forests

Review

# Gap Crossing in Flying Squirrels: Mitigating Movement Barriers through Landscape Management and Structural Implementation

**Jeremy M. Howard**

Department of Biology, University of Missouri St. Louis, St. Louis, MO 63121, USA; jh5ym@umsystem.edu

**Abstract:** Habitat fragmentation affects flying squirrels despite their ability to cross canopy gaps. If unable to cross gaps, flying squirrels may suffer from limited access to appropriate resources, inbreeding depression, and even extirpation. North American flying squirrels (*Glaucomys*) have been the focus of limited research on this issue when compared to other areas of the world tackling this problem. However, as all gliding mammals share similar conservation challenges, findings of other species on other continents can be applied to the *Glaucomys* species in North America. The purpose of this review is to take a metapopulation approach to the problem of gap crossing. This review first discusses necessary habitat conservation strategies for *Glaucomys* within the patches they reside. The review then discusses patch size and configuration, honing in on maintaining connectivity between habitat patches. Different structures (natural and manmade) used to maintain connectivity are reviewed using gliding mammal literature from around the world. This information is pertinent to North American conservation ecologists and landscape managers, who can use this information to improve habitat connectivity and facilitate crossings of *Glaucomys* flying squirrels within metapopulations.

**Keywords:** habitat fragmentation; gap crossing; flying squirrel; landscape management



**Citation:** Howard, J.M. Gap Crossing in Flying Squirrels: Mitigating Movement Barriers through Landscape Management and Structural Implementation. *Forests* **2022**, *13*, 2027. https://doi.org/10.3390/f13122027

Academic Editor: Jordan M. Marshall

Received: 8 September 2022
Accepted: 26 November 2022
Published: 30 November 2022



## 1. Fragmentation and Gliding Mammals

One of the biggest challenges small mammals face is habitat fragmentation. Fragmentation, whether due to agriculture, urban development, or timber harvesting, initiates change in a forest ecosystem. The most notable change is the creation of matrix habitat, which can contain roads, open fields, pastures, or recovering habitat from past disturbances [1–3]. On a population level, the matrix creates gaps for small mammals to cross for food, shelter, dispersal, or reproductive opportunities. Depending on the size and quality of a given forest stand or vegetation clump (i.e., patch), the home range size of small mammals may exceed the patch itself, necessitating movements to adjacent patches. Gap crossing comes with large amounts of risk for these small mammals, particularly from predation through exposure in open environments [4–6]. On a landscape level, fragmented landscapes may create a patchy network of habitat conducive to metapopulation dynamics. Metapopulations consist of multiple smaller populations existing together in different habitat patches of varying quality [7]. For small mammal metapopulations to persist, they must be able to move between fragmented landscapes to recolonize extirpated patches and interbreed. The number of individuals in a given patch is dictated by a variety of factors, including connectivity, isolation distance, intrinsic rate of extinction, colonization, patch size, patch shape, and patch quality [7]. Sustaining small mammal populations in these fragmented landscapes requires a metapopulation focus. Of the small mammals, flying squirrels are an underrepresented group in the literature yet are heavily affected by fragmentation and gap crossing and require additional attention.

Flying squirrels face distinct challenges unlike other small mammals because of their specialized morphology. The evolutionary design of flying squirrels has allowed for energetically cheap gliding through use of a retractable patagium and development of longer humeri and femora [8–11]. However, flying squirrels are not efficient runners because of this design, and expend significantly more energy running when compared to other small mammals [12]. With these morphological and energetic trade-offs, ground crossings are particularly challenging. As a result, flying squirrels are easy prey for avian and mammalian predators (e.g., owls, martens, foxes) when running over open areas [13]. To avoid ground crossings, flying squirrels rely on trees to move through their environment. When gaps such as roads and open fields are encountered, gliding across may be feasible if a tall enough structure is present or the distance is within the gliding capability of the species [14]. This gliding capability is represented by the glide ratio, which is the horizontal distance covered per unit of vertical drop for a given species. The height of the launch structure and glide ratio both factor into gap crossing potential for flying squirrels. If gaps are too large or if no plausible structures to glide from exist, ground crossings will be inevitable [15].

Flying squirrels need to cross gaps for a number of reasons. For example, food resources within a single patch may be inadequate, necessitating movement to new areas to forage [16] or retrieve food from caches [17]. This increased foraging range is reflected in the larger home range sizes seen in both Northern and Southern Flying Squirrels in various patchy landscapes around North America resulting from development and logging [18–21]. Additionally, dispersal across gaps by juveniles is necessary to access breeding sites and avoid inbreeding [22,23]. Differences between male and female reproductive strategies also affect crossing decisions. For instance, male flying squirrels typically roam through a forest to optimize copulatory encounters [24–26], which may involve crossing between forest patches. Unlike males, females typically establish territories to rear young [24–26].

Due to the fragmented landscapes flying squirrels inhabit, and the trade-offs of their morphology, mitigating the effect of gaps is crucial for their conservation in North America. If left unchecked, habitat fragmentation will interrupt gene flow. A variety of gliding mammals (including flying squirrels) suffer from genetic isolation and low genetic variability in these landscapes [27–31]. There is much to consider when addressing the issue of gap crossing, and research within North America is limited. The purpose of this review is to identify habitat improvement strategies from the international literature on gliding mammals for landscape managers and conservation ecologists of *Glaucomys* flying squirrels. These recommended strategies incorporate findings of the *Glaucomys* species habitat requirements in North America and studies on gliding mammals and gap crossing around the world. This review covers vital material that will ensure metapopulations of *Glaucomys* can access appropriate resources, resist inbreeding depression, and avoid extirpation.

