Space-use and nest selection of southern flying squirrels (*Glaucomys volans*) at the edge of their geographic range

by

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Abstract

Southern flying squirrels (*Glaucomys volans*, hereafter “flying squirrels”) are common throughout the eastern United States, with the western edge of their geographic range extending into the Great Plains where deciduous forest transitions into grassland. Studies have documented flying squirrel space-use patterns and nest selection within the core of their range, though it is unclear if these patterns persist along their western range edge. I used VHF radiocollars to track 10 flying squirrels (six males, four females) in southeastern Kansas, USA to estimate home-range sizes and identify local-scale patterns in nest-site and nest-tree selection during summer and winter 2024. Flying squirrels had a mean home-range size of 1.55 ha (male = 1.56 ha, female = 1.54 ha) for 95% minimum convex polygon and 5.44 ha (male = 6.44 ha, female = 3.94 ha) for 95% kernel density estimate. Flying squirrels selected nest sites based on tree richness (number of unique genera of trees) and diameter at breast height (DBH). Greater tree richness and average tree DBH increased probability of local-scale habitat use. Flying squirrels selected nest-trees based on tree type (hard mast-producing tree or non-hard mast-producing trees) and DBH. Non-hard mast-producing trees and greater tree DBH showed increased probability of nest-tree use. Based on my results, I recommend that forest diversity in Kansas should be maintained, while allowing hard mast-producing trees to reach full maturity and retaining snags when faster developing trees die. This would allow large diameter and mature trees of many different species to persist without disturbance to quality nesting habitat for flying squirrels.

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Dedication

To Barbara Bernhardt and Curt Kane, who without their love, support, and encouragement over many years of seasonal technician work, I would never have gotten to this point. To Caylen Wolfer, who has always been there for me through distance and time apart, there is no one else I want to spend the rest of my life with. To Shash Georgi, who was my biggest fan, thank you for shining the herbal light on me.

Chapter 1 - Southern Flying Squirrels: A Glide Through History

Introduction – Southern flying squirrels (*Glaucomys volans*) have not been studied along their western range limit. As a result, comparisons between these peripheral populations and core populations have not been discussed. In the following chapter, I overview two well-known hypotheses describing possible differences between core and peripheral populations and the importance of understanding their relationships. Then, I discuss what is currently known about southern flying squirrel natural history and ecology before putting them in context of these hypotheses.

Evolution and Biogeography – The New World flying squirrels (*Glaucomys* spp.), of the family *Sciuridae*, are glissant, nocturnal species of rodents native to North America. They are known for their unique skin flap, called a patagium, connecting to their wrists and ankles that gives them the ability to glide when leaping from a high launch point (Thorington et al., 1998). New World flying squirrels diverged from Asian Old World flying squirrel genera (within tribe *Pteromyini*) around 14 million years ago during the late Miocene era (Mercer and Roth, 2003). North America is home to three distinct species of New World flying squirrels: the northern flying squirrel (*Glaucomys sabrinus*), the southern flying squirrel, and the Humboldt's flying squirrel (*Glaucomys oregonensis*; Arbogast, 2007; Arbogast et al., 2017). The Humboldt's flying squirrel was once thought to be a subspecies of the northern flying squirrel, but was designated as a distinct species by Arbogast et al. (2017) based on deep divergence of mitochondrial DNA between the two taxa. Further, northern and southern flying squirrels are considered sister species based on the mitochondrial DNA phylogeny with the Humboldt's flying squirrel the most divergent of the three species (Arbogast, 2007; 2017). The geographic range of southern flying squirrels includes most of the eastern half of the United States, with northern limits within

parts of eastern Canada and southern limits through northern Mexico (Dolan and Carter, 1977). The geographic range of the northern flying squirrel overlaps southern flying squirrel in the Great Lakes region, New England, and some high elevation forest pockets through Appalachia (Wilson and Ruff, 1999). Despite regional sympatry, these species are ecologically divergent, with distinct habitat preferences leading to niche separation (Hutchinson, 1957). Southern flying squirrels typically occupy deciduous hardwood forests that dominate eastern portions of the contiguous United States, although populations persist within mixed conifer-deciduous stands (Dolan and Carter, 1977; Fridell and Litvaitis, 1991; Gilmore and Gates, 1985; Muul, 1968; Taulman and Smith, 2004). Where southern flying squirrels are found in mixed-forest habitats they more frequently select for hardwood trees over softwood (Holloway and Malcolm, 2007a, 2007b; Muul, 1968; O'Brien et al., 2021; Taulman and Smith, 2004). Conversely, northern flying squirrels prefer softwood conifer forests common across the Boreal zone of Canada and parts of the western United States (Carey et al., 1997; Holloway and Malcolm, 2007b, 2007a; O'Brien et al., 2021).

Availability of suitable habitat is part of a large suite of environmental factors that may affect the distribution of a species (Lee-Yaw et al., 2016). Brown et al. (1984) posited that environmental conditions become less favorable towards the edge of a species' distribution, resulting in lower population abundance and greater relative isolation. These differences in population demographics support the hypothesis that genetic differentiation across peripheral populations is increased, while genetic diversity, gene flow, and fitness are reduced (Brown, 1984; Hengeveld and Haeck, 1982; Sagarin and Gaines, 2002). These characteristics have been explored by scientists dating as far back as Darwin (Darwin, 1859; Pironon et al., 2017) and have

become the basis for many ecological and evolutionary hypotheses (Holt and Keitt, 2005; Pironon et al., 2017; Sagarin et al., 2006).

The ‘abundant center’ hypothesis and ‘center-periphery’ hypothesis, are two of the more prominent biogeographical hypotheses that have been invoked to explain differences between core and peripheral populations (Brown, 1984; Brown et al., 1995; Hengeveld and Haeck, 1982; Pironon et al., 2017; Sagarin and Gaines, 2002). The ‘abundant center’ hypotheses states that species have more abundant populations at their geographic center (Brown, 1984; Sagarin and Gaines, 2002). The ‘center-periphery’ hypothesis also postulates increased abundance but in addition includes that central populations have increased genetic diversity and gene flow (Brown, 1984; Pironon et al., 2017). Many studies have been conducted to test and attempt to confirm these hypotheses (e.g., Dallas et al., 2020; Pironon et al., 2017). However, results across studies have been mixed and at times contradictory, suggesting that although both hypotheses have merit, there remains little understanding of the fundamental dynamics behind these relationships, likely due to species-specific, or place-based idiosyncrasies (Dallas et al., 2020; Pironon et al., 2017; Sagarin and Gaines, 2002).

Eckert et al. (2008) reviewed 134 studies on genetic differences between peripheral and central populations and found that ~64% of studies reported decreased genetic diversity within peripheral populations, although modest, and ~70% of those studies also reported greater genetic differentiation of peripheral populations relative to core populations. San Juan et al. (2021) examined genetic diversity and differentiation in kissing bug (*Mepraia spinolai*) populations in Chile and found lower genetic diversity across peripheral populations, but no difference in relative genetic differentiation. Results from Xu et al. (2021) studying Chinese emmenopterys (*Emmenopterys henryi*) in China parallels results from San Juan et al. (2021), but in addition

found increased densities in core populations. Carey et al. (1995) also reported lower population abundances of purple fescue (*Vulpia ciliata ambigua*) at its northern range limit in England when compared to central populations.

Conversely, most disagreement among these hypotheses is from lack of support regarding differences in population demographics between peripheral and central populations. For instance, Sagarin and Gaines (2002) revealed that only 39% of tests in empirical studies on the 'abundant center' hypothesis supported it. Sexton et al. (2009) reviewed empirical tests on different range limit models to assess what influences a species' range, and while they did find support for decreased genetic diversity and increased differentiation at a species range limit, support was lacking for decreases in population abundance and fitness towards their range edge. Blackburn et al. (1999) did not find differences in abundances between peripheral and central populations across multiple British bird species. When reviewing range contractions of 245 species, Channell and Lomolino (2000) reported that a majority of declining species persisted in remnant populations at their range edge in the face of extinction, contrary to belief that range contraction would occur from the edges of their range inward.

Even though these hypotheses may be controversial, peripheral populations still hold critical value for continued persistence of a species over their entire geographic range. Peripheral populations are often the remaining strongholds for species nearing extinction (Channell and Lomolino, 2000) and promoting genetic diversity among these populations may lead to increased adaptive potential towards the continuing process of speciation (Lesica and Allendorf, 1995). One common assumption is that differences between peripheral and central populations are driven more by differences in ecological conditions and historical processes than by differences in geography and the spatial distance between populations (Duncan et al., 2015; Jin et al., 2020;

San Juan et al., 2021). If optimal ecological conditions persist throughout a species distribution, then demographic and genetic differences may not manifest (Chardon et al., 2015; Ntuli et al., 2020; Soulé, 1973). Thus, it is important to understand how ecological and environmental gradients are changing with increased disturbances. For example, climate change has pushed some southern flying squirrel populations further north where northern flying squirrels are more prevalent (Bowman et al., 2005), resulting in a zone of hybridization developing in recent years (Garroway et al., 2010). Consequently, populations at the northern edge of the southern flying squirrel geographic range are facing different ecological pressures than interior populations. Although research on interior populations of southern flying squirrels is abundant (Bendel and Gates, 1987; Borgo et al., 2006; Brady et al., 2000; Doty et al., 2022; Fridell and Litvaitis, 1991; Gilmore and Gates, 1985; Heidt, 1977; Howard et al., 2020; Jacques et al., 2017; Layne and Raymond, 1994; Muul, 1974, 1968; Reynolds et al., 2009; Steinhoff et al., 2012; Stone et al., 1997; Taulman, 1999; Taulman and Smith, 2004; Woodworth et al., 2000), a distinct lack of research focusing on peripheral populations suggests that further study along all range limits of southern flying squirrels could yield insights into stressors for this species that may at some point be experienced by currently more stable interior populations.

