Spatial behavior of northern flying squirrels in the same social network

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Abstract

North American flying squirrels (*Glaucomys* spp.) are social species that communally den and exhibit home range overlap. However, observations on home range overlap tend to come from live-trapped individuals and it is unknown whether overlap occurs among individuals belonging to the same social network. Since flying squirrels communally den with familiar individuals, their use of artificial nest boxes allows for the radio-collaring and tracking of squirrels within the same social network. We captured and radio-collared northern flying squirrels (*G. sabrinus* Shaw) found communally denning in nest boxes in the Appalachian Mountains in the eastern United States. We tracked squirrels captured from the same nest box (i.e., nest box groups) to determine home range overlap and subsequent den sharing between familiar individuals within those nest box groups. We found that amount of home range overlap did not differ between male–male, male–female, and female–female dyads, indicating that non-reproductive females and scrotal males are not territorial at the 95% or 50% home range level. Regardless of sex, all dyads had a significantly higher probability of home range overlap (PHR) at the 95% than the 50% home range level (i.e., overlap between squirrels decreases in core areas of their home range). We also found flying squirrels subsequently denned with familiar individuals during 20.9% of occasions post-collaring. Our study provides important information for understanding space use within flying squirrel social networks. Further work should be conducted to determine space use between familiar individuals including seasonal shifts in space use, degree of individual relatedness, and potential territoriality in females denning with young up to and following juvenile dispersal.

KEYWORDS

communal denning, *Glaucomys sabrinus*, home range overlap, nest boxes, social species

1 | INTRODUCTION

In social species, intraspecific spatial dynamics can be determined by interactions between conspecifics, which may influence survival, mating success, and resource competition. Intraspecific spatial behavior can be contingent on the social organization and social complexity of a species, which may differ depending on factors such as life history, territoriality, mating system, seasonality, and individual characteristics (e.g., age, sex; Blumstein & Armitage, 1998; Cudworth

& Koprowski, 2010; Fridell & Litvaitis, 1991; Mazzamuto et al., 2020). For nocturnal, arboreal species, understanding space use between individuals within the same social network can be problematic since social interactions may be difficult to observe. However, communal denning is known to play a role in social organization for certain species, wherein communal denning sites can act as potential contact points for conspecifics and may increase cohesion between individuals within a social network (i.e., the relationships and social interactions among all conspecifics belonging to a group; Gibbons &

Lindenmayer, 2002; Silvis et al., 2014). Within social, non-territorial species, individuals sharing den sites may be more likely to exhibit home range overlap (Ebensperger et al., 2006; Lacey et al., 2019; Silvis et al., 2014). Since communal denning may increase familiarity among individuals occupying shared areas and reflect social connections (e.g., Selonen et al., 2014; Thorington & Weigl, 2011; Winterrowd et al., 2005), individuals occupying the same den may be considered as belonging to the same social network.

Flying squirrels (*Glaucomys spp.*) are small, nocturnal, social mammals native to North American forests (Dolan & Carter, 1977; Wells-Gosling & Heaney, 1984). They are known to communally den throughout the year (Layne & Raymond, 1994; Reynolds et al., 2009; Stihler et al., 1987) and exhibit overlap in home ranges (Bendel & Gates, 1987; Holloway & Malcolm, 2007b). Thorington and Weigl (2011) hypothesized that squirrels with overlapping home ranges may be more likely to share den sites. Flying squirrels that communally den with younger individuals (e.g., nestlings, young of the year) are typically related to most or all of their den mates, whereas adults denning together may or may not be related (Garroway et al., 2013; Murrant et al., 2014; Thorington et al., 2010; Winterrowd et al., 2005). However, the degree of relatedness between familiar individuals that share dens may vary seasonally due to thermoregulation needs (Carey et al., 1997; Muul, 1968; Thorington et al., 2010). Other observed social interactions in flying squirrels include shared foraging forays (Layne & Raymond, 1994; Murrant et al., 2014), fights over food (Wells-Gosling, 1985), mating chases (Muul, 1969), and traveling together through shared habitat (Weigl et al., 1992).

Although home range overlap and den sharing have been reported in wild flying squirrels (Bendel & Gates, 1987; Diggins et al., 2017; Holloway & Malcolm, 2007b; Smith et al., 2011), it is unknown whether most individuals with overlapping home ranges in these studies were a part of the same social network since interactions between individuals are difficult and rare to observe. Home range overlap data tend to come from radio-collared flying squirrels captured via live-trapping, where observations of den sharing between individuals can be infrequent (Bendel & Gates, 1987; Holloway & Malcolm, 2007a, 2007b; but see Carey et al., 1997). And since observations of other types of interactions (e.g., flying squirrels foraging or traveling together) are even rarer (Murrant et al., 2014; Weigl et al., 1992), communal denning is the best indicator that one flying squirrel has a social connection (i.e., is familiar with) with another flying squirrel in the wild. Therefore, determining social connections between individuals and understanding social dynamics in wild populations are inherently problematic for flying squirrels. However, tracking home range overlap between individuals that exhibit den sharing can determine space use between flying squirrels belonging to the same social network.