## 2. Landscape Management Considerations

### *2.1. Habitat Quality*

High habitat quality within a patch is necessary to sustain flying squirrel subpopulations and its maintenance should be top priority. In North America, *Glaucomys* populations have declined in heavily harvested areas. Northern Flying Squirrels (*Glaucomys sabrinus*) occur in greater numbers in old growth forests with more habitat cover [32–34] versus thinned and logged stands [35,36]. Stands with larger diameter and larger snag trees also yield higher populations, many of which reside close to water sources [37]. High value foods items (e.g., conifer seeds, truffles, and lichens) are more prevalent in these old growth forests [38] and timber harvests negatively affect their growth [38,39]. When food resources are sparse, Northern Flying Squirrels must move to new patches [39]. Similar findings on Southern Flying Squirrels (*Glaucomys volans*) are reported. Southern Flying Squirrels avoid logged areas and prefer undisturbed mature stands when available [18,40] Additionally, habitat near water sources is crucial for survival [18,41]. Secondary growth patches resulting from development are less sufficient for food, predator protection, or shelter [42]. When resources are limited, Southern Flying Squirrels also increase their home ranges to compensate [18,21].

Habitat conservation for flying squirrels starts with protecting specific trees. Northern Flying Squirrels require trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and yellow birch (*Betula alleghaniensis*) in hardwood dominated areas [43]. As hypogeous fungi are a major food source of Northern Flying Squirrels, spruce-fir and mixed spruce-fir habitats have been identified as areas of high fungal growth. Trees with high fungal growth include red spruce (*Picea rubens*), beech (*Fagus grandifolia*), red oak (*Quercus rubra*), and yellow birch (*Butea lutea*), and should be protected whenever possible [44]. Southern Flying Squirrels require mature hardwood forest for mast (nuts and seeds) [18,41] which includes oak (*Quercus*), hickory (*Carya*), and beech (*Fagus*) [43,45–47]. For both Northern and Southern Flying Squirrels, larger (>50 cm dbh), decaying and snag trees should be left standing for cavities, as well as trees near streams (<150 m) for easy water access [18,37,41,43]. In more managed stands, leaving extra canopy (overstory) cover and planting shrubs provides more cover against predators [48]. In the case of Northern Flying Squirrels, this will also promote additional fungal growth [32]. Lastly, taller trees with less cover in the understory should be maintained to create more open glide paths within a patch for both species [42,48].

The maintenance of high-quality forest habitat for *Glaucomys* is a key first step in sustaining metapopulations. With access to adequate food, shelter, and predator protection, habitat patches can sustain subpopulations for longer periods of time. These high quality “source” patches can counterbalance other low quality “sink” patches in a landscape that is recovering from disturbances.

### *2.2. Size and Configuration*

Patch size and landscape configuration are also vital to understand flying squirrel gap crossing capabilities and decisions. Larger patches are more likely to have the required resources to support a subpopulation of flying squirrels [49]. Decreasing patch size leads to lower numbers as a result of fewer resources [50,51], necessitating movement between patches to ensure survival. For example, smaller patch sizes have led to increased crossings by Siberian Flying Squirrels (*Pteromys volans*) to find necessary resources in the agriculture landscapes of Finland [16]. It has been recommended that patch sizes should be >10 $m^2$ per hectare of live residual stand structure in mature forests to support flying squirrels [35].

Landscape configuration includes three components: patch distribution, connectivity, and patch surroundings (e.g., natural, agricultural, urbanized, suburban). First, patch distribution refers to how close individual habitat patches are in relation to one another. Patches located close together have higher flying squirrel occupancy over distant patches, irrespective of quality [49,51–53]. Patches closer together should be treated as higher priority for protection over distant patches. Second, patch connectivity is the level of accessibility of adjacent patches in the landscape. Prior studies report patch size and quality as more important over landscape configuration to support flying squirrels [33,54]. However, landscapes are largely heterogeneous because of human interference, and the size and quality of habitat patches cannot always be maintained. When this is the case, maintaining connectivity between patches is imperative to flying squirrel metapopulation persistence. An example of the importance of connectivity can be seen through the disruption of Siberian juvenile flying squirrel dispersal pathways. Juveniles that normally disperse in a straight line to another patch in connected landscapes must move longer distances amongst unconnected patches and roost in low quality patches, expending valuable energy and creating fitness losses [22]. Similar trends are seen in Southern Flying Squirrels in Indiana when moving to smaller sized patches (<3.7 ha). These patches can have greater distances between them (less connectivity), and incur greater latencies in movement [55]. Third, patch surroundings can influence crossing. Not all surroundings are the same, and this can affect crossing decisions. An example of this can been seen in urban habitats. Urban habitats cause flying squirrels to travel farther distances to suitable habitat, moving through urbanized areas at faster rates over non-urbanized areas to cover the greater distances [56], likely as a result of fewer trees and cover. Flying squirrels may also have to cross more roads and heterogeneous landscapes because of human infrastructure and development [57,58], which may prevent crossings or lead to fatalities.

When given a more contiguous landscape configuration, flying squirrels will avoid gaps altogether. Translocation experiments of Northern Flying Squirrels in Canada effectively illustrate this point. These experiments aimed to understand the pathways squirrels take to reach their home territory upon displacement [59]. A major predictor in Northern Flying Squirrel gap crossing from this study was detour efficiency, which considers both gap distance and the distance to go around the gap. Northern Flying Squirrels were found to predominantly move around gaps even when the distance to cross was approximately one-seventh the distance of the gap detour. Similar results were suggested with Siberian Flying Squirrels in their response to gaps and high occupation of forest edges [60]. The decision to spend considerably more time and energy moving around gaps is revealing, as it highlights the importance of cover for movement when traveling. From the translocation study, Female Northern Flying Squirrels were more likely to cross gaps than males, due to female avoidance of other female territories [59]. This differs from expectations between male and female flying squirrels. Males typically have larger home range sizes from moving among multiple female territories, which can include more than one patch [19–21,45,56,61]. While there may be nuances between male and female gap crossing decisions, flying squirrels avoid gaps whenever possible.

