern flying squirrels, *G. sabrinus* (0.12–3.3 animals/ha—Rosenberg and Anthony 1992; Waters and Zabel 1995; Carey et al. 1997), and higher

than density estimates for *Pteromys volans* (0.04–0.08 animals/ha—Hanski et al. 2000). In addition, hard mast is a primary food source for SFS throughout the year (Harlow and Doyle 1990) and an adequate supply of nuts and acorns is essential for overwinter survival of squirrels (Van Voorhees 1976; Weigl 1978). Overstory oak (81 trees/ha) and hickory (61 trees/ha) tree densities within core areas of our study area were comparable to those considered relatively low-quality habitat characteristics along the northern range limit of SFS (Fowells 1965; Fridell and Litvaitis 1991). Moreover, snags provide secure seasonal resting places during unfavorable environmental conditions and are important for seasonal thermoregulation (Stapp et al. 1991). Though speculative, SFS across our study site may have selected areas with a greater abundance of snags during summer for opposing reasons. Cavities used as feeding stations are seldom converted to maternity dens (Gilmore and Gates 1985; Sawyer and Rose 1985). Additionally, females may have selected snags in more advanced stages of decay to minimize exposure to high ambient temperatures while rearing young or to minimize contact with conspecifics or predators (e.g., black rat snakes, *Pantherophis obsoletus*) during the summer season (Bendel and Gates 1987; Fridell and Litvaitis 1991). Low squirrel densities across our study site also may have reduced competition for den sites or triggered a greater effort by males to locate potential mates, thereby explaining the use of areas with high snag abundance during summer.

Our results were not consistent with the tendency for females to occupy areas with concentrated food resources to meet the energetic demands of lactation during summer. Rather, males and females appeared to make greater use of these areas during winter, which may be a behavioral adaptation characteristic of low-density squirrel populations occurring in fragmented landscapes. Increased use of areas characterized by higher relative abundance of food in winter likely minimizes search and travel time for mast, especially since SFS sometimes nest in groups of conspecifics at this time, and predation risk may be especially important for isolated populations of SFS exhibiting characteristics of closed populations. As such, availability of mast-producing trees in close proximity to nesting cover (e.g., snags, natural cavities) is an important factor influencing reproductive output by SFS, home range use, and patterns of core area overlap (Weigl 1978; Sonenshine and Levy 1981; Fridell and Litvaitis 1991) across fragmented forested landscapes. SFS may compensate for reduced availability of overstory mast-producing trees that characterize unproductive habitats and low-density populations by exhibiting similar intersexual movement patterns and use of available habitat throughout the year (Harestad and Bunnell 1979).

Contrary to previous studies, our results provide weak support for communal nesting behavior during winter months as reflected by limited (7%) co-occupancy of diurnal nest trees ($n = 109$) by radiocollared animals. During our study, average winter temperatures during 2014 and 2015 were -0.9°C and 2.7°C , respectively (weather station: Carthage, Illinois—State Climatologist Office for Illinois 2016), and were within the range of ambient temperatures triggering communal nesting

behavior in SFS populations (Stapp et al. 1991; Stapp 1992). Thus, winter temperatures appeared weakly associated with communal nesting patterns and observed space use patterns during our study. However, limited communal nesting may have been a consequence of resource availability and low animal density across fragmented landscapes. Snag density (76.5–82.6/ha) across our study site was consistent with low-productivity habitats along the northern range limit of flying squirrels (Fridell and Litvaitis 1991), yet 71% ($n = 5$) of shared (and concurrently occupied) diurnal nest locations contained standing dead trees. Nest availability is one of the structural features that may limit reproductive output of flying squirrels in managed landscapes (Taulman et al. 1998; Selonen et al. 2001; Holloway and Malcolm 2007). Consequently, reduced abundance of nesting cavities across low-productivity and fragmented landscapes may affect communal nesting activities during winter months, and have longer-term implications for conservation of flying squirrels across its geographic range.

Survival.—Our estimated overall survival of SFS (0.71 using model S_{constant}) was higher than previous estimates of survival (0.12–0.64). This may reflect limited ($n \leq 17$) sample sizes or time intervals (single season) reported in previous studies (Taulman et al. 1998; Taulman and Smith 2004). Potential hybridization induced by climate change and associated range expansion may affect flying squirrels in the future (Bowman et al. 2005; Garroway et al. 2010); thus, estimates of annual survival of SFS in different landscapes and climates will be valuable for their conservation. We documented substantial rates (36%) of premature collar loss, the majority ($n = 15$) of which occurred between February and April each year. Researchers should therefore capture and radiocollar approximately 33% more animals than target sample sizes to ensure a sufficient number of individuals remain collared to achieve study objectives. Alternatively, periodic recapture of study animals during winter (October, February) and summer (June) to refit radiocollars in response to seasonal mass changes (Stapp 1992) may increase the likelihood of collar retention over a 12-month period.

Conservation implications.—Our results underscore the concurrent effects of habitat productivity and animal density on seasonal home range dynamics and space use patterns by flying squirrels in fragmented landscapes (Hanski et al. 2000; Selonen et al. 2001; Pyare et al. 2010). Because several aspects of SFS ecology and life history strategies are associated directly with forest structure (Bendel and Gates 1987) and its potential vulnerability to isolation as a consequence of habitat fragmentation (Pyare et al. 2010), SFS is an ideal species for evaluating population-level responses across Midwestern landscapes. That winter communal nesting appears to be influenced by availability of cavity trees underscores the importance of standing snags in contributing essential habitat to flying squirrel populations in fragmented forests. Similarly, maintaining large overstory mast trees is fundamental to sustaining productivity of females in closed populations and fragmented forest patches because of the dependence on hard mast for parturition, rearing young, and overwinter survival. At present, direct effects of habitat

fragmentation on seasonal survival of flying squirrels, particularly due to predation, are unknown. Consequently, future research to identify the threshold whereby habitat isolation and area loss adversely affect flying squirrel home range use and annual survival across fragmented forested landscapes is warranted. Evaluation of home range and core area patterns in relation to the interspersion of mast-producing trees and snags using compositional analyses may provide greater insight into SFS home range dynamics across fragmented Midwestern landscapes.

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