



Review article

Management of the Tongass National Forest in Southeast Alaska increases extinction risk of island endemics

Winston P. Smith ^{a,b,*} 

^a Independent Researcher, Glacier Highway, Juneau, AK, 99801, USA

^b Former Principal Wildlife Scientist (retired), USDA Forest Service, Pacific Northwest Research Station, Portland, OR, 97204, USA

ARTICLE INFO

Keywords:

Clearcut logging
Glaucomys sabrinus
 Island endemics
 Local extirpations
 Metapopulation
 Temperate rainforest
 Viable populations

ABSTRACT

After decades of clearcut logging the most productive old-growth forests, the Tongass National Forest developed a new forest plan in 1997 with expectations of maintaining viable populations of native wildlife species. The northern flying squirrel (*Glaucomys sabrinus*) was selected as an indicator species for the 1997 plan because of its dependence on old-growth forest. Numerous ecological studies of this viability proxy and an analysis of forest policies revealed untenable assumptions and deficiencies of the 1997 wildlife conservation strategy. I review numerous published studies of the island endemic *G. s. griseifrons*, including multiscale habitat relations, diet, demography, perceptual range, dispersal, and viability within isolated reserves or as metapopulations among old-growth remnants. *Glaucomys s. griseifrons* avoided logged areas and selected for larger patches of contiguous old-growth. Viable breeding populations occurred only in Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) old-growth, $\geq 40\%$ of which has been harvested. *G. s. griseifrons* requires $\approx 250,000$ ha of old-growth spruce-hemlock forests to sustain viable, isolated populations. At least 50% of old-growth reserves are not functionally connected because effective dispersal is limited by landscape resistance, a consequence of limited perceptual range, increased locomotor energetic costs, availability of food resources, and higher risks of predation. I conclude that *G. s. griseifrons* populations have been substantially reduced by incalculable local extirpations and offer 4 recommendations: 1) discontinue logging of old-growth forests; 2) restore logged forests through intermediate stand management of second-growth; 3) conduct a formal review of the conservation framework and assumptions; 4) and implement a comprehensive monitoring plan.

1. Introduction

European settlement drastically transformed the composition and structure of North America's landscapes (Steiner and Huettmann, 2025), especially the amount and distribution of forest cover (Cole et al., 2003, Smith 2007a, Albert and Schoen, 2012, Bellante et al., 2025). Over 60% of North American forests have undergone a change in major land-cover classification, the vast majority of which were logged and remained unforested because of human development or were converted to second-growth timber plantations (Smith 2007a, 2012a). Habitat loss and fragmentation are expected to continue reducing diversity of native vertebrates through increasing extinction probabilities (Crooks et al., 2017, Püttker et al., 2020). Among ecological communities, loss of a predator, prey, competitor,

* Correspondence to: 10915 Glacier Highway, Juneau, AK 99801, USA.

E-mail address: winstonpaulsmith@gmail.com.