A substantial challenge for flying squirrels within fragmented landscapes is dealing with larger gaps. The level of connectivity between patches changes gliding tactics. For instance, Siberian Flying Squirrels often cross gaps 30–70 m in a single glide. However, when gaps exceed this size range, multiple smaller glides are performed using isolated trees to move between habitat patches [22]. A parallel scenario has been described for petaurid gliders in agricultural areas of Australia. Most (95%) occupied woodlands patches were within 75 m of occupied linear woodland strips, suggesting treeless gaps of >75 m set a physical limit to habitat connectivity [62]. Unfortunately, not every landscape is structured in a way that allows for multiple small glides. Roads are a major hurdle that often require a single glide to cross. Van der Ree (2006) [63] has shown this in Squirrel Gliders (*Petaurus norfolcensis*) that cross highways and freeways between forest sections. Freeways were found to act as larger deterrents than highways, as they are six times wider and contain much higher traffic volumes. Larger gaps over these road environments may prove deadly for gliders as falling short on a glide results in mid-air collisions with automobiles or being run over. Glides can also prove deadly when large gaps are present in timber harvesting areas. Northern Flying Squirrels have been documented colliding with barbed wire fences when there is not enough height to clear the obstacle [64].

The challenge for gliding mammals, and thus flying squirrels, lies in the landscape altered by fragmentation that has created gaps too large to safely cross. These gaps, as mentioned above, not only create inconveniences for travel but are actively avoided when possible to mitigate the risk. Maintaining *Glaucomys* flying squirrel metapopulations requires essential habitat be conserved within patches, and that patches maintain high levels of connectivity to ensure effective colonization and dispersal. Strategically adding structures to key points along gaps while factoring flying squirrel morphology and behavior into the design can successfully re-establish connectivity between forest patches over the long term.

#### 2.2.1. Types of Structures and Their Specifications

Gliding mammals have shown great flexibility in their structure usage, including a variety of trees and manmade supports. Four different types of structures have been identified to assist with gap crossing (Table 1): median trees, canopy rope bridges, log bridges, and gliding poles. All of these structures have been used to successfully connect landscapes for various gliding mammal species worldwide, including North American flying squirrels.

1. Median trees. Median trees are individual trees retained in the median of roads or open fields to create "stepping stones" between habitat patches. Siberian Flying Squirrels in Europe, Southern Flying Squirrels in North America, and Mahogany Gliders (*Petaurus gracilis*), Squirrel Gliders, and Sugar Gliders (*Petaurus breviceps*) in Australia have been documented using median trees [16,22,57,58,65–68]. Trees provide cover and are a natural part of a gliding mammal's environment, making them easy to recommend. However, it is necessary to consider the long waiting period following planting. Median tree effectiveness will depend on the size of the gap and tree placement. If placed between habitat patches, trees facilitate crossing by creating several smaller gaps instead of one large gap.

2. Canopy rope bridges. Canopy rope bridges are horizontal rope meshes suspended as direct paths over gaps. These bridges have been used in a variety of locations by Australian gliding mammals, including above land bridges and below highway bridges [15,67,69–72]. Canopy rope bridges are lightweight and easily cover the distance of a gap, allowing for gliding mammals to simply cross regardless of the height of the rope bridge [15,69–71]. One drawback to these bridges is that there is greater exposure to predators, unlike with the natural foliage trees provide.

3. Log bridges. Log bridges involve using wooden utility poles and are similar to canopy rope bridges [73,74]. Wooden poles are positioned horizontally under bridges or above roads to create beams to run across ( Figure 1) [73,74]. Though made of a different material, log bridges confer similar benefits and drawbacks as canopy rope bridges.

**Figure 1.** Example of a log bridge used by the Siberian Flying Squirrel (*Pteromys volans*) in Japan. The photograph shows a log bridge running through a culvert under a road for crossing. Photo captured and provided by Dr. Yushin Asari from Obihiro University of Agriculture and Veterinary Medicine.

4. Gliding poles. Gliding poles are wooden poles placed vertically, either on opposite ends of a gap (such as a road), or at set intervals along a gap to make "stepping stones" similar to median trees (Figure 2) [15,67,72–80]. Though unintended, powerline poles have also been documented to serve the same purpose [66]. Gliding poles can confer many of the benefits of trees, without the extended waiting period associated with planting.

**Table 1.** Summary table of all crossing structures used by gliding mammals, which includes Mahogany Gliders, Squirrel Gliders, Sugar Gliders, Feathertail Gliders, Yellow-Bellied Gliders, Southern Flying Squirrels, Northern Flying Squirrels, and Siberian Flying Squirrels. Crossing structures are broken down into four categories: median trees, canopy rope bridges, log bridges, and gliding poles. All recorded species and their associated studies are included with the listed crossing structure.