Nutrition – Southern flying squirrels have similar morphology to northern flying squirrels but are more diminutive, being roughly half the size (Arbogast, 2007). Despite small size, southern flying squirrel are more carnivorous than other North American sciurids (Dolan and Carter, 1977) and their diet consists of a wide variety of resources, including nuts, seeds, fruits, berries, fungi, lichen, buds, bark, insects, eggs, carrion, and even nestling birds (Dolan and Carter, 1977). A preference specifically for carnivory has mainly been observed in captive populations (Harlow and Doyle, 1990). The first study on wild southern flying squirrel diet was

from Connor (1960), who found the total food mass collected from southern flying squirrels in New York consisted of 78% plant material (mast, fungi, buds, and lichen) and 22% insects or other invertebrates (beetles and slugs). Harlow and Doyle (1990) identified stomach contents of southern flying squirrels from South Carolina. In their study, acorns were the most common food material, comprising 74% of total food mass collected and appearing in 100% of the stomachs collected across the entire 12-month sampling period of the study. Insects were found in 11% of the stomachs collected, but only 1% of the total food mass collected. Other food material collected included fruits, seeds, fungal spores, lichen, moss, and other unidentified plant material. These studies indicate that wild southern flying squirrels rely more on plant materials than animal materials, and that acorns and other masts are their most critical food resource, associated with variable levels of tannins, fats, and proteins (Shimada and Saitoh, 2006).

Reproduction – The general consensus is that southern flying squirrels can breed twice annually (Dolan and Carter, 1977), however the timing of reproduction varies between locations (Goertz et al., 1975). Reynolds et al. (2009) reported parturition events in early spring and late summer in Virginia. Goertz et al. (1975) reported peak parturition in late winter and late summer, but as early as January and as late as November in Louisiana. Heidt (1977) reported litter production in later winter and later summer in Arkansas. Raymond and Layne (1988) reported parturition events between August and January, with two main peaks in late summer and early fall and a smaller peak in late fall. Gilmore and Gates (1985) reported parturition periods in spring and late summer. Across their range, litter sizes range from two to seven pups and generally these squirrels exhibit female uniparental care (Dolan and Carter, 1977). Mothers are very protective their young and will defend territory from other females, while males are usually not territorial (Dolan and Carter, 1977; Madden, 1974).

Nesting Behavior – Southern flying squirrels nest in either tree cavities or open nests, called dreys (Muul, 1974). However, they are more likely to use tree cavities over dreys, especially in colder environments (Holloway and Malcolm, 2007b; Muul, 1974; O'Brien et al., 2021). In comparison, northern flying squirrel selection of nest type varies, and they are more willing to use dreys if tree cavity availability is low (Carey et al., 1997; Holloway and Malcolm, 2007b; Menzel et al., 2004; O'Brien et al., 2021). While other taxa, such as birds, use nests specifically for breeding and raising young, nests for flying squirrels go beyond a singular use for breeding. Southern flying squirrels use nests throughout the entire year, regardless of season (Muul, 1968). Muul (1968) suggested that southern flying squirrels have primary nests that are almost continuously occupied, at least seasonally, and secondary nests that were occasionally used as food cache sites, latrine sites, refuge from predators, or due to disturbances at the primary nests. Steinhoff et al. (2012) found that, on average, southern flying squirrels in Wisconsin switched nests twice across four weeks in the summer. In Ontario, Holloway and Malcolm (2007b) observed southern flying squirrels using an average of 3.5 nests over the summer, with some individuals using a single nest the entire sampling period and others switching between nests every one to two weeks. Nest switching tends to decrease in the fall and winter months (Garroway et al., 2013).

Another unique function of nests is the formation of aggregations, or communal nesting (Layne and Raymond, 1994; Muul, 1968). This behavior is typically associated with thermoregulation and energy conservation (Doty et al., 2022; Layne and Raymond, 1994; Muul, 1968; Reynolds et al., 2009; Stapp et al., 1991; Thorington and Weigl, 2011). Stapp et al. (1991) showed that aggregations reduced energy loss by 26-33% in the winter and increasing the size of aggregations increased the difference in temperature between occupied and empty nests. The

warmth created by the increased number of bodies within a single nest allowed for less insulation required from nesting material, saving on energy costs of collecting this material. Aggregation sizes typically peak in the fall and winter, but less often are also formed in the spring and summer (Garroway et al., 2013; Goertz et al., 1975; Holloway and Malcolm, 2007b; Layne and Raymond, 1994; Muul, 1968; Stapp et al., 1991; Woodworth et al., 2000). Aggregations can also consist of individuals of different sex, family groups, and age classes (Doty et al., 2022; Garroway et al., 2013; Layne and Raymond, 1994; Thorington and Weigl, 2011), suggesting that socialization and reproduction may also play a role in aggregation formation. Relatedness and familiarity between individuals are both important factors when southern flying squirrels form aggregations (Garroway et al., 2013; Layne and Raymond, 1994; Thorington and Weigl, 2011).

Habitat Selection – Southern flying squirrels are secondary cavity nesters, so they do not create their own cavities for nests and they rely on cavities created from natural decay or by woodpeckers (Bendel and Gates, 1987; Holloway and Malcolm, 2007b; Muul, 1974). As a result, selection of nesting cavities can parallel selection from different woodpecker species (Conner et al., 1996; DeFazio et al., 1987; Holloway and Malcolm, 2007b; Loeb, 1993), so much so that southern flying squirrels are sometimes removed to ease competition for threatened woodpecker species, such as red-cockaded woodpeckers (*Leuconotopicus borealis*; DeFazio et al., 1987). However, Mitchell et al. (1999) concluded that removal of southern flying squirrels does not increase red-cockaded woodpecker nest success. Loeb et al. (1993) examined southern flying squirrel selection of tree cavities excavated by threatened red-cockaded woodpeckers in South Carolina and found that southern flying squirrels are one of the primary users of woodpecker excavated cavities. In fact, southern flying squirrels used those cavities mainly because the entrances are too small for other species to use, similar to selection by red-cockaded

woodpeckers. As such, one would expect southern flying squirrel habitat selection to parallel that of woodpecker habitat. Bush et al. (2009) found that pileated woodpeckers (*Dryocopus pileatus*) in Ontario foraged on larger trees and snags, especially those with higher decay, and were not influenced by forest type. Harestad and Keisker (1989) also found that various woodpecker species in British Columbia selected nest cavities in trees with more decay, larger diameters, and snags. Shackelford and Conner (1997) found that, in eastern Texas, hardwood forests were associated with higher occurrences of northern flickers (*Colaptes auratus*), red-headed woodpeckers (*Melanerpes erythrocephalus*), yellow-bellied sapsuckers (*Sphyrapicus varius*), downy woodpeckers (*Picoides pubescens*), and hairy woodpeckers (*Leuconotopicus villosus*). Overall, habitat selection by woodpeckers was mainly influenced by large snags, mature forests, and logs. Various studies have identified microhabitat that influences selection from southern flying squirrels that mirror these results for woodpeckers. For example, Campuzano-Chávez-Peón et al. (2014), Holloway and Malcolm (2007b), Taulman (1999), and Zweep et al. (2018) all identified snags as an important factor in nest selection for flying squirrels. Bendel and Gates (1987), Holloway and Malcolm (2007b), Howard et al. (2020), and Zweep et al. (2018) all identified diameter at breast height as an important factor in nest selection for flying squirrels as well.

Conclusions and Research Needs – As discussed above, there is a plethora of studies focused on interior and northern peripheral populations of southern flying squirrels. However, information regarding populations at the western range limit is completely unknown. The western range limit for the southern flying squirrel occurs in the Great Plains region due to a sharp gradient from deciduous hardwood forests to native prairie grasslands. Given that this transition is also coincident with strong environmental gradients, notably precipitation (Wishart

2004), and a complete loss of available habitat for an obligate arboreal mammal, it is reasonable to predict that southern flying squirrel ecology in this region significantly differs from eastern populations. This makes Kansas, which has a long history as a Great Plains prairie-dominated state (Wishart 2004), a quintessential region to study flying squirrel populations at their range periphery.

Before the arrival of European settlers, 8.5% of Kansas was covered by old growth deciduous hardwood forests, particularly hard mast-bearing tree species such as oak (*Quercus* spp.) and hickory (*Juglandaceae* spp.; Ware & Smith 1939). By the 1930's, forest coverage was reduced to 2.4% (Ware & Smith 1939). While modern Kansas land cover is mostly grasslands and agriculture, forest cover has now rebounded to at least 4% of total land cover (Moser et al. 2013). However, much of the recent forest recovery reflects expansion of eastern red cedar (*Juniperus virginiana*). While cedar encroachment on grasslands is a concern for management of native prairies, cedar encroachment may also have a negative effect on hardwood forests in the Midwest because its rapid spread and growth in the overstory may shade out seedings of mast-producing trees, threatening to reduce the amount of high-quality forest available to southern flying squirrels (Fridell and Litvaitis, 1991; Van Els et al., 2010; Campuzano-Chávez-Peón et al., 2014; Moser et al., 2013). Management to increase oak basal area in forest stands may reduce the number of eastern red cedar seedlings (Moser et al., 2013). In Kansas, oak stock has increased ~28% since 1981 but has declined in most recent years (Moser et al., 2013). Additionally, a majority of Kansas forests are relatively young (~30-60 years old), so not yet at their peak age for acorn production (Moser et al., 2013; Sander, 1990; Tirmenstein, 1991). Maintaining growth and regeneration of large hard mast-producing trees like oaks, while reducing the numbers of eastern red cedar, could limit detrimental woody encroachment while also promoting beneficial

forests for southern flying squirrels. Based on information gleaned from Kansas, there is strong potential to inform management of southern flying squirrels along their western range limit where negative impacts from eastern red cedar are increasing (Bidwell et al., 2009).

In recent years, southern flying squirrels have only been observed at a few localities along the easternmost border of Kansas where most of the deciduous forest remains, although incidental historical records from ~100 miles further west, combined with Kansas' history of reduced hardwood forests and youth of current hardwood stands, suggests a perceived eastward distributional contraction. However, there has never been an assessment of their populations in Kansas, so the true southern flying squirrel distribution and abundance in the state is still poorly defined. Due to all these factors, the Kansas Department of Wildlife and Parks (KDWP) listed the southern flying squirrel as a 'species in need of conservation.' Data gathered from my thesis will hopefully give both local and regional managers baseline information for management of the species, not just in Kansas, but across their entire western range limit.