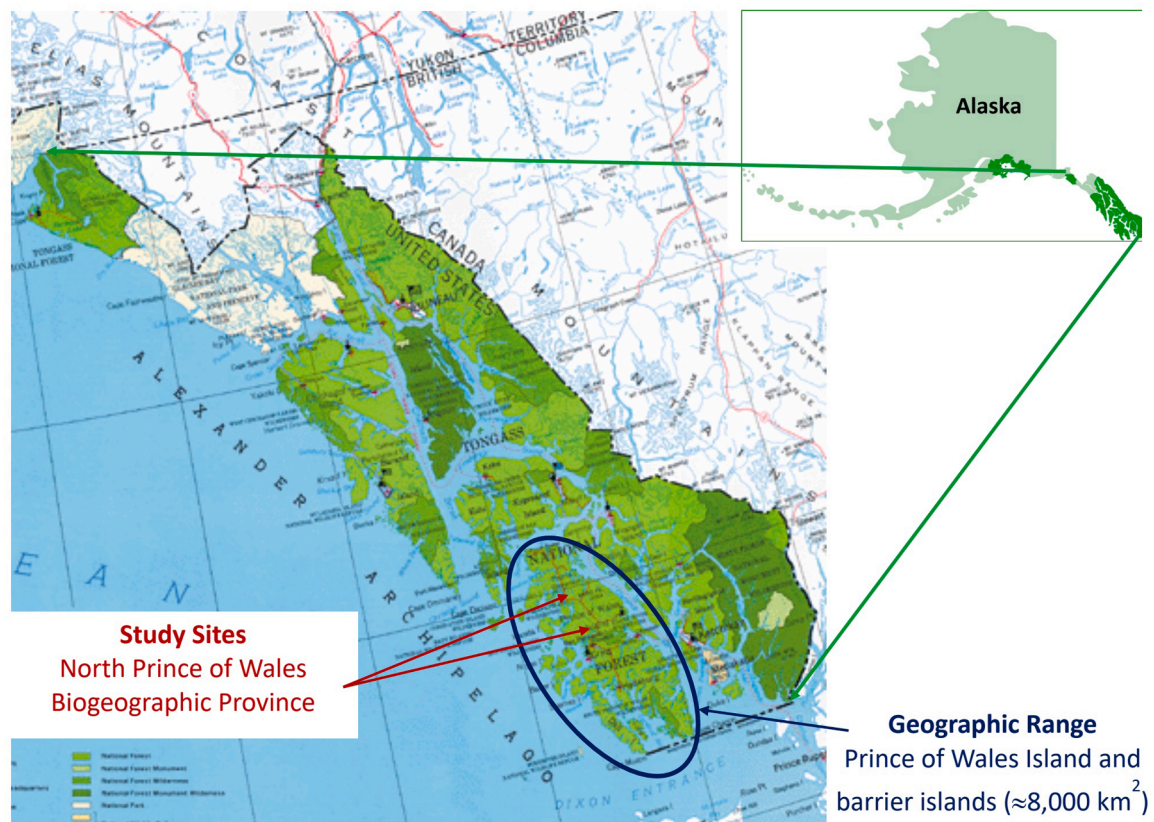
<https://doi.org/10.1016/j.gecco.2026.e04393>

Received 19 July 2026; Received in revised form 30 July 2026; Accepted 28 August 2026

Available online 23 September 2026

2351-9894/© 2026 The Author. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

The Tongass National Forest (Fig. 1) lies within one of the largest temperate rainforests in the world, spanning 800 km across Southeast Alaska, with thousands of islands comprising the Alexander Archipelagos (DellaSala et al., 2011, 2022). The forest canopy is dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) in uplands (upland-OG), but includes shore pine (*Pinus contorta*), mountain hemlock (*Tsuga mertensiana*), western redcedar (*Thuja plicata*), and Alaska-cedar (*Chamaecyparis nootkensis*) in wetlands (Alaback, 1982, Nowacki and Kramer, 1998). About 90% of forests available for logging are upland Sitka spruce–western hemlock forests (USFS 1997, 2008, 2016). The Tongass National Forest (hereafter Tongass) has experienced expansive clearcut logging since the 1950s (Beier et al., 2009) with significant changes in landscape attributes that were recently documented using the Land Change Monitoring System (Bellante et al., 2025) and the National Land Cover Database (Steiner and Huettmann, 2025). Historically, 47% of North Prince of Wales Biogeographic Province (North POW) was comprised of patches of contiguous, productive (medium and high volume) old-growth forests, some of which exceeded 80,000 ha. Over several decades, $\geq 40\%$ of productive old-growth forests have been clearcut logged (Fig. 2), and the remaining forest fragments are $< 18,000$ ha. Albert and Schoen (2012) reported a pattern of disproportionate logging at multiple spatial scales across the Tongass, targeting large-tree stands and contiguous landscapes of the most productive old-growth spruce-hemlock forests. The largest harvests were most frequently among landform associations and biogeographic provinces that originally contained the greatest concentrations of the most