| Method | Species Documented | Studies |
|---|---|---|
| Median trees | Siberian Flying Squirrel (*Pteromys volans*) | [16,22,65] |
| | Mahogany Glider (*Petaurus gracilis*) | [66] |
| | Squirrel Glider (*Petaurus nolfolcensis*) | [67,68] |
| | Southern Flying Squirrel (*Glaucomys volans*) | [57,58] |
| Canopy rope bridges | Squirrel Glider (*Petaurus norfolcensis*) | [15,67,69–72] |
| | Sugar Glider (*Petaurus breviceps*) | [15,70,71] |
| | Feathertail Glider (*Acrobates pygmaeus*) | [15,69] |
| Log bridges | Siberian Flying Squirrel (*Pteromys volans*) | [73,74] |
| Gliding poles | Siberian Flying Squirrel (*Pteromys volans*) | [73,74] |
| | Mahogany Gliders (*Petaurus gracilis*) | [66] |
| | Squirrel Glider (*Petaurus norfolcensis*) | [15,67,72,75–78,80] |
| | Sugar Glider (*Petaurus breviceps*) | [15,80] |
| | Feathertail Glider (*Acrobates pygmaeus*) | [15,80] |
| | Yellow-bellied Glider (*Petaurus australis*) | [15,80] |
| | Northern Flying Squirrel (*Glaucomys sabrinus*) | [79] |

**Figure 2.** Example of a set of gliding poles utilized by various gliding mammals in Australia. This photograph shows poles on opposite sides of a highway, designed for glider crossing by species such as Squirrel Gliders (*Petaurus nolfolcensis*), Sugar Gliders (*Petaurus breviceps*), Feathertail Gliders (*Acrobates pygmaeus*), and Yellow-Bellied Gliders (*Petaurus australis*). Photo captured and provided by Dr. Ross Goldingay at Southern Cross University.

Gliding poles should be made tall enough to allow the species to land on the trunk of the receiving structure (a tree or another gliding pole). If roads are present, the glider should clear the height of a truck (~4 m) when crossing [81]. Failure to clear this height can result in mid-flight collisions with automobiles or falling short and becoming roadkill [63]. In addition to the necessary height, poles need appropriate spacing. Poles should be placed at even intervals across the width of the gap when possible, with placement informed by glide ratios. This design creates "stepping stones" to use, and one long, risky or unachievable glide becomes a series of smaller, more manageable glides. Such an approach has found success with Australian Squirrel Gliders in a variety of environments, including pastures, land bridges, and roads [14,15,75–78]. Additionally, suitable launch points are needed atop poles. On trees gliders use horizontal branches to maximize take-off forces when jumping for more successful glides [82]. Launch points can be incorporated as horizontal platforms at the top of poles, as described by Kelly et al. (2013) [79] for Northern Flying Squirrels, and Goldingay and Taylor (2017) [70] for Squirrel Gliders and Sugar Gliders. Incorporating these platforms into structures maximizes the height and potential energy for gliding.

### 2.2.2. Gliding Performance

While structural features and placement require consideration for trees and gliding poles, they mean nothing if the gliding performance of the species has not been reviewed. Every gliding mammal species is characterized by a range of gliding performance values, referred to earlier as the glide ratio. These ratios represent horizontal distance covered per unit of vertical drop and are highly variable, with higher ratios indicating longer glide distances. Southern Flying Squirrels have a ratio of 1.53 [83], Northern Flying Squirrels 1.98 [84], Siberian Flying Squirrels 1–1.5 [85], Red Giant Flying Squirrels (*Petaurista petaurista*) 3.1 [86], Japanese Giant Flying Squirrels (*Petaurista leucogenys*) 1.87 [87], Indian Giant Flying Squirrels (*Petaurista philippensis)* 2.32 [88], Squirrel Gliders 1.84 [81], Yellow-Bellied Gliders (*Petaurus australis*) 2.0 [89], and Sugar Gliders and Mahogany Gliders, 1.82 and 1.91 respectively [11]. When implementing gap crossing structures, the launch height must factor in the species' glide ratio. The height of a launch structure designed for one species may not meet the requirements of another species. This is illustrated in Taylor and Goldingay (2009) [81], who examined Squirrel Glider performance and made recommendations for the height of structures with road crossing. The authors state two-lane roads require poles 13 m tall and four-lane roads require poles 25 m tall. However, pole placement and number also need consideration for the Squirrel Glider, as pole use is negatively associated with pole number and distance [90]. While such glide pole suggestions apply to the Squirrel Glider species, there is no universal design applicable to all species. Within forests of Australia, multiple glider species such as Squirrel Gliders, Mahogany Gliders, and Sugar Gliders may occupy a single patch, all with different glide ratios. In North America, where Northern and Southern Flying Squirrels reside, the gliding poles must factor in each individual species. These species have different height requirements to cross the same distance. Structure height and placement will have to be tailored to a specific regional species to maximum crossing efficacy while minimizing material costs.

### 2.2.3. Habituation to Structures

When implementing novel management techniques (canopy rope bridges, log bridges, gliding poles), it is important to note these additions may not be used immediately. Canopy rope bridges designed for Squirrel Gliders did not re-establish gene flow across a highway until the 5-year mark [72]. Siberian Flying Squirrels were noted to take two years to regularly use gliding poles [74]. With newly installed gliding poles, Northern Flying Squirrels in the United States were only found to increase from 0 crossings to 14 crossings over a 15-month monitoring period [79]. Yellow-Bellied Gliders were not detected at gliding poles until 18 months after installation [80]. Regardless of the species involved, there will be an extended adjustment period before structural enhancements are fully utilized. Moreover, these structures will need continuous monitoring to ensure that they remain effective. Previous studies that implemented manmade crossing structures noted the importance of further observation and documentation to obtain accurate data on long-term usage [15,67,69,75–79].