Northern flying squirrels (*G. sabrinus*) are listed as state and federally endangered in the central and southern Appalachians (U.S. Fish and Wildlife Service (USFWS), 1985) and capture rates of northern flying squirrels using live-trapping tend to be low (Diggins et al., 2017). However, long-term nest box programs have

been established in several eastern states to monitor listed subspecies of northern flying squirrels (Mahan et al., 2010; Reynolds et al., 1999; Stihler et al., 1995; Weigl et al., 1992). Within this region, northern flying squirrels (*G. sabrinus* Shaw) are known to den communally wherein two to ten individuals may share a nest box (Reynolds et al., 1999; Weigl, 1974; Weigl et al., 1992; Craig Stihler, West Virginia Department of Natural Resources, pers. comm.; Christine Kelly, North Carolina Wildlife Resources Commission, pers. comm.). These long-term nest box monitoring programs thereby allow for the capture of familiar individuals within the same social network when they communally den in a nest box. Our objective was to examine home range overlap between familiar individuals of northern flying squirrel captured in the same nest box. We wanted to determine whether northern flying squirrels exhibit individual territoriality or the lack thereof between familiar individuals within the same social network. We also tracked subsequent den sharing in familiar individuals and compared den sharing rates in this study to other studies.

2 | METHODS

Our study took place in high elevation red spruce (*Picea rubens* Sarg.)—northern hardwood forests of the Allegheny and Blue Ridge Mountains sub-physiographic provinces of the central and southern Appalachian Mountains in the eastern United States. Within the Allegheny Mountains, our study sites were located on Middle Mountain in the Monongahela National Forest and Kumbrabow State Forest in Randolph County, West Virginia. Our Blue Ridge Mountain sites in North Carolina were located in the Great Balsam Mountains and Roan Mountain Highlands of Pisgah National Forest in Haywood County and Mitchell County, respectively. We opportunistically conducted nest box surveys at Kumbrabow State Forest in spring and fall 2013, Middle Mountain in spring 2014, Great Balsam Mountains in winter 2012 and winter 2014, and Roan Mountain Highlands in spring 2014.

We checked long-term nest box lines, originally established by the West Virginia Division of Natural Resources (WVDNR) in 1985 and by the North Carolina Wildlife Resources Commission (NCWRC) in 1996, used to monitor population status and distribution of northern flying squirrels (Ford et al., 2015; Ford et al., 2010). Constructed of plywood, WVDNR nest boxes were 33 cm × 12.7 cm × 12.7 cm with a 4.4–5.7 cm circular entrance (Stihler et al., 1987), whereas NCWRC nest boxes were 30 cm × 18 cm × 15 cm with an 5 cm × 5 cm square entrance (Kelly et al., 2013). Both WVDNR and NCWRC nest box transects contained 10–20 nest boxes located 25–100 m apart (Ford et al., 2004, 2015). Nest boxes were placed on the boles of trees located approximately 3–4.5 m off the ground. We accessed nest boxes with a 3-m tall aluminum tree ladder (Model D1510-1; Werner Ladder Company¹). We removed all squirrels from the nest box and placed

¹Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

each squirrel into individual bags. We recorded weight, sex, age, and hind foot length of all captures. We determined age (i.e., juvenile or adult) by weight and pelage characteristics (Villa et al., 1999). We ear-tagged each individual with a uniquely numbered ear tag (Monel No. 1005-1; National Band and Tag Co.). We radio-collared individuals weighing >80 g with 2.1 BD-2C or 3.4–4.0 g PD-2C radio transmitters (Holohil Systems Ltd.). We radio-collared all individuals from each nest box, with the exception of one female juvenile due to insufficient body size. After tagging and radio-collaring, we placed all individuals back into the nest box from which they were extracted. We considered all squirrels captured in the same nest box during radio-collaring as individuals belonging to the same social network and hereafter refer to them as “nest box groups.” However, nest box groups do not include all members of a social network as indicated by recaptured squirrels denning with uncaptured individuals during several decades of long-term nest box monitoring by WVDNR and NCWRC. Due to the constraints of the study, we were unable to obtain genetic information to determine the relatedness of nest box groups. The Virginia Tech Institutional Animal Care and Use Committee approved all capture and tagging protocols (#11-120-FIW and #14-120-FIW).