2

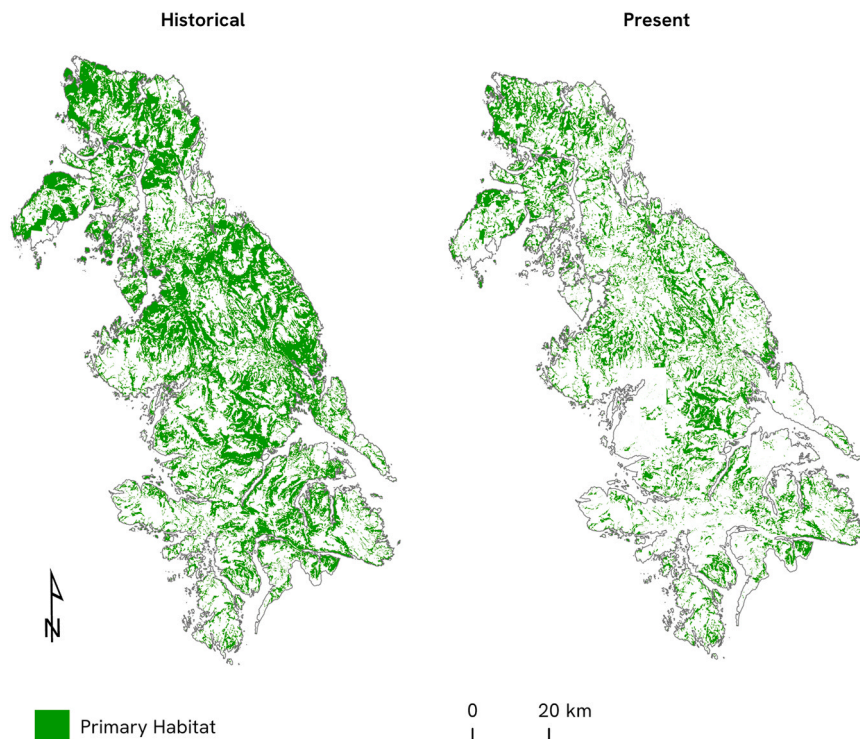


Fig. 2. Historical and present distribution of high-volume Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) old-growth forests throughout North Prince of Wales Biogeographic Province. High-volume Sitka spruce–western hemlock forests is the primary habitat of the island endemic *Glaucomys sabrinus griseifrons* (Smith et al. 2004, Smith and Person, 2007). The Tongass National Forest Size Density Model (Caouette and DeGayner, 2005) was used to map forest volume classes and management history. An estimate of timber harvest on Non-Federal lands was supplemented with a Land Change Monitoring System score > 50% (Bellante et al., 2025). An assumption was made that previously harvested areas were historically primary habitat. This GIS analysis revealed clearcut logging over the last several decades has reduced the primary habitat of *G. s. griseifrons* in the North Prince of Wales Biogeographic Province by 40%.

productive old-growth spruce-hemlock forests. Landscapes with the highest volume of old-growth spruce-hemlock forests have been reduced by 66.5% (Albert and Schoen, 2012).