## 3. Conclusions

Ongoing urbanization, agricultural development, and timber harvesting in North America have altered landscapes for *Glaucomys* flying squirrels. Habitat quality within patches has declined, and larger gaps encompassing roads, fields, and bridges are more prominent. These obstacles put flying squirrels at a tremendous disadvantage and threaten the persistence of their metapopulations. Protecting high quality habitat such as mature forest near water sources provides better food and habitat. In more managed stands, retaining larger trees and snags and providing cover is vital. Larger patches of forest stands should be conserved wherever possible, with stands left in close proximity to one another for ease of access by flying squirrels. Furthermore, maintaining connectivity between patches is necessary to sustain metapopulations. Four types of structures can be implemented: median trees, canopy rope bridges, log bridges, and gliding poles. While the four structures have advantages and disadvantages to consider, each has the ability to restore connectivity between forest fragments. Of these, gliding poles are the most widely documented and are heavily modifiable to accommodate the gliding species in question, making them one of the best solutions for addressing gap crossing. Gliding poles should be the necessary launch height, spaced appropriately, and possess launch platforms. Structures such as gliding poles should also factor in the morphology and behavior of *Glaucomys*. Finally, it is important to remember that any structure added to a flying squirrel's environment will require an adjustment period and will not be immediately used. For North American flying squirrel conservation, lessening the effects of fragmentation on local populations will be a slow process, but maintaining high habitat quality and connectivity is the answer to maintain squirrel persistence within these landscapes.

**Funding:** This research received no external funding.

**Acknowledgments:** I thank Richard Essner at Southern Illinois University Edwardsville for all his guidance and support with the manuscript. Special thanks to Ross Goldingay at Southern Cross University and Yushin Asari at Obihiro University of Agriculture and Veterinary Medicine for providing photographs of crossing structures. Lastly, I would like to thank the reviewers for taking time to provide feedback to improve the manuscript.

**Conflicts of Interest:** The author declares no conflict of interest.

## References

1. Friedenburg, L.K. *Chapter 4: Physical Effects of Habitat Fragmentation*; Fiedler, P.L., Kareiva, P.M., Eds.; Conservation Biology: For the Coming Decade; Chapman and Hall: New York, NY, USA, 1998; pp. 66–79.
2. Pardini, R. Effects of forest fragmentation on small mammals in an Atlantic forest landscape. *Biodivers. Conserv.* **2004**, *13*, 2567–2586. [CrossRef]
3. Potapov, P.; Hansen, M.C.; Laestadius, L.; Turubanova, S.; Yaroshenko, A.; Thies, C.; Smith, W.; Zhuravleva, I.; Komarova, A.; Minnemeyer, S.; et al. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.* **2017**, *3*, e1600821. [CrossRef] [PubMed]
4. Bakker, V.J.; van Vuren, D.H. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conserv. Biol.* **2004**, *18*, 689–697. [CrossRef]
5. Haynes, K.J.; Cronin, J.T. Interpatch movement and edge effects: The role of behavioral responses to the landscape matrix. *Oikos* **2006**, *113*, 43–54. [CrossRef]
6. Zugmeyer, C.A.; Koprowski, J.L. Severely insect-damaged forest: A temporary trap for red squirrels? *For. Ecol. Manag.* **2009**, *257*, 464–470. [CrossRef]
7. Hanski, I. Metapopulation Dynamics. *Nature* **1998**, *396*, 41–49. [CrossRef]
8. Norberg, U.M. Evolution of vertebrate flight: An aerodynamic model for the transition from gliding to active flight. *Am. Nat.* **1985**, *126*, 303–327. [CrossRef]
9. Endo, H.; Yokokawa, K.; Kurohmaru, M.; Hayashi, Y. Functional anatomy of gliding membrane muscles in the sugar glider (*Petaurus breviceps*). *Ann. Anat.* **1998**, *180*, 93–96. [CrossRef]