After a 24-hr adjustment period, we tracked squirrels with Wildlife Material TR4-2000S receivers and three-element folding yagi antennas (Wildlife Materials) to determine the location of diurnal dens and the location of individuals during nighttime foraging activity. We tracked all individuals from the same nest box group during the same night tracking session. To obtain home ranges, we typically tracked collared squirrels one to three times every 1–2 weeks until the squirrel dropped their collar, the radio transmitter signal was lost, or the animal was predated. Before each nighttime tracking session, we tracked all individuals to their diurnal den sites. We tracked squirrels starting at civil twilight and continued until individuals ceased moving, usually occurring two to three hrs after the beginning of the tracking session (Ford et al., 2014). We used close-range biangulation to obtain telemetry fixes by manning two fixed stations and simultaneously locating the squirrel to minimize temporal error (Schmutz & White, 1990) and to avoid behavior alteration that occurs when tracking a squirrel on foot (Witt, 1992). We located telemetry stations >50 m apart to reduce bearings taken at <90° (White, 1985). This method was successfully used for arboreal squirrels with small home ranges (<20 ha; Koprowski et al., 2008; Shanley et al., 2013), as an individual can move frequently in a short amount of time within their home range (Diggins & Ford, 2017; Weigl et al., 1992). We obtained bearings on individual flying squirrels every 10–20 min, allowing us to determine frequent movements related to nocturnal activity for all radio-collared individuals from same nest box group within the same night and over the multi-night effort. We tested personnel for telemetry bias in the field using known radio-collar locations (White & Garrott, 1990). Our telemetry error ranged from 1–3°.

Using UTM coordinates obtained during tracking sessions, we used biangulation bearings and locations of tracking stations for

each individual squirrel and input them into LOCATE II (Pacer Co.) to obtain location coordinates. We calculated kernel density home ranges for the 50% (core area) and 95% (high-use area) probability contours. After calculating home ranges, we estimated the percentage of overlap (% overlap) and probability of overlap (PHR; Fieberg & Kochanny, 2005) between male–male, female–male, and female–female dyads within each nest box group. PHR calculates the probability of one animal being located within another animal's home range (Fieberg & Kochanny, 2005). PHR ranges from 0 to 1, where 0 indicates no probability of home range overlap and 1 indicates a 100% probability of home range overlap. Home range estimates, % overlap, and PHR were calculated using package adehabitatHR (Calenge, 2020) in Program R version 3.1.2 (R Core Development Team). We compared the PHR for squirrel dyads using a Kruskal–Wallis test and compared PHR for all squirrels between the 95% and 50% levels using a Wilcoxon rank-sum test.

3 | RESULTS

During our nest box surveys, we found seven nest box groups ranging from two to five flying squirrels per group ($N = 26$ squirrels; 9 females, 16 males). We only captured individuals from one nest box per site during each nest box survey, with the exception of two nest boxes with flying squirrels captured during the same nest box line check on Middle Mountain. However, the two nest boxes at Middle Mountain were located 0.5 km apart and no individuals from one nest box exhibited home range overlap or den sharing with individuals from the other nest box over the course of tracking. The sex composition of the majority of nest box groups was mixed M-F (four nest box groups, three to five individuals per group), whereas two nest box groups were all males (two to three individuals per group) and one was all females (three individuals). Mixed nest box groups had scrotal males and non-reproductive females. A single mixed nest box group had one juvenile male with one adult female and one adult male. All male nest box groups were composed of only adults, whereas the all-female nest box group had two adults and one juvenile.

We collected 1,347 telemetry points on 25 individuals (average 61.4 ± 3.2 SE, range 38–86). We tracked flying squirrels from 5 to 15 weeks. Female flying squirrels had an average home range of $8.09 \text{ ha} \pm 1.60$ SE (range 3.11–17.87) at 95% and 1.6 ± 0.3 (range 0.5–3.2) at 50% home range level, respectively. Males had an average of $12.2 \text{ ha} \pm 2.3$ SE (range 2.1–32.4) at 95% and 2.31 ± 0.37 (range 0.4–5.5), respectively. There was no difference in home range size between the sexes at the 95% ($W = 51$, $p = .25$) or 50% levels ($W = 56$, $p = .39$). For dyads, % overlap and PHR are reported in Table 1. Examples of home range overlap within a nest box group are shown in Figure 1. There was not any significant difference in percentage of home range overlap between any dyads at the 95% ($\chi^2 = 69.22$, $df = 70$, $p = .504$) or 50% level ($\chi^2 = 60.65$, $df = 62$, $p = .525$). The average PHR for all flying squirrels was 0.67 ± 0.03 (range: 0.01–0.95) at 95% and 0.29 ± 0.07 (0.11–0.43) at 50% level.

TABLE 1 Home range overlap for northern flying squirrel (*Glaucomys sabrinus* Shaw) dyads obtained from nest boxes in the central and southern Appalachian Mountains in 2012–2014

Dyad	N	% overlap 95	% overlap 50	PHR 95	PHR 50
Female–female	5	65.4 ± 9.5	52.9 ± 9.8	0.76 ± 0.06	0.28 ± 0.05
Male–female	17	53.8 ± 4.6	35.3 ± 5.4	0.64 ± 0.04	0.18 ± 0.03
Male–male	15	58.2 ± 5.1	34.6 ± 6.1	0.66 ± 0.05	0.41 ± 0.06

Note: Reported below are the number dyads (N), as well as the % of overlap and probability home range overlap (PHR) at the 95% and 50% home range levels.