Loss of forest types has increased the risk of extirpation of species dependent on old-growth forests (Smith, 2005, Smith and Fox, 2017), notably among arboreal squirrels (Bidlack and Cook, 2001, 2002; Arbogast, 2007, Steiner and Huettmann 2023b). Cumulative habitat disturbance is particularly impactful within island biogeographic provinces because habitat across archipelagos is already naturally fragmented. Total population size is predictably smaller among islands than in mainland habitats (MacArthur and Wilson, 1967, Conroy et al., 1999, Cook et al., 2001, Cook et al., 2006, Androski et al., 2024), and viable breeding populations are isolated (Burkey, 1995, Smith et al., 2011a). Furthermore, demographic stochasticity and inbreeding depression increase risk of extinction, especially among endemic taxa (Frankham, 1998, Bidlack and Cook, 2001, 2002; Cook and MacDonald, 2001, Arbogast, 2007, Androski et al., 2024). Smaller populations are more frequently and more severely impacted by habitat disturbance, and the likelihood of rescue following extirpation depends on the number and proximity of source populations (MacArthur and Wilson, 1967, Laurance, 1991, Burkey, 1995, Conroy et al., 1999, Androski et al., 2024) and functional connectivity (Fahrig and Merriam, 1985, Fahrig et al., 2021, Smith et al., 2011a, b; Trapp et al., 2019). Most worldwide vertebrate extinctions during the last 400 years were island endemics (Cook and MacDonald, 2001).

In 1997, the Tongass Land Management Plan (TLMP) revision team were directed by the viability rule of the National Forest Management Act (NFMA; U.S. Forest Service 1982) to manage the forest in a manner that maintains viable, widely distributed populations of existing native vertebrate species. Procedures for complying with the expectations of NFMA viability provisions included identifying and collecting information on species of viability concern. *Glaucomys sabrinus* was selected as a management indicator species for the revision of the 1997 Tongass Land Management Plan (Everest et al., 1997, U.S. Forest Service, 1997) because of its recognition as a species of viability concern and as a sentinel of local community and landscape-scale ecological processes (Smith, 2012a).

The northern flying squirrel (*Glaucomys sabrinus*) is an arboreal rodent of boreal and montane coniferous forests of North America, with several endemics of island archipelagos or fragmented montane forests (Wells-Gosling and Heaney, 1984, Arbogast, 2007). At least 6 subspecies are state- or federally-listed as imperiled (Arbogast, 2007, Androski et al., 2024). *Glaucomys sabrinus* has several life-history traits typical of k-selected species (sensu MacArthur and Wilson, 1967): a reliance on old-growth forest (Smith, 2007b, Holloway and Smith, 2011, Holloway et al., 2012); relatively long-lived (7 years; Villa et al., 1999); delayed development and age at

first reproduction; seasonal breeder with 1 litter per year in Southeast Alaska (Smith and Nichols, 2003) averaging 2 young after a relatively long (37- to 42-day) gestation (Wells-Gosling and Heaney, 1984); females invest substantial energy during gestation (Smith, 2007b); undergoes density-dependent population growth (Fryxell et al., 1998, Lehmkuhl et al., 2006); and locomotor limitations (Flaherty et al., 2010a) that delimit effective dispersal distances (Smith 2007b, Smith 2012a, Trapp et al., 2019). Furthermore, flying squirrels in the Pacific Northwest and Alaska are vital prey for several predators (Forsman et al., 1984, Rosenberg et al., 2003, Lewis et al., 2006) and facilitate an obligate symbiotic relationship between mycorrhizal fungi and dominant tree species, providing an essential ecosystem service supporting healthy forests (Maser and Maser, 1988). Thus, *G. sabrinus* is an essential link in the food chain and dynamics of coniferous forests (Smith, 2007b); a sentinel of ecological processes (Smith, 2012a) informing ecosystem management of western coniferous forests (Lehmkuhl et al., 2006, Holloway et al., 2012).

The objectives of this review are to 1) assess whether currently available data indicate that northern flying squirrels have maintained widely distributed viable populations as mandated under the 1997 TLMP, and 2) determine if the findings of this assessment satisfy requirements under the legal definition of threatened or endangered in the U.S. Endangered Species Act (Vucetich et al., 2006).