10. Runestad, J.A.; Ruff, C.B. Structural adaptations for gliding in mammals with implications for locomotor behavior in Paromomyids. *Am. J. Phys. Anthropol.* **1995**, *98*, 101–119. [CrossRef] [PubMed]
11. Jackson, S.M. Glide angle in the genus Petaurus and a review of gliding in mammals. *Mammal Rev.* **1999**, *30*, 9–30. [CrossRef]
12. Flaherty, E.; Ben-David, M.; Smith, W.P. Quadrupedal locomotor performance in two species of arboreal squirrels: Predicting energy savings of gliding. *J. Comp. Physiol. B* **2010**, *180*, 1067–1078. [CrossRef] [PubMed]
13. Carey, A.B. Ecology of northern flying squirrels: Implications for ecosystem management in the Pacific Northwest, USA. In *Biology of Gliding Mammals*; Scheibe, J.S., Goldingay, R.L., Eds.; Filander Verlag: Fürth, Germany, 2000; pp. 45–61.
14. Van der Ree, R.; Cesarani, S.; Sunnucks, P.; Moore, J.L.; Taylor, A. Large gaps in canopy reduce road crossing by gliding mammal. *Ecol. Soc.* **2010**, *15*, 35. [CrossRef]
15. Goldingay, R.L.; Taylor, B.D.; Parkyn, J.L. Use of tall poles by four species of gliding mammal provides further proof of concept for habitat connection. *Aust. Mammal.* **2019**, *41*, 255–261. [CrossRef]
16. Selonen, V.; Hanski, I.K. Movements of the flying squirrel *Pteromys volans* in corridors and in matrix habitat. *Ecography* **2003**, *26*, 641–651. [CrossRef]
17. Murrant, M.N.; Bowman, J.; Wilson, P.J. A test of non-kin social foraging in the southern flying squirrel (*Glaucomys volans*). *Biol. J. Linn. Soc.* **2014**, *113*, 1126–1135. [CrossRef]
18. Taulman, J.F.; Smith, K.G. Home range and habitat selection of southern flying squirrels in fragmented forests. *Mamm. Biol.* **2004**, *69*, 11–27. [CrossRef]
19. Holloway, G.L.; Malcolm, J. Northern and southern flying squirrels use of space within home ranges in central Ontario. *For. Ecol. Manag.* **2007**, *242*, 747–755. [CrossRef]
20. Diggins, C.A.; Silvis, A.; Kelly, C.A.; Ford, W.M. Home range, den selection and habitat use of Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*). *Wildl. Res.* **2017**, *44*, 427–437. [CrossRef]
21. Jacques, C.N.; Zweep, J.S.; Jenkins, S.E.; Klaver, R.W. Home-range use and survival of southern flying squirrels in fragmented forest landscapes. *J. Mammal.* **2017**, *98*, 1479–1488. [CrossRef]
22. Selonen, V.; Hanski, I.K. Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests. *Behav. Ecol.* **2004**, *15*, 564–571. [CrossRef]
23. Hanski, I.K.; Selonen, V. Female-biased natal dispersal in the Siberian flying squirrel. *Behav. Ecol.* **2008**, *20*, 60–67. [CrossRef]
24. Martin, K.; Anthony, R. Movements of northern flying squirrels in different-aged forest stands of western Oregon. *J. Wildl. Manag.* **1999**, *63*, 291–297. [CrossRef]
25. Selonen, V.; Hanski, I.K.; Stevens, P.C. Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. *Ecography* **2001**, *24*, 588–600. [CrossRef]
26. Brommer, J.; Wistbacka, R.; Selonen, V. Immigration ensures population survival in the Siberian flying squirrel. *Ecol. Evol.* **2017**, *7*, 1858–1868. [CrossRef] [PubMed]
27. Arbogast, B.S.; Browne, R.A.; Weigl, P.D.; Kenagy, G.J. Conservation genetics of endangered flying squirrels (*Glaucomys*) from the Appalachian Mountains of eastern North America. *Anim. Conserv.* **2005**, *8*, 123–133. [CrossRef]
28. Lampila, S.; Kvist, L.; Wickback, R.; Orell, M. Genetic diversity and population differentiation in the endangered Siberian flying squirrel (*Pteromys volans*) in a fragmented landscape. *Eur. J. Wildl. Res.* **2009**, *55*, 397–406. [CrossRef]
29. Taylor, A.C.; Walker, F.M.; Goldingay, R.L.; Ball, T.M.; van der Ree, R. Degree of landscape fragmentation influences genetic isolation among populations of a gliding mammal. *PLoS ONE* **2011**, *6*, e26651. [CrossRef]
30. Goldingay, R.L.; Harrisson, K.A.; Taylor, A.C.; Ball, T.M.; Sharpe, D.J.; Taylor, B.D. Fine-scale genetic response to landscape change in a gliding mammal. *PLoS ONE* **2013**, *8*, e80383. [CrossRef]
31. Knipler, M.L.; Dowton, M.; Clulow, J.; Meyer, N.; Mikac, K.M. Genome-wide SNPS detect fine-scale genetic structure in threatened populations of squirrel glider *Petaurus norfolcensis*. *Conserv. Genet.* **2022**, *23*, 541–558. [CrossRef]
32. Meyer, M.D.; Kelt, D.A.; North, M.P. Microhabitat associations of northern flying squirrels in burned and thinned forest stands of the Sierra Nevada. *Am. Midl. Nat.* **2007**, *157*, 202–211. [CrossRef]
33. Ritchie, L.E.; Betts, M.G.; Forbes, G.; Vernes, K. Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. *For. Ecol. Manag.* **2009**, *257*, 1920–1929. [CrossRef]
34. Holloway, G.L.; Smith, W.P.; Halpern, C.B.; Gitzen, R.A.; Maguire, C.C.; West, S.D. Influence of forest structure and experimental green-tree retention on northern flying squirrel (*Glaucomys sabrinus*) abundance. *For. Ecol. Manag.* **2012**, *285*, 187–194. [CrossRef]
35. Herbers, J.; Klenner, W. Effects of logging pattern and intensity on squirrel demography. *J. Wildl. Manag.* **2007**, *71*, 2655–2663. [CrossRef]
36. Manning, T.; Hagar, J.C.; McComb, B.C. Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades. *For. Ecol. Manag.* **2012**, *264*, 115–124. [CrossRef]
37. Meyer, M.D.; Kelt, D.A.; North, M.P. Nest trees of northern flying squirrels in the Sierra Nevada. *J. Mammal.* **2005**, *86*, 275–280. [CrossRef]
38. Flaherty, E.A.; Ben-David, M.; Smith, W.P. Diet and food availability: Implications for foraging and dispersal of Prince of Wales northern flying squirrels across managed landscapes. *J. Mammal.* **2010**, *91*, 79–91. [CrossRef]
39. Gomez, D.M.; Anthony, R.G.; Hayes, J.P. Influence of thinning of Douglas-fir forest on population parameters and diet of northern flying squirrels. *J. Wildl. Manag.* **2005**, *69*, 1670–1682. [CrossRef]