Chapter 2 - Nest Selection and Home Ranges

Introduction

Patterns in species' population demography at range edges often differ from populations occurring near the center of their geographic range (Brown 1994; Brown et al. 1996). Understanding how these demographic patterns differ, and the mechanistic reasons that alter these patterns, is necessary to assess population responses to novel land-use or climate changes (Holt and Keitt 2005, Wait and Ahlers 2020). The 'center-periphery hypothesis' (CPH) states populations at range edges exhibit more limited gene flow, less genetic diversity, reduced fitness, and lower densities compared to populations near the center of their range (Brown, 1984; Hengeveld and Haeck, 1982; Pironon et al., 2017). These patterns are presumed driven by different environmental conditions from center to periphery (Brown, 1984) where peripheral populations should be more sensitive to changes given they occur close to their environmental limits (Alvarez, 2001; Goldstein et al., 2017; Hardie and Hutchings, 2010). However, multiple reviews have challenged the CPH (Channell and Lomolino, 2000; Dallas et al., 2017; Pironon et al., 2017; Sagarin and Gaines, 2002). The 'Olympic Village effect' (Phillips et al., 2008), similar to the concept of 'spatial sorting' (Shine et al., 2011), proposes individuals at range peripheries are more fit and better dispersers due to reduced competition and enhanced phenotypes beneficial for persistence in harsher environmental conditions. Despite these inconsistences, ecological and evolutionary distinctions between peripheral and core populations motivate regional management along range limits (Brown, 1984; Brown et al., 1996; Channell and Lomolino, 2000; Lesica and Allendorf, 1995).

Southern flying squirrels (hereafter "flying squirrels") are small (~46-85g), arboreal, glissant mammals native to eastern deciduous forests of North America (Dolan and Carter, 1977;

Weigl, 1978) whose western periphery extends to the Great Plains region, where forest habitat sharply transitions to grassland-dominated prairies. Multiple previous studies have revealed ecological insight for population demographics through the core of their range (e.g., Bendel and Gates, 1987; Borgo et al., 2006; Brady et al., 2000; Doty et al., 2022; Fridell and Litvaitis, 1991; Gilmore and Gates, 1985; Heidt, 1977; Howard et al., 2020; Jacques et al., 2017; Layne and Raymond, 1994; Muul, 1974, 1968; Reynolds et al., 2009; Steinhoff et al., 2012; Stone et al., 1997; Taulman, 1999; Taulman and Smith, 2004; Woodworth et al., 2000), though understanding of populations at their range limits, such as through Kansas USA, remain limited (Bowman et al., 2005; Campuzano-Chávez-Peón et al., 2014; Garroway et al., 2013, 2011, 2010; Holloway and Malcolm, 2007a, 2007b; O'Brien et al., 2024, 2021). Additionally, most studies at that did focus on peripheral populations were northern range limits, often due to management concerns of sympatric competition with northern flying squirrels (Holloway and Malcolm, 2007b, 2007a; Garroway et al., 2010; O'Brien et al., 2024; Garroway et al., 2011; O'Brien et al., 2021). As a result, comparisons between western peripheral and core populations are limited. For flying squirrels, which play a key role within forest ecosystems through consumption and dispersal of nuts, seeds, and fungi (Muul 1968; Dolan & Carter 1977; Steele 2008; Steele & Yi 2020), understanding their habitat requirements at this periphery should contribute to maintenance of healthy forests. For instance, healthy forests include areas with suitable availability of nesting trees. Flying squirrels use nests daily throughout the year as diurnal resting locations, and multiple nest sites are often active concurrently (Muul, 1968). They are vital for flying squirrel survival because, in addition to using nests for reproduction and rearing young, they are also used for thermoregulation in cold temperatures, predator avoidance, and food

caching (Brady et al., 2000; Dolan and Carter, 1977; Holloway and Malcolm, 2007b; Muul, 1968; Steinhoff et al., 2012; Taulman, 1999; Weigl, 1978; Zweep et al., 2018).

My objectives were to 1) compare home-range extents of core populations of flying squirrels with populations occurring in Kansas and 2) assess the role of forest structure and composition in nest selection of flying squirrels in Kansas. Changes in habitat composition, resource availability, and fragmentation have been linked to changes in home range size (Börger et al., 2008; Gardiner et al., 2019; Mitchell and Powell, 2004; van Beest et al., 2011). Home-range sizes for other species of mammals and birds have been shown to be larger in areas where habitat and resource availability are lower (Ferguson et al., 1999; Morellet et al., 2013; Séchaud et al., 2022; Viana et al., 2018). Given that Kansas is located at the edge of the flying squirrel range, I predicted flying squirrel home range sizes in Kansas are larger than home range sizes from interior populations. I also hypothesized that selection of nest site depends both on tree type, and tree characteristics. Flying squirrels rely on mast produced from many different tree species for food (Dolan and Carter, 1977; Harlow and Doyle, 1990; Muul, 1968), but during winter rely most heavily on hard masts, such as acorns and nuts, which are stored in food caches (Dolan and Carter, 1977; Muul, 1974). Therefore, I predicted that flying squirrels select nest trees at sites with increased availability of hard-mast trees. Coupled with this, larger, mature live trees and standing dead trees, or snags, tend to have more cavities from natural decay and woodpeckers, which are used by flying squirrels as nest sites (Bendel and Gates, 1987; Bush et al., 2009; Loeb, 1993). Therefore, I predicted that flying squirrels would select nest trees at sites with larger live trees and availability of snags. Finally, northern flying squirrels select cavities in live trees located beneath dense canopies providing protection from predators and weather

(Carey et al., 1997; Smith, 2007). Therefore, I predicted flying squirrels select nest trees in sites with dense canopy cover, over more open sites.

Study Area

My study occurred on Grand Osage Wildlife Area (3891 ha), a Kansas Department of Wildlife and Parks (KDWP) managed property in southeast Kansas, USA (37°26’ N, 95°19’ W; Figure 2.1). This area was characterized by oak (*Quercus spp.*), hickory (*Carya spp.)*, and floodplain riparian forest of early successional woodland co-dominated by osage orange (*Maclura pomifera*), honey locust (*Gleditsia triacanthos*), green ash (*Fraxinus pennsylvanica*), elm (*Ulmus spp.*), hackberry (*Celtis occidentalis*), dogwood (*Cornus spp.*), sumac (*Rhus spp.*), and blackberry (*Rubus fruticosus*). Remaining landcover consisted of shrubland, native grasses and fescue, crops including wheat (*Triticum aestivum*), soybean (*Glycine max*), corn (*Zea mays*), and sunflower (*Helianthus annuus*), wetland, water, and human infrastructure. Mean temperature was 24.6°C in summer 2024, with averages ranging from 20° C in May to 27.3° C in July. In December 2024 for my winter sampling, mean temperature was 4.2° C. Mean precipitation was 0.18 cm in May-July 2024 and 0.02 cm in December 2024. Sympatric sciurid species included gray squirrel (*Sciurus carolinensis*) and fox squirrel (*Sciurus niger*). Potential predators included bobcat (*Lynx rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), black rat snake (*Pantherophis obsoletus*), barred owl (*Strix varia*), eastern screech owl (*Megascops asio*), and great horned owl (*Bubo virginianus*).

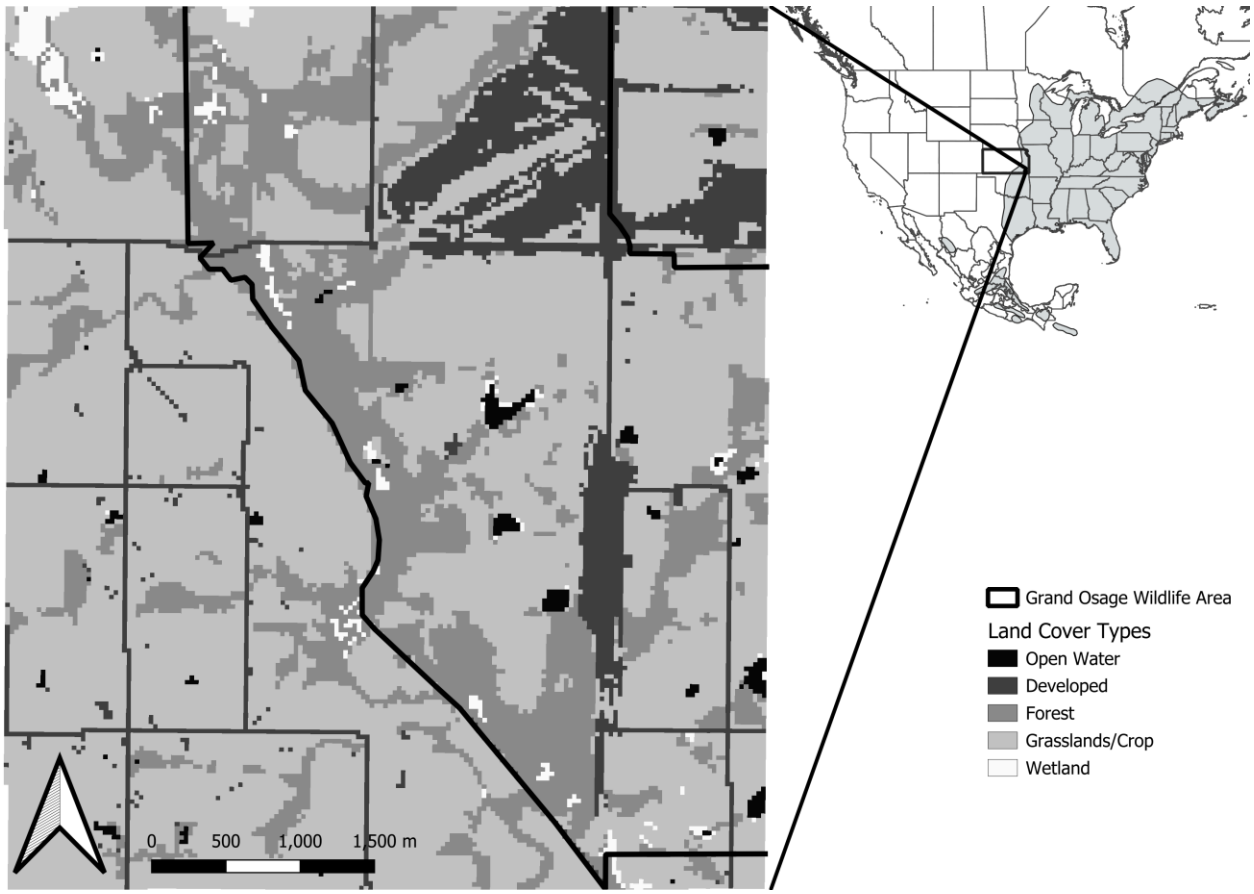

Figure 2.1 Geographic range of southern flying squirrels (*Glaucomys volans*; shaded map inset; International Union for Conservation of Nature, 2008) and location of my study area (3891 ha) in Kansas, USA. Land cover types include open water, human development, forest, grasslands/crop, and wetland.