For all dyads, the PHR was significantly different between the 95% and 50% level home range ($W = 875.5$, $p = .000$).

Additionally, we tracked flying squirrels to 65 diurnal den sites on 134 occasions. We tracked radio-collared squirrels on 79.1% of occasions wherein they were not denning with another radio-collared squirrel, although we were unable to definitively determine if they were denning alone or with uncollared individuals. We found pairs of familiar squirrels denning in the same den on 28 occasions post-radio-collaring, including 2 female–female, 2 male–female, and 5 male–male dyads. We never observed more than two flying squirrels denning together post-radio collaring. Of the nine dyads that communally denned post-radio-collaring, five were only observed denning together once and two were found co-denning on 2–3 occasions. For two dyads of flying squirrels (one male–female, one male–male), we found them denning together on eight and ten occasions, respectively, at two different den sites each. While the majority of flying squirrels (81.3%) found denning with familiar individuals post-collaring only denned with one other individual, we found three males denning with two different individuals from their respective nest box groups. Of those three males, only one denned with both male and female familiar individuals, whereas the other two other males only denned with other males.

4 | DISCUSSION

During our study, we found that the home range overlap for northern flying squirrel dyads was similar between males and non-reproductive females at the overall home range and core home range scale, indicating neither sex is territorial. Northern flying squirrels were less likely to have overlapping core home ranges within nest box groups, although some overlap did occur for all dyads. Since our dataset only allowed for us to determine whether overlap was occurring, not the mechanisms behind the overlap decrease, we cannot definitively state why this decrease occurred. We conjecture that this decrease is most likely not due to some level of territoriality at the core home range level. Since core home ranges occur over a very small area of less than a few hectares, the probability of overlap with other individuals may be reduced. Additionally, although nest box groups represented a subsample of familiar individuals from the same social network, we did not capture all individuals within a social network at each study site. Therefore, is it possible an individual's core home range could be completely overlapped by multiple individuals within their social network, including the individuals they were denning

with when collared for this study. We suggest further work be conducted to determine mechanisms for differences in spatial overlap at the 95% and 50% home range levels.

Similar to our study, Holloway and Malcolm (2007b) found no difference in home range overlap for neighboring radio-collared male or female northern flying squirrels obtained from live traps in Canada. Their study also found greater home range overlap at the 95% compared to the 50% home range level. However, we observed higher average overlap at the 95% home range level for familiar squirrel dyads (53.8%–65.4%) than they did for neighboring live-trapped squirrel dyads (16.5%–27.9%; Holloway & Malcolm, 2007b). Although male–male and male–female 50% home range overlap was similar between our two studies, female–female dyads had much lower core home range overlap (11.4%; Holloway & Malcolm, 2007b) than our study (52.9%). However, Holloway and Malcolm (2007a, 2007b) most likely tracked several lactating females during their study, although they do not specify whether lactating females were included in home range overlap estimates. If they did tracking lactating females, it could explain the female–female overlap difference between our two studies. Regardless, while social familiarity may influence spatial organization in northern flying squirrels, especially for females, other factors, such as reproductive condition and presence of young, may influence the amount and probability of home range overlap in females even with familiar individual within their social network.

Since we did not capture reproductive females during this study, we could not determine how reproductive condition or the presence of neonates might influence spatial dynamics between familiar individuals. Several studies on southern flying squirrels (*G. volans* L.) noted that female flying squirrels had little or no home range overlap with other females (Bendel & Gates, 1987; Jacques et al., 2017) and females were observed to defend natal den trees, especially from other females (Madden, 1974; Muul, 1968; Sollberger, 1943). In pregnant or lactating Humboldt's flying squirrels (*G. oregonensis* Bachman), females maintained activity close to their natal den tree when young were present and home range overlap with other females only increased after young were weaned (Smith et al., 2011). They concluded female Humboldt's flying squirrels with neonates shared foraging areas, but were territorial around natal den trees. Although no study has determined nest guarding in female northern flying squirrels, it is likely that this species also exhibits territoriality around their natal den tree and more work is required to determine changes in spatial dynamics during

pregnancy and lactation to understand factors influencing those dynamics within a social network.