2. Methods

2.1. Review early research and forest plan investigation

Following implementation of the 1997 TLMP, field studies were undertaken to obtain previously unavailable information on the life history and ecology of *G. sabrinus* in Southeast Alaska (Smith and Nichols, 2003). The previous federal listing of *G. s. griseifrons* (Arbogast, 2007), failure of the Tongass to implement a comprehensive monitoring plan, and findings of early ecological (Smith et al., 2004, Smith and Person, 2007) and genetic (Bidlack and Cook, 2001, 2002) research prompted additional field and laboratory studies to investigate underlying assumptions of the TLMP Wildlife Conservation Strategy to sustain widely-distributed, viable populations of native wildlife species (Smith and Flaherty, 2023).

Insufficient evidence that TLMP’s landscape conservation strategy would achieve multiple expected outcomes prompted additional research because of the following assumptions regarding the viability of native wildlife: 1) old-growth reserves are effective habitat conservation areas and ensure functional connectivity; 2) forest management and conservation policies are implemented at appropriate ecological scales; 3) forest planning assessments of wildlife viability were realistic; and 4) forest-wide standard and guidelines ensure sufficient habitat for sensitive species in managed landscapes (Smith and Flaherty, 2023). Recognition that TLMP did not adequately consider the vulnerability of island communities to cumulative broad-scale disturbance, or acknowledge numerous local extirpations of island endemic populations or interruption of functional connectivity across managed landscapes reinforced concerns that insular populations were being negatively impacted (Smith et al., 2011a, Smith and Flaherty, 2023). Without a comprehensive monitoring plan to document outcomes of management actions, the Tongass accumulated little information to evaluate the effectiveness of its new landscape conservation plan (Everest et al., 1997, Smith et al., 2011a) and ensuing consequences for island endemics (Smith and Flaherty, 2023). Thus, a comprehensive, detailed review of published findings from numerous behavioral and ecological studies of a Tongass wildlife viability proxy seemed warranted.

2.2. Literature and landcover search

To thoroughly consider the published literature on the topic of northern flying squirrel management in the Tongass, I used a Web of Science™ word search conducted on 27 February 2025 using the search terms of TS = ((northern flying squirrel OR *Glaucomys sabrinus*) AND (Tongass OR Alaska). I conducted a second Web of Science™ word search 22 April 2026 to search for more recent publications using the search terms of TS = ("northern flying squirrel*" OR "*Glaucomys sabrinus*" OR "*G. sabrinus*") and limited it to publications during 2020–2026. Both searches produced 57 results of which a total of 46 were relevant. I removed publications that did

Table 1
Existing and historical landscape composition (ha) and structure of available habitat types across Prince of Wales Island for *Glaucomys sabrinus griseifrons* based on existing vegetation map products (Caouette and DeGayner, 2005, Bellante et al. 2025) and demography (Smith and Nichols, 2003), ecological correlates of relative abundance (Smith et al., 2004), and population dynamics (Smith and Person, 2007). Fragment number (n) and patch size (ha) represent number and mean total area of separate polygons of existing (E) and historical (H) primary habitat that exceeded *G. s. griseifrons* occupancy threshold (≥ 73 ha; Shanley et al., 2013). Historical composition and structure assumed that existing old second-growth (Old SG: 61 – 100 yr) and young second-growth (Young SG: 0 – 60 yr) represented primary habitat based on old-growth volume classes that were clearcut logged (U.S. Forest Service, 1997), and other portions of the landscape have undergone little change (Bellante et al., 2025). Primary Habitat represents medium- and high-volume Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) old-growth rainforests. Non-habitat represents non-commercial forests, non-forested muskegs, and other non-forested landscapes.