Methods

Trapping

In 2024, I live-trapped flying squirrels during a two-month period from mid-May to mid-July and a two-week period in mid-December. I chose trap sites (n = 15) near flying squirrel nest boxes (boxes installed in previous years) or in nearby areas where flying squirrels were previously detected. During summer, I used Sherman live traps (Slade et al., 1993) baited with an oatmeal and peanut butter mixture, sweet horse feed, or sunflower seeds (Bendel and Gates, 1987; Holloway and Malcolm, 2007a, 2007b; Howard et al., 2020; Jacques et al., 2017;

Kuykendall and Keller, 2011; Nelson and Sagot, 2018). At each trap site, I established a 40-90 m transect (Pearson and Ruggiero, 2003) consisting of paired traps spaced 10 m apart. For each pair, I cable-tied one trap on a wooden platform attached to a tree ~2-3 m above the ground (Bendel and Gates, 1987; Engel et al., 1992; Keefe and Giuliano, 2004) and placed the second trap on the ground at the base of the same tree. Traps at the base of the tree were intended to capture non-target species such as white-footed mice (*Peromyscus leucopus*) to reduce by-catch in platform traps, which were my main traps targeting flying squirrels (Loeb et al., 2001). I placed every trap on the northeast side of the tree to avoid overheating and to increase capture success (Jacques et al., 2017). Traps were operational 5-7 nights per week and checked once a day in the mornings to minimize prolonged periods of containment and stress for individuals (Powell and Proulx, 2003). I replaced bait every 2-3 days or when wet, moldy, or missing. Trap success during this time was relatively low, so I adjusted my live-capture efforts in December, and relied solely captured flying squirrels at established nest boxes constructed similarly to Althoff and Althoff (2001). Flying squirrels form aggregations in the winter to aid in thermoregulation and reproductive success (Dolan and Carter, 1977; Layne and Raymond, 1994; Muul, 1968; Thorington and Weigl, 2011; Weigl, 1978). They often use nest boxes for aggregations, which provides an opportunity for scientists to increase capture success (Heidt, 1977; Layne and Raymond, 1994; Reynolds et al., 2009; Woodworth et al., 2000). I used an endoscope camera (Depstech, Hong Kong, China) fixed to the top of an extendable (1.8–3.6 m) painter's pole (Ace Hardware, Oak Brook, IL, USA) to assess nest box occupancy while minimizing disturbance (Kolowski et al., 2023). If I observed a flying squirrel, I inserted cotton balls dosed with 1 cc isoflurane each into the nest box opening and plugged the hole with a rag to reduce movement and stress on flying squirrels during removal (Jacques et al., 2017; Steinhoff et

al., 2012). After 2-3 minutes, I opened the nest box and removed the flying squirrels. I ensured nest boxes retained as much nesting material as possible and replaced any nesting material that fell out during removal.

I handled captured flying squirrels using American Society of Mammologist guidelines (Sikes et al, 2016) and in line with Kansas State University IACUC (permit #4801). I transferred captured flying squirrels to a nylon bag and kept them in a shaded, dry area. In December, flying squirrels were kept inside a nylon bag within a handler's jacket to keep individuals warm. I recorded reproductive condition, weight, sex and age of the individual (Linzey and Linzey, 1979). I fit flying squirrels weighing ≥46 g with a VHF radio-tracking collar (Lotek PicoPip Ag376, 2.3g, Lotek, Newmarket, ON, Canada), with this minimum weight calculated to keep the collar at <5% of body weight). Flying squirrels lighter than this weight were not collared. I fit collars so they rotated freely around the neck and allowed individuals to breathe normally. Once the cable tie on the collar was fitted, I trimmed the excess and used super glue (Loctite, Rocky Hill, CT, USA) to prevent tightening after release. I also marked each flying squirrel with a Passive Integrated Transponder tag (Harper and Batzli, 1996) inserted subcutaneously between the shoulder blades and/or a metal ear tag (National Band and Tag Co., Newport, KY, USA) to identify subsequent recaptures in the event a collar slipped off an individual. Once handling was completed, I placed flying squirrels back in the nylon bag and released them at their point of capture.

Tracking

Collared flying squirrels were tracked using an ATS yagi antenna (Advanced Telemetry Systems, Inc., Isanti, Minnesota) and Telonics receiver (Telonics Inc., Mesa, Arizona). Prior to

the study, I estimated telemetry error by tracking 10 hidden transmitters using homing methods with the help of other observers. One observer hid transmitters in trees as high as possible using a step ladder so the transmitter could not be seen. Observers tracked the signal until they chose a tree believed to contain the transmitter. I measured distance (m) between the chosen tree and the tree with the transmitter. After I averaged distances from each of the 10 trials, I found telemetry error was minimal (0.0 – 0.5m).

All nighttime tracking occurred after sunset and before sunrise to identify the extent of home-ranges per night. I recorded 2-6 locations on each flying squirrel per night, with each location recorded ~ 2 hours apart to account for any potential spatial autocorrelation between locations and differences in temporal movement behaviors. I homed into the nearest tree where flying squirrels were active (Kenward, 2000; White and Garrott, 2012) until individuals were observed or signal suggested marked individuals were directly overhead (Jacques et al., 2017; Taulman and Smith, 2004). Once a flying squirrel was located, I recorded locations using a handheld global positioning system unit (Garmin Ltd., Olathe, KS). During daylight hours, when flying squirrels were inactive, I used homing methods to track marked individuals to their exact nesting location. I observed nest locations for individuals 1-5 times a week until at least a minimum of five nest locations were found for each flying squirrel.

Habitat Surveys

I recorded habitat data at 1) all unique nest tree locations (n = 40; hereafter called “nest tree”), 2) the area within a 10-meter radius circle of the nest tree (0.03 hectares; n = 40; hereafter called “nest site”; Steinhoff et al., 2012; Zweep et al., 2018) and 3) paired, random locations (n = 85; hereafter called “random site”). I recorded diameter at breast height (DBH; Table 2.1) of

every tree ≥10 cm DBH using loggers' tape (cm; Spencer Logging Tape, US Tape Company, Pennsburg, PA) and identified them to genus, including the nest tree (Loeb, 1993; Steinhoff et al., 2012; Zweep et al., 2018). Genus-level identification was considered sufficient to delineate ecological roles from individual trees (Howard et al., 2020). I also counted number of snags at the nest site (Snags), and recorded percent canopy cover on the north side of the nest tree (Canopy Cover; Table 1) using a spherical convex densiometer (Forestry Suppliers, Inc., Jackson, MS, USA). These habitat characteristics were important to nest-site selection based on previous studies (Bendel and Gates, 1987; Fridell and Litvaitis, 1991; Holloway and Malcolm, 2007b; Howard et al., 2020; Taulman, 1999; Zweep et al., 2018).

I selected random sites 20-360 m away from the nest tree similar to Grisham (2012). I did not consider random distances ≤20m because I did not want to overlap any survey measurements with the nest site. Random site habitat survey methods were consistent with nest site habitat surveys, except percent canopy cover was measured at the center of random site, regardless of the presence of a focal tree.

Table 2.1 Description of variables used to predict nest-site and nest-tree selection of southern flying squirrels (*Glaucomys volans*) in Kansas, USA in 2024. Includes mean, standard deviation, minimum, and maximum values for each variable at nest tree, nest site, and random site levels.

Variable	Description	Mean	SD	Range
Nest Tree				
DBH	Diameter (cm) at breast height of nest tree	46.57	24.44	14.48 - 108.20
Canopy Cover	Percent canopy cover at nest tree	62.19	25.38	10.00 - 100.00
Nest Site				
DBH	Diameter (cm) at breast height of surveyed trees at nest site	26.12	16.98	10.16 - 108.33
Tree Density	Number of surveyed trees at nest site	14.67	4.97	4.00 - 24.00
Tree Richness	Number of unique genera of surveyed trees at nest site	5.63	1.56	2.00 - 8.00
Random Site				
DBH	Diameter (cm) at breast height of trees at random site	24.48	13.69	10.16 - 89.79
Tree Density	Number of surveyed trees at random site	13.35	6.02	4.00 - 33.00
Canopy Cover	Percent canopy cover at center of random site	61.38	26.4	5.00 - 100.00
Tree Richness	Number of unique genera of surveyed trees at random site	4.88	1.69	1.00 - 9.00

Data Analysis

I used the adehabitatHR package (Calenge, 2024) in Program R (R Core Team, 2024) to calculate 95% minimum convex polygon (MCP) and 95% kernel density estimate (KDE) home ranges for each marked flying squirrel. 95% KDE was calculated using the reference bandwidth (href) as a smoothing parameter (Silverman, 2018; Worton, 1989). I used these two home-range estimators to be consistent with other studies assessing home-range sizes for flying squirrels elsewhere in North America. I calculated mean seasonal home-range sizes for both males and females for each method. I used generalized linear models to examine effects of biotic variables (sex and number of nest sites), abiotic variables (season), and sampling effort (total number of locations) on home-range size. I fit each of these predictor variables as individual models, along with a null model, with home range size as the response variable.

I categorized tree identifications from nest site and random site habitat surveys (hereafter "tree type") as either hard-mast producing tree, soft-mast producing tree, snag, or other. Other tree type included seed-producing trees whose seeds are not developed as hard or soft mast. I recorded number of trees for each tree type at each nest site and random site. I estimated tree density for nest sites and random sites by counting the number of total trees surveyed for each nest site and random site (Tree Density; Table 1). I estimated tree richness by counting unique tree genera for each nest site and random site (Tree Richness; Table 1).