Observations of den sharing from telemetry studies are typically rare for flying squirrels (e.g., Diggins et al., 2017; Holloway & Malcolm, 2007a; Smith et al., 2011), although that may be contingent on the number of individuals radio-collared at a site (see Carey

et al., 1997; Table 2). In Pacific Northwest, 179 squirrels were radio-collared during a study, including 140 at one site, and only 34% of individuals were never found to den with other radio-collared squirrels (Carey et al., 1997). In western North Carolina, 12.2% of den sites were communally shared by radio-collared northern flying squirrels (Diggins et al., 2017); however, communal denning was

FIGURE 1 Examples of kernel density home range estimate overlap of communally denning, radio-collared northern flying squirrels (*Glaucomys sabrinus* Shaw) in the central and southern Appalachian Mountains, USA. A1 and A2 represent one mixed sex nest box group of 4 individuals from Roan Mountain Highlands, Pisgah National Forest, Mitchell County, North Carolina, at the 95% and 50% home range level, respectively. B1 and B2 represent one mixed sex nest box group of 4 individual from Middle Mountain Cabins, Monongahela National Forest, Randolph County, West Virginia, at the 95% and 50% home range level, respectively. The black square in each figure represents the nest box the squirrels were captured in at the beginning of the study. Each patterned line represents an individual squirrel at the 50% and 95% level for the North Carolina and West Virginia denning associations. The same line patterns were used for the North Carolina (A1–A2) and West Virginia (B1–B2) squirrels, but represent different individuals between these two sites

TABLE 2 Observed den sharing of radio-collared North American flying squirrels (*Glaucomys* spp.) from telemetry studies in the United States and Canada

Species	# individuals tracked	Capture method	Den sharing	Relationship between familiar individuals	Source
<i>Glaucomys oregonensis</i>	22	Live traps	1.1% den sites	Unknown	Smith et al., 2011
<i>G. oregonensis/sabrinus</i> ^a	179	Live traps	32.1% of observations	Unknown	Carey et al., 1997
<i>G. sabrinus</i>	36	Live traps	7.6% den sites	Unknown	Bakker & Hastings, 2002
	18	Live traps	0% of observations	.	Holloway & Malcolm, 2007a
	59	Live traps	Several occasions (# unspecified)	Unknown	Hough & Dieter, 2009
	6	Live traps	Several occasions (# unspecified)	Unknown	Weigl, 1974
	25	Nest boxes	20.9% of observations (26.2% den sites)	Unknown	This study
<i>G. volans</i>	12	Live traps	10.8% den sites	Most unknown w/possible mother-offspring	Bendel & Gates, 1987
	24	Live traps	1.4% of observations (1.3% of den sites)	Unknown	Holloway & Malcolm, 2007a

^aThe study by Carey et al. (1997) occurred prior to classification of *G. oregonensis* as a distinct species from *G. sabrinus*. Part of the study occurs within the range of *G. oregonensis*, although the more significant part occurred in a region where *G. oregonensis* and *G. sabrinus* are sympatric, making it difficult to ascertain den sharing of the two species from observations in this study.

only observed in squirrels obtained from nest boxes, but not live-trapped individuals. Northern flying squirrels tend to den switch and typically have an average of 3–5 den sites at any given time (Diggins et al., 2017; Hackett & Pagels, 2003; Holloway & Malcolm, 2007a). It is unknown how often northern flying squirrels den alone versus with conspecifics, although there certainly are records of solo denning squirrels via nest boxes (Maser et al., 1981; Reynolds et al., 1999). We found individuals from the same nest box group shared dens during 20.9% of occasions. This number is much larger than studies with comparable numbers of radio-collared individuals (Table 2), although it is similar to the Pacific Northwest study (Carey et al., 1997).

Demographic, seasonal, and behavioral factors may influence home range overlap and communal denning patterns in northern flying squirrels. The social dynamics of a flying squirrel network may change regularly, as social networks of short-lived social species tend to be instable via natality, migration, or mortality events (Ebensperger et al., 2009). Seasonal shifts in behavior occur throughout the year and are associated with breeding, juvenile dispersal, thermoregulatory needs, and changes in food resources. For example, although northern flying squirrels communally den year-round, there may be a smaller number of individuals sharing communal denning sites during the summer versus the winter (Reynolds et al., 2009; Selonen et al., 2014), although this has not been observed in northern flying squirrels (Maser et al., 1981; Reynolds et al., 1999). Home range size may also vary between seasons for northern flying

squirrels wherein larger home ranges occur in winter due to reduced availability of food resources (Ford et al., 2007; Hughes, 2006; Weigl et al., 1992). Home range size may be also influenced by social interactions, such as increased movement by males during the mating season (Weigl et al., 1992). During our study, we only tracked individuals for several weeks, which did not allow for long-term shifts in home ranges due to seasonal events (e.g., mating season or juvenile dispersal). While we tracked at least one nest box group during each of the four seasons, our sample sizes were too small to determine differences in home range overlap between seasons.