40. Taulman, J.F. Selection of nest trees by southern flying squirrels (Sciuridae: *Glaucomys volans*) in Arkansas. *J. Zool.* **1999**, *248*, 369–377. [CrossRef]
41. Campuzano-Chávez-Peón, D.; Zuria, I.; Castellanos, I.; Gates, J.E. Characteristics of nest-sites of the southern flying squirrel (*Glaucomys volans*) in a pine-oak forest of Central Mexico. *Southwest. Nat.* **2014**, *59*, 75–80. [CrossRef]
42. Keefe, E.M.; Giuliano, W.M. Effects of forest structure on the distribution of southern flying squirrels (*Glaucomys volans*) in urban parks. *Urban Ecosyst.* **2004**, *7*, 55–64. [CrossRef]
43. Holloway, G.L.; Malcolm, J.R. Nest-tree use by northern and southern flying squirrels in central Ontario. *J. Mammal.* **2007**, *88*, 226–233. [CrossRef]
44. Loeb, S.C.; Tainter, F.H.; Cázares, E. Habitat associations of hypogeous fungi in the southern Appalachians: Implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). *Am. Midl. Nat.* **2000**, *144*, 286–296. [CrossRef]
45. Fridell, R.; Litvaitis, J. Influence of resource distribution and abundance on home-range characteristics of southern flying squirrels. *Can. J. Zool.* **1991**, *69*, 2589–2593. [CrossRef]
46. Helmick, K.R.; Barrett, T.L.; Barrett, G.W. Dietary resource preference of the southern flying squirrel (*Glaucomys volans*). *Am. Midl. Nat.* **2014**, *171*, 371–374. [CrossRef]
47. Zweep, J.S.; Jacques, C.N.; Jenkins, S.E.; Klaver, R.W.; Dubay, S.A. Nest tree use by southern flying squirrels fragmented midwestern landscapes. *Wildl. Soc. Bull.* **2018**, *42*, 430–437. [CrossRef]
48. Bendel, P.R.; Gates, J.E. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). *J. Mammal.* **1987**, *68*, 243–255. [CrossRef]
49. Hurme, E.; Reunanen, P.; Mönkkonen, M.; Nikula, A.; Nivala, V.; Oksanen, J. Local habitat patch pattern of the Siberian flying squirrel in a managed boreal forest landscape. *Ecography* **2007**, *30*, 277–287. [CrossRef]
50. Mönkkõnen, M.; Reunanen, P.; Nikula, A.; Inkeröinen, J.; Forsman, J. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. *Ecography* **1997**, *20*, 634–642. [CrossRef]
51. Woodworth, C.J.; Bollinger, E.K.; Nelson, T.A. The effects of forest fragment size, isolation, and microhabitat variables on nest box use by southern flying squirrels (*Glaucomys volans*) in southern Illinois. In *Biology of Gliding Mammals*; Scheibe, J.S., Goldingay, R.L., Eds.; Filander Verlag: Fürth, Germany, 2000; pp. 135–147.
52. Santangeli, A.; Hanski, I.K.; Mäkelä, H. Integrating multi-source forest inventory and animal survey data to assess nationwide distribution and habitat correlates of the Siberian flying squirrel. *Biol. Conserv.* **2013**, *157*, 31–38. [CrossRef]
53. Deslauriers, S. *Effects of Forest Characteristics and Landscape Configuration on Flying Squirrel Occurrence and Abundance in Rouge National Urban Park*; Graduate Department of Forestry University of Toronto: Toronto, ON, Canada, 2021.
54. Walpole, A.A.; Bowman, J. Patch occupancy by squirrels in fragmented deciduous forest: Effects of behavior. *Acta Theol.* **2011**, *56*, 63–72. [CrossRef]
55. Rizkalla, C.; Swihart, R. Explaining movement decisions of forest rodents in fragmented landscapes. *Biol. Conserv.* **2007**, *140*, 339–348. [CrossRef]
56. Mäkeläinen, S.; de Knegt, H.J.; Ovaskainen, O.; Hanski, I.K. Home-range use patterns and movements of the Siberian squirrel in urban forests: Effects of habitat composition and connectivity. *Mov. Ecol.* **2016**, *4*, 5. [CrossRef] [PubMed]
57. Howard, J.M.; Essner, R.L. Gap crossing event in the southern flying squirrel (*Glaucomys volans*) in fragmented urbanized forest habitat. *Trans. Ill. State Acad. Sci.* **2020**, *113*, 23–26.
58. Howard, J.M.; Loos, J.E.; Essner, R.L. Movement and microhabitat selection in the southern flying squirrel (*Glaucomys volans*) in southwestern Illinois. *Northeast. Nat.* **2020**, *27*, 35–47. [CrossRef]
59. Smith, M.; Forbes, G.; Betts, M. Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). *Biol. Conserv.* **2013**, *168*, 176–183. [CrossRef]
60. Desrochers, A.; Hanski, I.K.; Selonen, V. Siberian flying squirrel responses to high-and low-contrast forest edges. *Landsc. Ecol.* **2003**, *18*, 543–552. [CrossRef]
61. Gilmore, R.; Gates, E. Habitat use by the southern flying squirrel at a hemlock-northern hardwood ecotone. *J. Wildl. Manag.* **1985**, *49*, 703–710. [CrossRef]
62. Van der Ree, R.; Bennett, A.F.; Gilmore, D.C. Gap-crossing by gliding marsupials: Thresholds for use of isolated woodland patches in an agricultural landscape. *Biol. Conserv.* **2003**, *115*, 241–249. [CrossRef]
63. Van der Ree, R. Road upgrade in Victoria a filter to the movement of the endangered squirrel glider (*Petaurus norfolcensis*): Results of a pilot study. *Ecol. Manag. Restor.* **2006**, *7*, 226–228. [CrossRef]
64. Findley, J.S. The interesting fate of a flying squirrel. *J. Mammal.* **1946**, *26*, 437. [CrossRef]
65. Selonen, V.; Hanski, I.K. Habitat exploration and use in dispersing juvenile flying squirrels. *J. Anim. Ecol.* **2006**, *75*, 1440–1449. [CrossRef]
66. Asari, Y.; Johnson, C.N.; Parsons, M.; Larson, J. Gap-crossing in fragmented habitats by mahogany gliders (*Petaurus gracilis*). Do they cross roads and powerline corridors? *Aust. Mammal.* **2010**, *32*, 10–15. [CrossRef]
67. Soanes, K.; Lobo, M.C.; Vesk, P.A.; McCarthy, M.A.; Moore, J.L.; van der Ree, R. Movement re-established but not restored: Inferring the effectiveness of road-crossing mitigation for a gliding mammal by monitoring use. *Biol. Conserv.* **2013**, *159*, 434–441. [CrossRef]
68. Taylor, B.D.; Rohweder, D.A. Radio-tracking three Sugar Gliders using forested highway median strips at Bongil Bongil National Park, north-east New South Wales. *Ecol. Restor. Manag.* **2013**, *14*, 228–230. [CrossRef]