I used logistic regression (Hosmer and Lemeshow, 2013; McCullagh and Nelder, 2019) to compare habitat characteristics (tree type abundance, mean DBH, tree density, canopy cover, and tree richness) between nest sites and random sites and also between nest trees and random trees. I fit models based on measured habitat covariates, season, and a null model. I randomly

selected single trees from each random site for tree type and DBH comparisons to do a one-to-one comparison with nest trees. When I randomly selected tree types, I removed random site trees ≤ mean nest tree DBH. I found no correlation between DBH and tree richness, and DBH and tree type in additive models.

I performed all statistical analyses using the AICcmodavg program (Mazerolle, 2023) in R. I used Akaike's Information Criterion corrected for small sample size (AICc) to rank models (Burnham and Anderson, 2002) and assessed AICc weights (ω) and ΔAICc to evaluate model support (Burnham and Anderson, 2002). I did not consider models with ΔAICc ≥2.00 to be supportive (Burnham and Anderson, 2002).

Results

I captured flying squirrels over 2,817 trap nights in May-July 2024 and 60 nest box nights in December 2024. From all sampling methods combined I captured 14 flying squirrels (three in summer from Sherman live traps, 11 in winter recovered from nest boxes) and radio-marked 10 individuals (six males, four females). Three juveniles did not meet the weight threshold for collaring, and one adult died by capture myopathy and was deposited as a voucher specimen in the Kansas State Biorepository. I marked three individuals (all females) in summer and seven (six males, one female) in winter. I recorded 431 total locations, with 346 of those at night and 85 during the day, for an average of 43.1 locations per individual (SE = 4.28, range = 36 - 79). I tracked individuals to 85 total nest detections from 40 unique nest localities (average = 4 nests per individual, SE = 0.69, range = 2 - 10).

Mean home-range size for all flying squirrels was 1.55 ha (SE = 0.31) for 95% MCP (range = 0.18 - 3.38 ha) and 5.44 ha (SE = 1.06) for 95% KDE (range = 0.90 - 11.18 ha). My

home-range estimates were smaller when compared to overall means from published literature, but comparable to some estimates from previous studies (Table 2.2, Figure 2.2). Mean home-range size based on six males was 1.56 ha (SE = 0.42) for 95% MCP (range = 0.25 - 2.92 ha), and 6.44 ha (SE = 1.53) for 95% KDE (range = 1.33 - 11.18 ha). Mean home-range size based on four females was 1.54 ha (SE = 0.69) for 95% MCP (range = 0.18 - 3.38 ha) and 3.94 ha (SE = 1.77) for 95% KDE (range = 0.90 - 9.06 ha). Mean home range size for summer 2024 based on three female individuals was 1.99 ha (SE = 0.70) for 95% MCP, ranging from 1.89 ha to 3.38 ha, and 4.95 ha (SE = 2.06) for 95% KDE, ranging from 2.72 ha to 9.06 ha. Mean home range size in winter 2024 based on 10 individuals was 1.36 ha (SE = 0.40) for 95% MCP, ranging from 0.18 ha to 2.92 ha, and 5.65 ha (SE = 1.51) for 95% KDE, ranging from 0.90 ha to 11.18 ha.

Table 2.2 Compiled mean home range estimates of southern flying squirrels (*Glaucomys volans*) from previous studies. Table includes: author and year of study; location of study; which seasons the studies occurred; method used for home range estimation (MCP = minimum convex polygon, KDE = kernel density estimation); mean home range size estimations (ha) for all flying squirrels, males and females; total sample size; and sample sizes of males and females. Home range estimates from Gilmore and Gates (1982) were not included in mean MCP or KDE home range sizes from all previous studies. Any non-numbered method uses either 95% MCP or 95% KDE method. Alternative home range estimation methods are listed below:

[1] Minimum home range or polygon method (Hayne, 1949)

[2] Adjusted range length method (Layne, 1954)

[3] Modified minimum home range area (Habvey and Barbour, 1965)

[4] Minimum home range area (Mohr, 1947)

Study	Location	Season	Method	Overall (ha)	Male (ha)	Female (ha)	Total Samples	Male Samples	Female Samples
Madden (1974)	New York, USA	All	MCP[1]	0.47	0.53	0.41	22	12	10
Gilmore and Gates (1982)	Maryland, USA	All	Adjusted range length[2]	2.38	3.49	1.89	13	4	9
Bendel and Gates (1987)	Maryland, USA	Summer	MCP[3]	2.26	2.45	1.95	8	5	3
Fridell and Litvaitis (1991)	New Hampshire, USA	Summer	MCP	6.65	9.90	3.40	8	4	4
Stone et. al (1997)	Arkansas, USA	Winter	MCP[4]	5.50	7.80	3.80	12	5	7
Taulman and Smith (2004)	Arkansas, USA	Summer	KDE	10.03	16.03	5.88	44	18	26

Holloway and Malcolm (2007)	Ontario, Canada	Summer	MCP	3.03	3.07	2.99	13	6	7
Holloway and Malcolm (2007)	Ontario, Canada	Summer	KDE	5.14	5.25	5.02	13	6	7
Jacques et al. (2017)	Illinois, USA	All	KDE	10.39	10.49	10.28	56	29	27
Howard et. al (2020)	Illinois, USA	Summer	MCP	1.72	2.11	1.46	10	4	6
Howard et. al (2020)	Illinois, USA	Summer	KDE	1.29	1.51	1.14	10	4	6
Mean from previous studies			MCP	3.27	4.31	2.34	-	-	-
Mean from previous studies			KDE	6.71	8.32	5.58	-	-	-
Current Study	Kansas, USA	Summer, Winter	MCP	1.55	1.56	1.54	10	6	4
Current Study	Kansas, USA	Summer, Winter	KDE	5.44	6.44	3.94	10	6	4

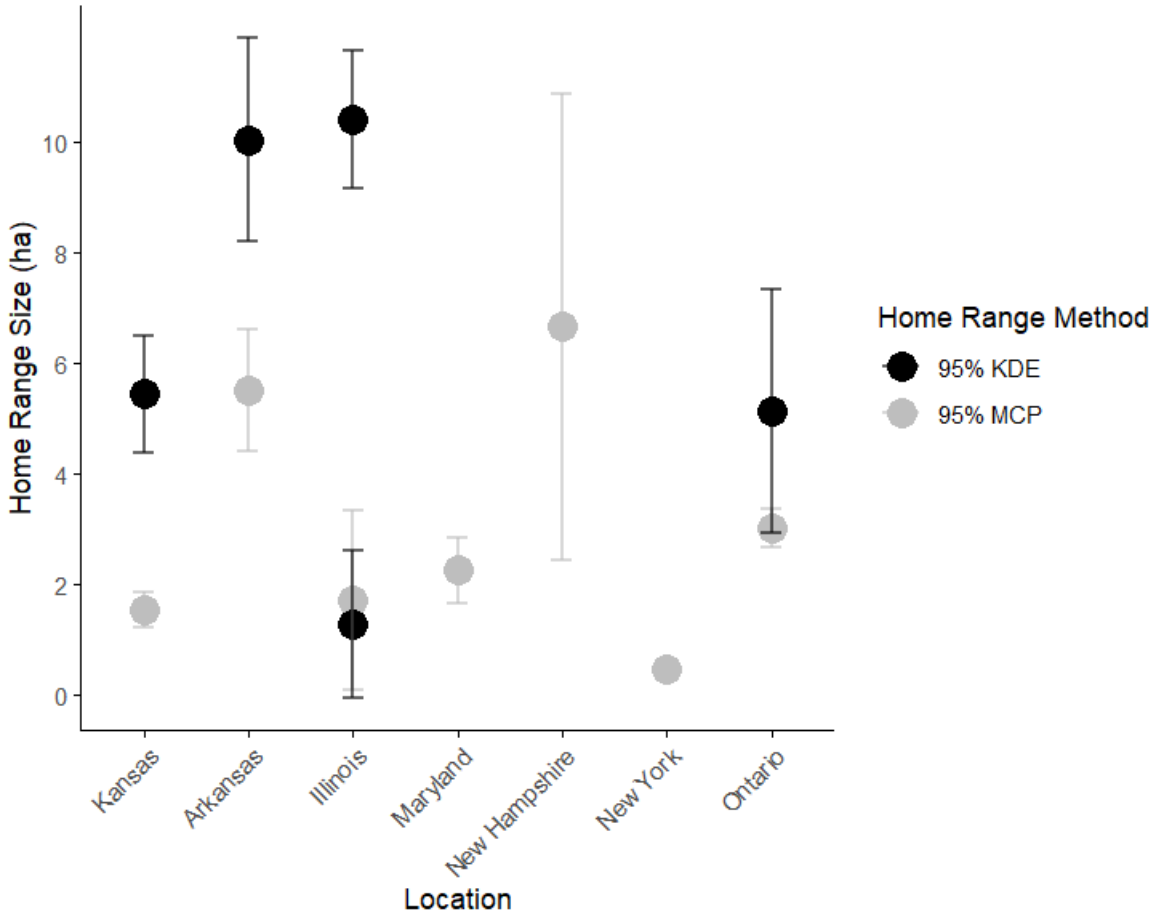

Figure 2.2 Mean 95% minimum convex polygon (MCP; black) and 95% kernel density estimate (KDE; gray) home range sizes (ha) of southern flying squirrels (*Glaucomys volans*) in locations of previous studies, including Kansas, USA. Standard errors are included as bars above and below each point. Arkansas and Illinois each include two studies, and all other locations include one study.

The most parsimonious model for factors influencing 95% MCP home range size was number of nest sites ($\omega = 0.62$; $\beta = 0.366$, SE = 0.143; Table 2.3). However, the second-best model (null) was also competitive ($\omega = 0.27$; Table 2.3). The most parsimonious model for factors influencing 95% KDE home range size was the null model ($\omega = 0.49$; Table 2.3). The number of nest sites model was also competitive ($\omega = 0.27$; Table 2.3) but this variable estimate included a wide 95% confidence interval ($\beta = 0.958$, SE = 0.562). Flying squirrel home-range size increased as more nest sites were occupied within the home-range (Fig. 2.3).