Due to the opportunistic nature of our study, it was limited, but nonetheless showed familiar individuals of northern flying squirrels from the same nest box group exhibit shared space use and denned together at higher rates than live-trapped squirrels from comparable studies. Further research is needed to determine spatial dynamics of social networks of flying squirrels and what mechanisms influence home range overlap and denning sharing. For example, we observed post-capture den sharing, but did not track groups daily and only captured a handful of individuals at each site, only allowing us to determine the minimum amount of den sharing events. However, it is possible that squirrels frequently denned with uncollared individuals and the den sharing is even more common than our observations suggest. The capture of multiple nest box groups of squirrels in the same area may further highlight spatial dynamics, especially over longer time periods which include biologically important seasonal events, such as mating, juvenile dispersal, seasonal den sharing

dynamics including winter aggregations, and space use shifts determined by seasonal resource availability. Additionally, genetic relations of northern flying squirrels may influence social dynamics and social cohesion, and determine the frequency, seasonality, and composition of individuals sharing communal denning in this species. Although we did not assess the genetic relationships between individuals in the nest box groups in this study, assessing genetic relatedness in future studies may help discern what mechanisms influence social contacts and interactions, especially since flying squirrels are known to communally den with both related and non-related individuals (Garroway et al., 2013; Murrant et al., 2014; Thorington et al., 2010; Winterrowd et al., 2005).

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ETHICAL APPROVAL

The methodology for trapping, radio-collaring, and tracking endangered subspecies of northern flying squirrels during this study followed U.S. Fish and Wildlife protocol outlined in permit #TE34778A-O and the Guidelines of the American Society of Mammalogists for the Use of Wild Mammals in Research and Education (Sikes et al., 2016). Our methodology was approved by the Virginia Tech Institutional Animal Care and Use Committee (permit #11-120-FIW and #14-120-FIW).

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REFERENCES

- Bakker, V. J., & Hastings, K. (2002). Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. *Canadian Journal of Zoology*, 80, 1623–1633.
- Bendel, P. R., & Gates, J. E. (1987). Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). *Journal of Mammalogy*, 68, 243–255. <https://doi.org/10.2307/1381463>
- Blumstein, D. T., & Armitage, K. B. (1998). Life history consequences of social complexity: A comparative study of ground-dwelling sciurids. *Behavioral Ecology*, 9, 8–19. <https://doi.org/10.1093/beheco/9.1.8>
- Calenge, C. (2020). Package 'adehabitatHR'. Retrieved from <https://cran.r-project.org/web/packages/adehabitatHR/adehabitatHR.pdf>
- Carey, A. B., Wilson, T. M., Maguire, C. C., & Biswell, B. L. (1997). Dens of northern flying squirrels in the Pacific Northwest. *Journal of Wildlife Management*, 61, 684–699. <https://doi.org/10.2307/3802176>
- Cudworth, N. L., & Koprowski, J. L. (2010). Influences of mating strategy on space use of Arizona gray squirrels. *Journal of Mammalogy*, 91, 1235–1241. <https://doi.org/10.1644/09-MAMM-A-426.1>
- Diggins, C. A., & Ford, W. M. (2017). Microhabitat selection of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus* Miller) in the Central Appalachians. *Northeastern Naturalist*, 24, 173–190.
- Diggins, C. A., Silvis, A., Kelly, C. A., & Ford, W. M. (2017). Home range, den selection, and habitat use of Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*). *Wildlife Research*, 44, 427–437. <https://doi.org/10.1071/WR16203>
- Dolan, P. G., & Carter, D. C. (1977). *Glaucomys volans*. *Mammalian Species*, 78, 1–6. <https://doi.org/10.2307/3504026>
- Ebersperger, L. A., Chesh, A. S., Castro, R. A., Tolhuysen, L. O., Quirici, V., Burger, J. R., & Hayes, L. D. (2009). Instability rules social groups in the communal breeder rodent *Octodon degus*. *Ethology*, 115, 540–554.
- Ebersperger, L. A., Taraborelli, P., Giannoni, S. M., Hurtado, M. J., León, C., & Bozinovic, F. (2006). Nest and space use in a highland population of the Southern Mountain cavy (*Microcavia australis*). *Journal of Mammalogy*, 87, 834–840. <https://doi.org/10.1644/05-MAMM-A-407R2.1>
- Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management*, 69, 1346–1359.
- Ford, W. M., Evans, A. M., Odom, R. H., Rodrigue, J. L., Kelly, C. A., Abaid, N., Diggins, C. A., & Newcomb, D. (2015). Predictive habitat models derived from nest-box occupancy for the endangered Carolina northern flying squirrel in the southern Appalachians. *Endangered Species Research*, 27, 131–140. <https://doi.org/10.3354/esr00662>
- Ford, W. M., Kelly, C. A., Rodrigue, J. L., Odom, R. H., Newcomb, D., Gilley, L. M., & Diggins, C. A. (2014). Late winter and early spring home range and habitat use of the endangered Carolina northern flying squirrel in western North Carolina. *Endangered Species Research*, 23, 73–82. <https://doi.org/10.3354/esr00561>
- Ford, W. M., Mertz, K. N., Menzel, J. M., & Sturm, K. K. (2007). *Winter home range and habitat use of the Virginia Northern Flying Squirrel (Glaucomys sabrinus fuscus)*. USDA Forest Service Research Paper NRS-4. Northern Research Station, Newtown Square, Pennsylvania, USA.
- Ford, W. M., Moseley, K. R., Stihler, C. W., & Edwards, J. W. (2010). Area occupancy and detection probabilities of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) using nest-box surveys. In J. S. Rentch, & T. M. Schuler (Eds.), *Proceedings from the Conference on the Ecology and Management of High Elevation Forests in the Central and Southern Appalachian Mountains* (pp. 37–47). General Technical Report NRS-P-64, USDA Forest Service.
- 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 Appalachian Mountains. *American Midland Naturalist*, 152, 430–438.
- Fridell, R. A., & Litvaitis, J. A. (1991). Influence of resource distribution and abundance on home-range characteristics of southern flying squirrels. *Canadian Journal of Zoology*, 69, 2589–2593. <https://doi.org/10.1139/z91-365>
- Garroway, C. J., Bowman, J., & Wilson, P. J. (2013). Complex social structure of southern flying squirrels is related to spatial proximity but not