69. Goldingay, R.L.; Rohweder, D.; Taylor, B.D. Will arboreal mammals use rope-bridges across a highway in eastern Australia? *Aust. Mammal.* **2013**, *35*, 30–38. [CrossRef]
70. Goldingay, R.L.; Taylor, B.D. Can field trials improve the design of road-crossing structures for gliding mammals? *Ecol. Res.* **2017**, *32*, 743–749. [CrossRef]
71. Soanes, K.; Mitchell, B.; van der Ree, R. Quantifying predation attempts on arboreal marsupials using wildlife crossing structures above a major road. *Aust. Mammal.* **2017**, *39*, 254–257. [CrossRef]
72. Soanes, K.; Taylor, A.C.; Sunnucks, P.; Vesk, P.A.; Cesarini, S.; van der Ree, R. Evaluating the success of wildlife crossing structures using genetic approaches and an experimental design: Lessons from a gliding mammal. *J. Appl. Ecol.* **2018**, *55*, 129–138. [CrossRef]
73. Yanagawa, H.; Asari, Y.; Kishida, K.; Kimura, S.; Kitase, T. Eco-bridge for flying squirrels. *Symp. Wildl. Traffic Proc.* **2004**, *3*, 13–18.
74. Asari, Y.; Yanagawa, H. The monitoring of 'conservation bridge' for the Siberian flying squirrel in Obihiro, Hokkaido. *Animate* **2008**, *7*, 44–49.
75. Ball, T.M.; Goldingay, R.L. Can wooden poles be used to reconnect habitat for a gliding mammal? *Landsc. Urban Plan.* **2008**, *87*, 140–146. [CrossRef]
76. Goldingay, R.L.; Taylor, B.D.; Ball, T.M. Wooden poles can provide habitat connectivity for a gliding mammal. *Aust. Mammal.* **2011**, *33*, 36–43. [CrossRef]
77. Taylor, B.D.; Goldingay, R.L. Restoring connectivity in landscape fragmented by major roads: A case study using wooden poles as "stepping stones" for gliding mammals. *Restor. Ecol.* **2012**, *20*, 671–678. [CrossRef]
78. Taylor, B.D.; Goldingay, R.L. Squirrel gliders use roadside glide poles to cross a road gap. *Aust. Mammal.* **2013**, *35*, 119–122. [CrossRef]
79. Kelly, C.; Diggins, C.; Lawrence, A. Crossing structures reconnect federally endangered flying squirrel populations divided for 20 years by road barrier. *Wildl. Soc. Bull.* **2013**, *37*, 375–379. [CrossRef]
80. Taylor, B.D.; Rohweder, D.A. Yellow-bellied gliders use glide poles to cross the Pacific highway at Halfway creek, north-east New South Wales. *Aust. Mammal.* **2020**, *42*, 385–387. [CrossRef]
81. Taylor, B.D.; Goldingay, R.L. Gliding performance and its relevance to gap crossing by the squirrel glider (*Petaurus norfolcensis*). *Aust. J. Zool.* **2009**, *57*, 99–104.
82. Paskins, K.E.; Bowyer, A.; Megill, W.M.; Scheibe, J.S. Take-off and landing forces and the evolution of controlled gliding in northern flying squirrels *Glaucomys sabrinus*. *J. Exp. Biol.* **2007**, *210*, 1413–1423. [CrossRef]
83. Scheibe, J.S.; Robins, J.H. Morphological and performance attributes of gliding mammals. In *Ecology and Evolutionary Biology of Tree Squirrels*; Steele, M.A., Meritt, J.F., Zegers, D.A., Eds.; Virginia Museum of Natural History: Martinsville, VA, USA, 1998; pp. 131–144.
84. Vernes, K. Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forest eastern Canada. *J. Mammal.* **2001**, *82*, 1026–1033. [CrossRef]
85. Asari, Y.; Yanagawa, H.; Osida, T. Gliding ability of the Siberian flying squirrel *Pteromys volans orii*. *Mammal. Study* **2007**, *32*, 151–154. [CrossRef]
86. Krishna, M.C.; Awadhesh, K.; Tripathi, O.P. Gliding performance of the red giant gliding squirrel *Petaurista petaurista* in the tropical rainforest of Indian eastern Himalaya. *Wildl. Biol.* **2016**, *22*, 7–12. [CrossRef]
87. Stafford, B.J.; Thorington, R.W.; Kawamichi, T. Gliding behavior of Japanese giant flying squirrels (*Petaurista leucogenys*). *J. Mammal.* **2002**, *83*, 553–562. [CrossRef]
88. Koli, V.K.; Bhatnagar, C.; Mali, D. Gliding behavior of Indian giant flying squirrel *Petaurista philippensis*. *Curr. Sci.* **2011**, *100*, 1563–1568.
89. Goldingay, R.L. Gliding performance in the yellow-bellied glider in low-canopy forest. *Aust. Mammal.* **2014**, *36*, 254–258. [CrossRef]
90. Soanes, K.; Vesk, P.A.; van der Ree, R. Monitoring the use of road-crossing structures by arboreal marsupials: Insights gained from motion-triggered cameras and passive integrated transponder (PIT) tags. *Wildl. Res.* **2015**, *42*, 241–256. [CrossRef]