Table 2.3 Model rankings for predicting home-range sizes (95% Minimum Convex Polygon and 95% Kernal Density Estimate) for radio-marked southern flying squirrels (*Glaucomys volans*) in Kansas, USA in 2024. Models are ranked by ascending ΔAICc (change in Akaike Information Criterion corrected for small sample sizes). K = number of estimable parameters, ω = model weight, LL = measure of model fit. Independent variables include Nest Sites (number of nesting sites used), Season (winter or summer), Total Locations (number of locations used to estimate home-range size), Sex (male or female). I also included an intercept-only model (Null) for each model set for comparison.

Model	***K***	**ΔAIC_c**	**ω**	**Log likelihood**
		95% Minimum Convex Polygon		
Nest Sites	3	0.00	0.62	-11.48
Null	2	1.70	0.27	-14.47
Season	3	5.17	0.05	-14.06
Total Locations	3	5.73	0.04	-14.35
Sex	3	5.98	0.03	-14.47
		95% Kernal Density Estimate		
Null	2	0.00	0.49	-26.72
Nest Sites	3	1.19	0.27	-25.17
Sex	3	2.97	0.11	-26.06
Total Locations	3	4.14	0.06	-26.65
Season	3	4.20	0.06	-26.68

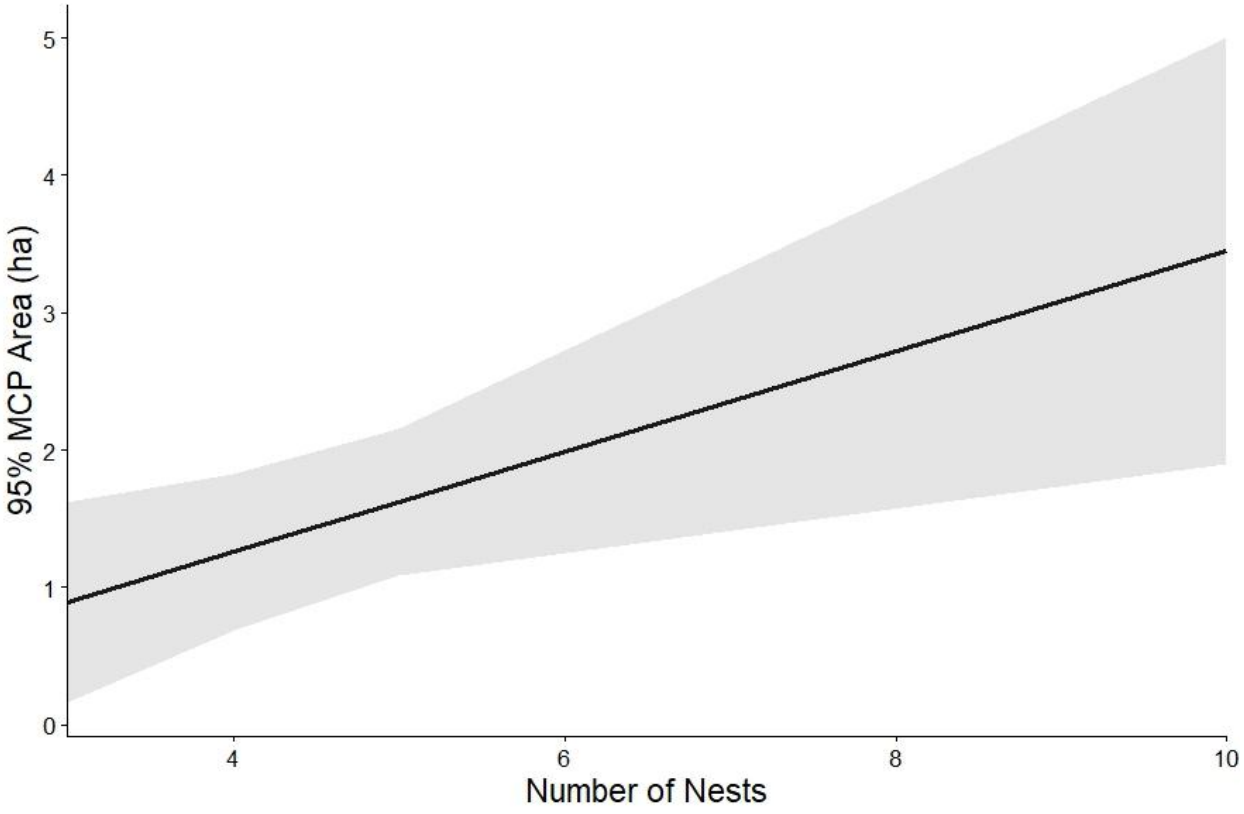

Figure 2.3 Home range size with 95% *CI* (shaded gray) by southern flying squirrels (*Glaucomys volans*) in Grand Osage Wildlife Area, Kansas, USA based on number of unique nest sites located during daytime tracking. Unique nest locations (n = 40) were located in summer and winter 2024 for an average of four nests per flying squirrel.

I surveyed 587 trees at nest-sites and 1,135 trees at random sites. The most parsimonious model ($\omega = 0.67$, Table 2.4) for predicting nest-site use included effects of tree richness ($\beta = 0.694$, SE = 0.234) and mean DBH ($\beta = 0.574$, SE = 0.218). Probability of nest-site use increased with greater tree richness and larger trees surrounding the nest tree (Figure 2.4a, b).

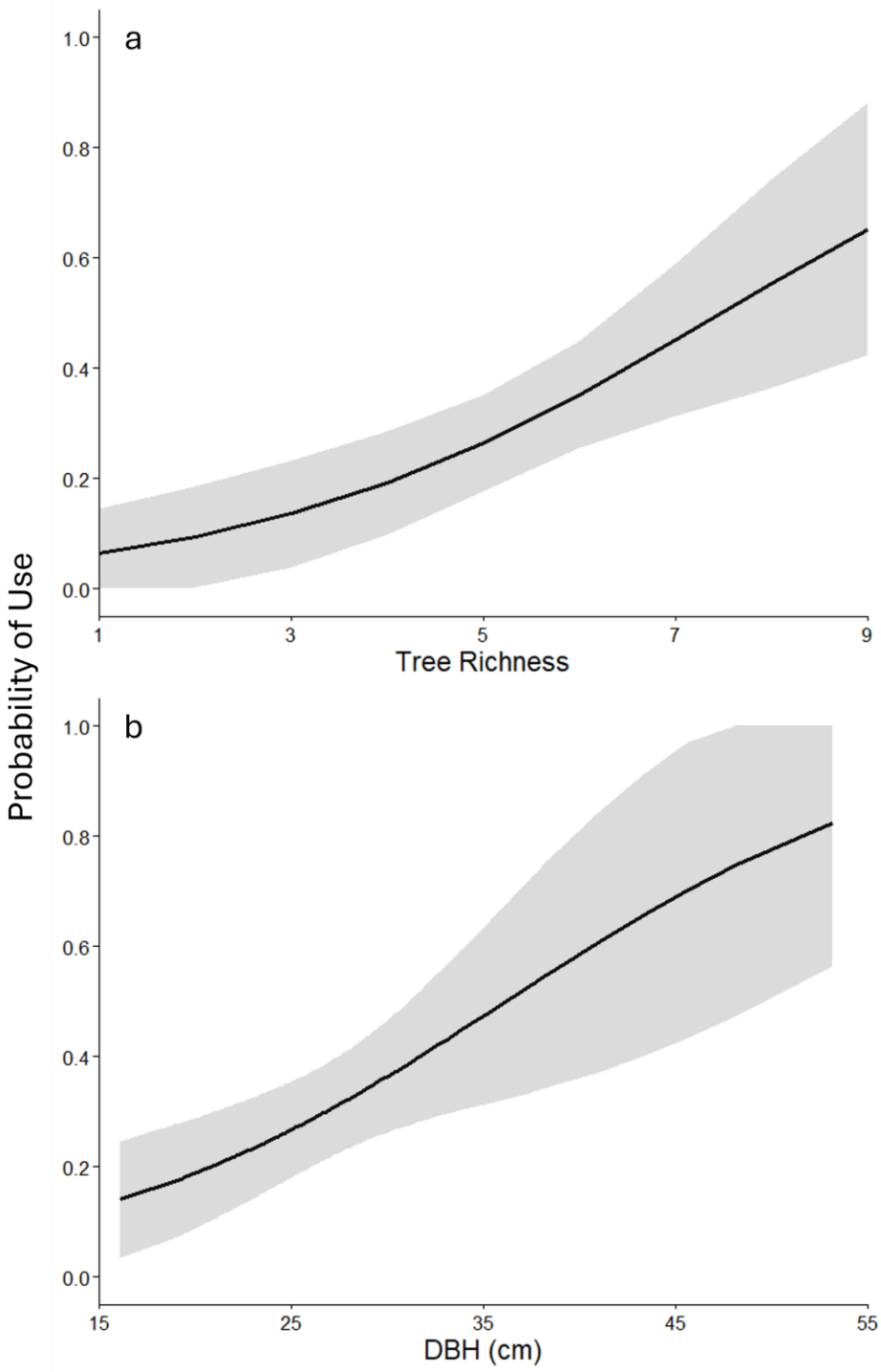

Figure 2.4 a) Probability of nest site use with 95% *CI* (shaded gray) by southern flying squirrels (*Glaucomys volans*) in Grand Osage Wildlife Area, Kansas, USA based on number of unique genera of trees surveyed (Tree Richness) within 0.03 ha area surrounding nest tree. Nest sites (n = 40) and random sites (n = 85) were located and surveyed for analysis in summer and winter 2024. b) Probability of nest site use with 95% *CI* (shaded gray) by southern flying squirrels (*Glaucomys volans*) in Grand Osage Wildlife

Area, Kansas, USA based on diameter of breast height (DBH) of trees surveyed within 0.03 ha area surrounding nest tree. Nest sites (n = 40) and random sites (n = 85) were located and surveyed for analysis in summer and winter 2024.

I recorded 40 independently used nest trees (20 hard mast-producing trees and 20 other tree types, Table 2.4) and 55 randomly selected available trees (33 hard mast-producing trees and 22 other tree types). The most parsimonious model ($\omega = 0.56$, Table 2.4) for predicting nest tree use included effects of tree type (hard-mast trees $\beta = -0.893$, SE = 0.347; other trees $\beta = 0.861$, SE = 0.798) and mean DBH ($\beta = 1.130$, SE = 0.276). Effect of 'Season' was included in the next-best model, however inclusion of 'Season' did little to improve model fit relative to the top-ranked model (Table 2.5). Flying squirrels were more likely to nest in trees with larger DBH (Figure 2.5). Flying squirrels were more likely to select other tree types (probability of use = 0.393, range = 0.247 – 0.560) over hard mast-producing trees (probability of use = 0.215, range = 0.113 – 0.368) as nest trees (Figure 2.6).