- kinship. *Behavioral & Ecological Sociobiology*, 67, 113–122. <https://doi.org/10.1007/s00265-012-1431-3>
- Gibson, P., & Lindenmayer, D. (2002). *Tree hollows and wildlife conservation in Australia*. CSIRO Publishing.
- Hackett, H. M., & Pagels, J. F. (2003). Nest site characteristics of the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*) in southwest Virginia. *American Midland Naturalist*, 150, 321–331.
- Holloway, G. L., & Malcolm, J. R. (2007a). Nest-tree use by northern and southern flying squirrels in central Ontario. *Journal of Mammalogy*, 88, 226–233. <https://doi.org/10.1644/05-MAMM-A-368R2.1>
- Holloway, G. L., & Malcolm, J. R. (2007b). Northern and southern flying squirrel use of space within home ranges in central Ontario. *Forest Ecology and Management*, 242, 747–755. <https://doi.org/10.1016/j.foreco.2007.02.020>
- Hough, M. J., & Dieter, C. D. (2009). Summer nest tree use by northern flying squirrels in the Black Hills, South Dakota. *American Midland Naturalist*, 162, 98–111.
- Hughes, R. S. (2006). Home ranges of the endangered Carolina northern flying squirrel in the Unicoi Mountains of North Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* (Vol. 60, pp. 19–24)
- Jacques, C. N., Zweep, J. S., Jenkins, S. E., & Klaver, R. W. (2017). Home range use and survival of southern flying squirrels in fragmented forest landscapes. *Journal of Mammalogy*, 98, 1479–1488. <https://doi.org/10.1093/jmammal/gyx089>
- Kelly, C. A., Diggins, C. A., & Lawrence, A. J. (2013). Crossing structures reconnect federally endangered flying squirrel populations divided for 20 years by road barrier. *Wildlife Society Bulletin*, 37(2), 375–379. <https://doi.org/10.1002/wsb.249>
- Koprowski, J. L., King, S. R. B., & Merrick, M. J. (2008). Expanded home ranges in a peripheral population: Space use by endangered Mt. Graham Red Squirrels. *Endangered Species Research*, 4, 227–232. <https://doi.org/10.3354/esr00026>
- Lacey, E. A., O'Brien, S. L., Sobrero, R., & Ebensperger, L. A. (2019). Spatial relationships among free-living cururos (*Spalacopus cyanus*) demonstrate burrow sharing and communal nesting. *Journal of Mammalogy*, 100, 1918–1927. <https://doi.org/10.1093/jmammal/gyz117>
- Layne, J. N., & Raymond, M. A. V. (1994). Communal nesting of southern flying squirrels in Florida. *Journal of Mammalogy*, 75, 110–120. <https://doi.org/10.2307/1382242>
- Madden, J. R. (1974). Female territoriality in a Suffolk County, Long Island, population of *Glaucomys volans*. *Journal of Mammalogy*, 55, 647–652. <https://doi.org/10.2307/1379554>
- Mahan, C. G., Bishop, J. A., Steele, M. A., Turner, G., & Myers, W. L. (2010). Habitat characteristics and revised GAP landscape analysis for the northern flying squirrel (*Glaucomys sabrinus*), a state endangered species in Pennsylvania. *American Midland Naturalist*, 164, 283–295. <https://doi.org/10.1674/0003-0031-164.2.283>
- Maser, C., Anderson, R., & Bull, E. L. (1981). Aggregation and sex segregation in northern flying squirrels in northeastern Oregon, an observation. *The Murrelet*, 62, 54–55. <https://doi.org/10.2307/3534176>
- Mazzamuto, M. V., Merrick, M. J., Bisi, F., Koprowski, J. L., Wauters, L., & Martinoli, A. (2020). Timing of resource availability drives divergent social systems and home range dynamics in ecologically similar tree squirrels. *Frontiers in Ecology and Evolution*, 8, 174. <https://doi.org/10.3389/fevo.2020.00174>
- Murrant, M. N., Bowman, J., & Wilson, P. J. (2014). A test of non-kin social foraging in the southern flying squirrel (*Glaucomys volans*). *Biological Journal of the Linnean Society*, 113, 1126–1135.
- Muul, I. (1968). *Behavioral and physiological influences on the distribution of the flying squirrel Glaucomys volans* (Vol. 134, pp. 1–66). University of Michigan Museum of Zoology Miscellaneous Publications.
- Muul, I. (1969). Mating behavior, gestation, and development of *Glaucomys sabrinus*. *Journal of Mammalogy*, 50, 121.
- Reynolds, R. J., Fies, M. L., & Pagels, J. F. (2009). Communal nesting and reproduction of southern flying squirrels in montane Virginia. *Northeastern Naturalist*, 16, 563–576.