Table 2.4 List of tree genera used by southern flying squirrels (*Glaucomys volans*) as nesting locations in Grand Osage Wildlife Area, Kansas, USA in 2024. Unique nest locations (n = 40) were located in summer and winter 2024 for an average of four nests per flying squirrel.

Tree Genera	Count
Red oak	10
Ash	6
Hickory	6
American elm	4
Snag	4
Maple	3
Walnut	3
Cottonwood	1
Osage orange	1
Sycamore	1
White oak	1

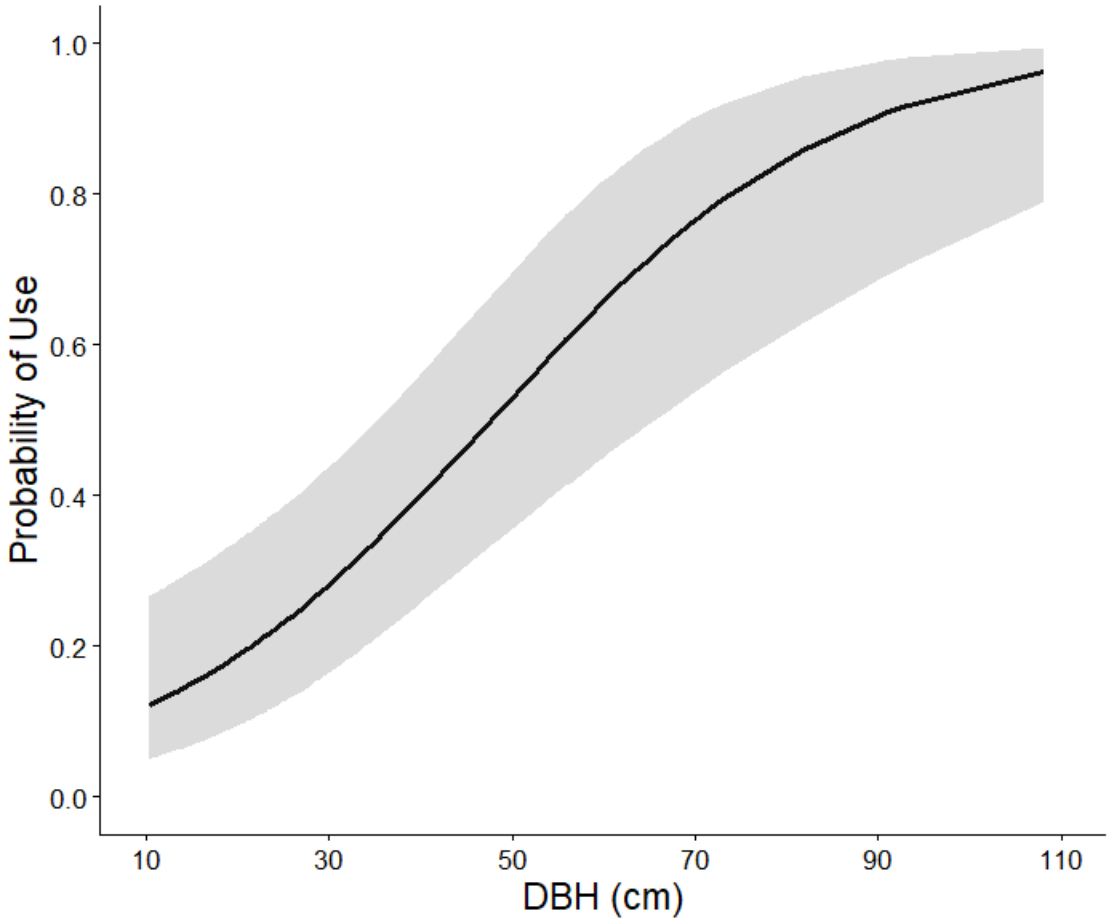

Figure 2.5 Probability of nest tree use with 95% *CI* (shaded gray) by southern flying squirrels (*Glaucomys volans*) in Grand Osage Wildlife Area, Kansas, USA based on diameter of breast height (DBH) of observed nest trees. Independent nest trees (n = 40) were observed and compared to randomly selected trees (n = 85) from surveyed random sites in summer and winter 2024.

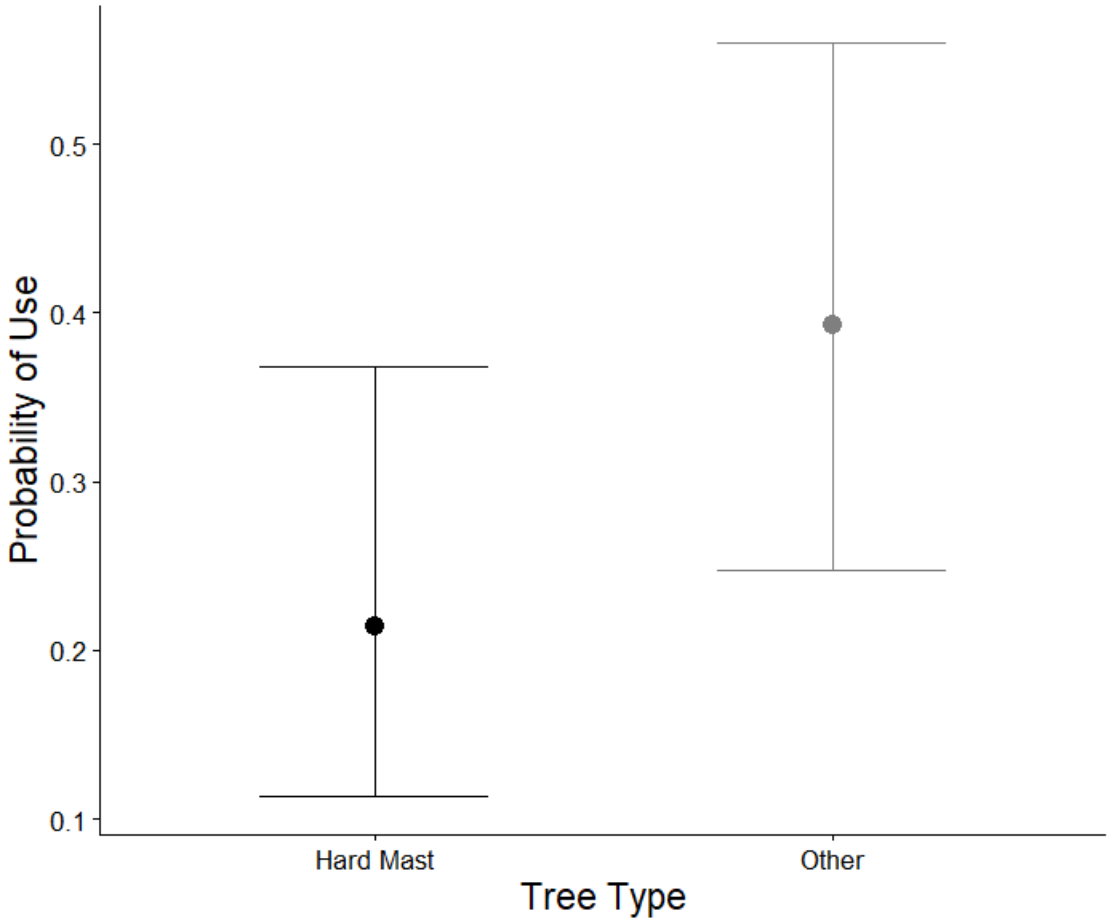

Figure 2.6 Probability of nest tree use with 95% *CI* (shaded gray) by southern flying squirrels (*Glaucomys volans*) in Grand Osage Wildlife Area, Kansas, USA based on categorized tree types. Hard mast includes all hard mast-producing trees and other includes non-hard and soft mast-producing trees and snags. Independent nest trees (n = 40) were observed and compared to randomly selected trees (n = 55) surveyed from random sites ≥ the mean diameter at breast height of observed nest trees in summer and winter 2024.

Table 2.5 Model rankings for predicting nest site and nest tree selection for radio-marked southern flying squirrels (*Glaucomys volans*) in Grand Osage Wildlife Area, Kansas, USA in 2024. Models are ranked by ascending ΔAICc (change in Akaike Information Criterion corrected for small sample sizes). K = number of estimable parameters, ω = model weight, LL = measure of model fit. Independent variables include Tree Richness (number of unique tree genera), DBH (diameter at breast height), Season (winter or summer), Tree Density (number of total trees surveyed), Hard Mast (number of hard mast-producing trees surveyed), Soft Mast (number of soft mast-producing trees surveyed), Other (number of other trees(non-hard or soft mast-producing trees surveyed), Snag (number of snags surveyed), Tree Type (categorical variable for number of hard mast-producing trees and all other trees surveyed which includes soft mast-producing trees, snags, and non-hard or soft mast-producing trees), and Canopy Cover (percent canopy cover at nest tree or random location) . I also included an intercept-only model (Null) for each model set for comparison.

Model	***K***	**ΔAIC_c**	**ω**	**Log likelihood**
		Nest-Site Selection		
Tree Richness + DBH	3	0.00	0.67	-71.99
Tree Richness + DBH + Season	4	2.10	0.23	-71.97
Tree Richness	2	5.15	0.05	-75.62
DBH	2	7.83	0.01	-76.95
Null	1	8.57	0.01	-78.36
Tree Density	2	9.18	0.01	-77.63
Hard Mast	2	9.27	0.01	-77.67
Soft Mast	2	9.98	0.005	-78.03
Other	2	10.13	0.004	-78.11
Snag	2	10.24	0.004	-78.16
		Nest-Tree Selection		
Tree Type + DBH	3	0.00	0.56	-52.37

Tree Type + DBH + Season	4	0.50	0.44	-51.53
DBH	2	17.31	0.0001	-62.11
Tree Type	2	21.50	0.00	-64.19
Null	1	47.74	0.00	-78.36
Canopy Cover	2	49.78	0.00	-78.35

Discussion

I found home-range sizes for flying squirrels were comparable to estimates from previous literature elsewhere in their range. While overall male and female mean home-range sizes from my study are smaller than mean values from previous studies combined, they are still within the range of estimates recovered elsewhere. My overall mean 95% MCP home range size is comparable to an estimate from Illinois, USA (Howard et al., 2020), and my overall mean 95% KDE home range size is comparable to an estimate from Ontario, Canada (Holloway and Malcolm, 2007). My moderate sample size is also consistent with previous studies. Thus, my prediction that home range sizes from my study would be larger than estimates from previous studies was not supported.

Home-range size can be a useful resource for understanding space and habitat requirements of species (Mitchell et al., 2002; Powell, 2000), which may in turn help to assess habitat quality coincident with a given home range (McLoughlin et al., 2000). McLoughlin et al. (2000) suggested home range sizes are smaller in high-quality habitat, because an individual can survive on available resources in close proximity (Bailey, 1974). This pattern is consistent with those seen from the central place foraging theory, where an individual would not need to travel

far from their central place (e.g. nest or den) when resources are abundant (Orians, 1979). Because my mean home-range sizes are lower than mean home range sizes from previous literature combined, it is plausible that habitat quality for flying squirrels in my study area is equal to or greater than habitat quality towards the interior of the flying squirrel's range. However, further research is required to evaluate habitat quality for flying squirrels in Kansas as related to other variables, including survival, population growth, and local densities (Fretwell and Lucas, 1969; Van Horne, 1983).

My study found that flying squirrel home-range sizes did not vary due to season or sex for either MCP or KDE methods. Mean 95% MCP home range size for males (1.56 ha) and females (1.54 ha) were similar, but more varied for 95% KDE home range sizes (male = 6.44 ha, female = 3.94 ha). While there appears to be some difference in mean home-range sizes between summer (MCP = 1.99 ha, KDE = 4.95 ha) and winter (MCP = 1.36 ha, KDE = 5.44 ha), season was not a competitive model. I only tracked three flying squirrels in the summer and all of them were female. In winter, I only tracked one female, and the other six were male. My results possibly reflect this disproportionate sample and make interpretation tenuous given that I do not know how home range size varies across seasons, or in relation to other variables such as reproductive activity. However, my estimates were derived using similar sample sizes from past studies and provide a good baseline for comparison of other peripheral populations throughout the range of flying squirrels.

Total number of locations detected for an individual flying squirrel also did not influence either MCP or KDE home range sizes. However, 95% MCP home-range size was positivity related to the number of nest sites individual flying squirrels maintained within their home range. This parallels the relationship observed between muskrat (*Ondatra zibethicus*) home-range size

and the number of burrows they occupy (Ahlers et al., 2010), suggesting that flying squirrels are possibly acting as multiple central-place foragers (Ahlers et al., 2010; Orians, 1979) through nest switching (Steinhoff et al., 2012). As a result, flying squirrel home-range size may be less influenced by amount of food resources available, and more by availability of cavities for nest sites and abundance of other flying squirrels within a home range.

My study suggests flying squirrels selected areas with greater tree richness. Though flying squirrels may be considered as habitat generalists without a requirement of a specific stand type (Muul, 1968), there are no studies indicating tree species richness near the nest-site influenced site selection (Campuzano-Chávez-Peón et al., 2014; Steinhoff et al., 2012; Zweep et al., 2018). My results support suggestions that nesting requirements could be filled by having a wide range of resources (Taulman, 1999). This is important in the context of a population occurring at their range limit, where forest diversity is generally considered to be lower than in the interior of their range (Litte, 1999).

My prediction that flying squirrels would select nest sites in areas of increased availability from hard mast-producing trees was not supported. While flying squirrels used hard mast-producing trees, mainly oaks, and other tree types (soft mast-producing trees, snags, and other seed-producing trees) an equal amount as nest trees, they selected other tree types over hard mast-producing trees of a similar DBH, relative to availability. This pattern is not consistent with previous studies suggesting hard mast-producing trees play a major role in nest-tree selection (Campuzano-Chávez-Peón et al., 2014; Holloway and Malcolm, 2007b; Zweep et al., 2018). In other parts of their range, oak and beech (*Fagus* spp.) were the most used live trees for cavity nests (Bendel and Gates, 1987; Holloway and Malcolm, 2007b; Taulman, 1999; Zweep et al., 2018). Given that the geographic range of beech does not include Kansas (Tubbs and

Houston, 1990), use of hard mast-producing trees overall in Kansas could be limited by their availability, forcing squirrels to select for other types of trees. Howard et al. (2020) found flying squirrels selected for soft mast-producing trees over hard mast-producing trees more than expected. Their study was conducted during spring and summer when soft mast-producing trees would be fruiting and before hard masting season begins (Thorington and Ferrell, 2006), and they suggested that food resources provided by each tree type could have influenced selection of these trees. However, my study was conducted during summer and late winter, giving opportunities for both tree types to provide resources for flying squirrels during the study, and yet I did not find season to influence nest-tree selection. This supports selection of tree species based on tree structure more than availability of resources provided.

Hard mast-producing trees exhibit slow growth (Buckley et al., 1998), so they reach maturity later than other species. This is evident in Kansas, where eight of the ten fastest growing species are non-hard mast-producing trees: hackberry, osage orange, eastern redcedar, American elm (*Ulmus americana*), green ash, black walnut (*Juglans nigra*), honey locust, plains cottonwood (*Populus deltoides*), red mulberry (*Morus rubra*), and pecan (*Carya illinoinensis*) (Moser et al., 2013). Of the two hard mast-producing trees on this list, pecans are not widely distributed in Kansas, and timber removals and tree pathogens (e.g., thousand cankers disease) have limited population increases for the black walnut (Moser et al., 2013; Peterson, 1990). Additionally, while Kansas forests continue to mature, they are still young overall, with a majority of stands aged 30-60 years (Moser et al., 2013). Because tree maturity can result in more decay and availability of cavities, paired with younger-aged forests in Kansas, flying squirrels may be selecting for non-hard mast-producing trees that reach maturity faster than hard mast-producing trees.

My prediction that flying squirrels would select nest sites with increased tree diameter was supported, but availability of snags was not. Flying squirrels selected for larger DBH trees surrounding the nest tree and for the nest tree itself. This is consistent with results elsewhere (Campuzano-Chávez-Peón et al., 2014; Holloway and Malcolm, 2007b; Taulman, 1999; Zweep et al., 2018). Increased tree diameters have been linked to increased tree maturity (Łukaszkiewicz et al., 2005) and number of available cavities for nest sites due to natural decay coupled with woodpecker activity (Bendel and Gates, 1987; Bush et al., 2009; Loeb, 1993). Bendel and Gates (1987) suggested the availability of cavities influences nest-site selection more than structure of the surrounding forest. Additionally, larger DBH trees can reduce the energetic costs of climbing and gliding (Howard et al., 2020; Scheibe et al., 2006). Large trees are more stable for take-off (Howard et al., 2020; Suzuki and Yanagawa, 2019), provide a wider target for landing (Bendel and Gates, 1987; Howard et al., 2020; Krishna et al., 2016), and often have textured bark for climbing (Bendel and Gates, 1987). These advantages in the area surrounding the nest site would allow easy access and movement for an almost exclusively arboreal species. Cavities inside large diameter trees might also allow for more stable temperatures across all seasons when compared to smaller trees (Coombs et al., 2010). Larger DBH trees are also more likely to develop dead branches creating natural cavities for nesting when limbs break (Bendel and Gates, 1987; Holloway and Malcolm, 2007b).

Snag availability was thought to potentially influence flying squirrel nest-tree selection because natural and woodpecker-excavated cavities are commonly found in these dead standing trees (Muul 1968, Holloway and Malcolm 2007*a*, Jacques et al. 2017, Zweep et al. 2018). However, this was not supported by my results at the nest-site level. This could be a result of lower overall snag density in relatively young forest of Kansas, compared to other parts of their

geographic range (Jacques et al., 2017, Moser et al., 2013). At the nest-tree level, I included snags in the other tree type category which collectively was considered important for nest site choice. However, my results likely reflect selection of seed-producing trees rather than snags, as snags made up only 10% of nest trees used in my study. Non-hard mast-producing trees are also more likely to become snags than hard mast-producing trees (Moser et al., 2013) given their relative age versus longevity. But, based on the evidence from previous literature, I would still recommend snag retention as a forest management practice benefiting flying squirrels in Kansas going forward.

My prediction that flying squirrels would select for nest sites with reduced predation risk from increased canopy cover was not supported. This result concurs with Zweep et al. (2018). The lack of support in my study is most likely due to age homogeneity of the younger-aged forest stand (Moser et al., 2013). My study area has likely not had enough time for complex canopy layers to develop, resulting in similar canopy cover measurements across used and random sites. Also, much of my data collection was during winter, after most leaves had fallen off trees, further complicating estimates of canopy cover between used and random areas.

There are some biases that exist in my study that may have affected results. Some flying squirrels were captured out of the same box (four from one box and two from another). Additionally, these flying squirrels were often observed sharing the same diurnal nests during winter tracking and located at the same locations at night. This could be due to familial relatedness or familiarity from socialization while forming aggregations (Garroway et al., 2013; Layne and Raymond, 1994; Thorington and Weigl, 2011). Nonetheless, my results are mixed regarding consistency with previous studies on flying squirrels. In central and northern parts of their range, flying squirrel nesting habitat is characterized by an abundance of mature hard mast-

producing trees and snags that provide ample cavities for nests. At my study site, nesting habitat requirements were fulfilled through younger, more diverse forest stands with larger DBH trees regardless of species. Even though tree diversity and abundance of quality habitat may be assumed lower at the flying squirrel range periphery in Kansas, as stated by the center-periphery and abundant-center hypotheses, this may not limit their nest selection and space use at smaller densities. Given the influence of nest availability on home-range size from my study, this can be critical habitat to conserve. In order to maintain quality nesting habitat for flying squirrels as Kansas forests age, it can be good for managers to retain snags and consider multiple metrics of forest diversity as hard mast-producing trees continue to mature. This can include managing tree richness to be ≥8 genera per 300 m^2 for a probability of use ≥0.5 at those sites and allowing hard mast-producing trees to develop a minimum of 50 cm DBH for a probability of use ≥0.5 at both the nest-site and nest-tree levels.

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