- Reynolds, R. J., Pagels, J. F., & Fies, M. L. (1999). Demography of northern flying squirrels in Virginia. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* (Vol. 53, pp. 340–349).
- Schmutz, T. M., & White, G. C. (1990). Error in telemetry studies: Effects of animal movement on triangulation. *Journal of Wildlife Management*, 54, 506–510. <https://doi.org/10.2307/3809666>
- Selonen, V., Hanski, I. K., & Wistbacka, R. (2014). Communal nesting is explained by subsequent mating rather than kinship or thermoregulation in Siberian flying squirrel. *Behavioral Ecology and Sociobiology*, 68, 971–980.
- Shanley, C. S., Pyare, S., & Smith, W. P. (2013). Response of an ecological indicator to landscape composition and structure: Implications for function units of temperate rainforest ecosystem. *Ecological Indicators*, 24, 175–186.
- Sikes, R. S., & Animal Care and Use Committee of the American Society of Mammalogists (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97, 663–688. <https://doi.org/10.1093/jmammal/gyw078>
- Silvis, A., Ford, W. M., Britzke, E. R., & Johnson, J. B. (2014). Association, roost and social networks of *Myotis septentrionalis* maternity colonies. *Behavioral Processes*, 103, 283–290.
- Smith, J. R., Van Vuren, D. H., Kelt, D. A., & Johnson, M. L. (2011). Spatial organization of northern flying squirrels, *Glaucomys sabrinus*: Territoriality in females? *Western North American Naturalist*, 7, 44–48.
- Sollberger, D. E. (1943). Notes on the breeding habitats of the eastern flying squirrel (*Glaucomys volans volans*). *Journal of Mammalogy*, 24, 163–173.
- Stihler, C. W., Knight, K. B., & Urban, V. K. (1987). The northern flying squirrel in West Virginia. *Proceedings of the 3rd Southeastern Nongame and Endangered Wildlife Symposium* (pp. 176–183).
- 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.
- Thorington, K. K., Metheny, J. D., Kalcounis-Rueppell, M. C., & Weigl, P. D. (2010). Genetic relatedness in winter populations of seasonally gregarious southern flying squirrels, *Glaucomys volans*. *Journal of Mammalogy*, 91, 897–904.
- Thorington, K. K., & Weigl, P. D. (2011). Role of kinship in the formation of southern flying squirrel winter aggregations. *Journal of Mammalogy*, 92, 179–189. <https://doi.org/10.1644/10-MAMM-A-062.1>
- U.S. Fish and Wildlife Service (USFWS) (1985). Final rule for listing Carolina northern flying squirrel and Virginia northern flying squirrel as endangered. *Federal Register*, 50, 27002.
- Villa, L. J., Carey, A. B., Wilson, T. M., & Glos, K. E. (1999). *Maturation and reproduction of northern flying squirrels in Pacific Northwest forests* (p. 68). General Technical Report PNW-GTR-444, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture.
- Weigl, P. D. (1974). Study of the northern flying squirrel, *Glaucomys sabrinus*, by temperature telemetry. *American Midland Naturalist*, 92, 482–486. <https://doi.org/10.2307/2424313>
- Weigl, P. D., Knowles, T. W., & Boynton, A. C. (1992). *The distribution and ecology of the northern flying squirrel, Glaucomys sabrinus coloratus, in the southern Appalachians*. North Carolina Wildlife Resources Commission Publication.

- Wells-Gosling, N. (1985). *Flying squirrels: Gliders in the dark*. Washington, DC, USA: Smithsonian Institution Press.
- Wells-Gosling, N., & Heaney, L. R. (1984). *Glaucomys sabrinus*. *Mammalian Species*, 299, 1–8. <https://doi.org/10.2307/3503926>
- White, G. C. (1985). Optimal locations of towers for triangulation studies using biotelemetry. *Journal of Wildlife Management*, 49, 190–196.
- White, G. C., & Garrott, R. A. (1990). *Analysis of wildlife radio-tracking data*. Academic Press.
- Winterrowd, M. F., Gergits, W. F., Laves, K. S., & Weigl, P. D. (2005). Relatedness within nest groups of southern flying squirrels using microsatellite and discriminant function analyses. *Journal of Mammalogy*, 86, 841–846.
- Witt, J. W. (1992). Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon. *Journal of Mammalogy*, 73, 921–929. <https://doi.org/10.2307/1382217>

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