Habitat type	Existing (ha)	Historical (ha)	Fragments (n)		Patch size (ha)	
			E	H	E	H
Primary	166,965	279,690	246	197	538	1290
Old SG	14,562	0	— ^a	—	— ^a	—
Young SG	98,163	0	— ^a	—	— ^a	—
Non-habitat	320,721	320,721	— ^a	—	— ^a	—

^a Data unavailable.

not involve *Glaucomys sabrinus* or those not located in Southeast Alaska. Publications from research conducted in California, western Oregon, western Washington, and southern British Columbia prior to 2018 were no longer directly relevant because of the discovery of the cryptic congeneric species *Glaucomys oregonensis* by Arbogast et al. (2017). Still, there was evidence that the life history and ecology of both species are similar, especially the manner in which each responds to extensive harvesting of old-growth coniferous forests (Smith 2007b, Holloway and Smith, 2011, Smith 2012a). Relevant literature from other portions of the geographic range of *G. sabrinus* is included to provide a broader perspective of the life history and ecology of *G. sabrinus* in forest habitats in other portions of its geographic range. The expansion of *G. volans* northward and its hybridization with *G. sabrinus* where the two species are sympatric (Persad et al., 2025) limited the inclusion of some published studies.

To further understand the nature and extent of cumulative changes in landscape composition and structure over the last several decades, I undertook a GIS (ESRI, Redlands CA) analysis of existing landcover of Prince of Wales Island. I followed the lead of recent investigators who quantified historical changes in vegetative cover (Bellante et al., 2025) to understand impacts to the habitat and populations of arboreal squirrels (Steiner and Huettmann 2023a, b; 2025). Using the results of a demographic analysis by Smith and Person (2007), I used the GIS spatially-explicit analysis to document the extent of *G. s. griseifrons* primary habitat that had been lost by decades of expansive clearcut logging of POW (Table 1).

3. Results

3.1. Life history, natural history, and environmental context

Glaucomys s. griseifrons is an island endemic subspecies, the geographic range of which is limited to Prince of Wales Island and barrier islands (Fig. 1; MacDonald and Cook, 1996, Bidlack and Cook, 2001, 2002). Analyses of genetic data produced corroborating results that *G. s. griseifrons* is genetically distinct and indicated a general pattern of isolation among insular populations of *G. sabrinus* in Southeast Alaska (Bidlack and Cook, 2002). *Glaucomys s. griseifrons* exhibits severely reduced mitochondrial (Demboski et al., 1998a, Bidlack and Cook, 2001) and nuclear (Bidlack and Cook, 2002) genetic variation that is likely the result of an early Holocene founder event from a mainland source population (Bidlack and Cook, 2001, Arbogast, 2007). *Glaucomys s. griseifrons* is a subspecies of ecological concern in the Tongass and is listed by the International Union for the Conservation of Nature as potentially endangered (Demboski et al., 1998b, Hafner et al., 1998). It was federally listed as a C2 candidate in 1974, but was delisted by the US Fish and Wildlife Service in 1986 for reasons that remain unclear (Arbogast, 2007). Since then, the cumulative loss of productive old-growth forests has substantially increased (Albert and Schoen, 2012). A petition to list *G. s. griseifrons* was submitted to the U.S. Fish and Wildlife Service in 2011 (WildEarth Guardians, 2011). A recent GIS analysis of North POW revealed that 40% of this endemic’s primary habitat has been lost (Table 1, Fig. 2) because of expansive clearcut logging over the past several decades (Smith and Flaherty, 2023). Clearcutting of western coniferous forests reduces food, cover, and stand structure attributes for *Glaucomys sabrinus* and other arboreal sciurids (Sullivan and Sullivan, 2024). Old-growth Sitka spruce – western hemlock forests that are clearcut logged require ≥ 300 years to regenerate structure and composition typical of mature forests via ecological succession (Nowacki and Kramer, 1998).

3.2. Demography, habitat use, and ecological correlates of abundance

Smith and Nichols (2003) studied populations of *G. s. griseifrons* across North POW, providing the first quantitative estimates of *G. sabrinus* demography in rainforest of Southeast Alaska (Table 2). They observed a significant habitat-by-season interaction during autumn, with mean squirrel density higher in upland-OG forest (3.7/ha) than in muskeg forests (1.7/ha), described as peatland-mixed

Table 2
Crisp summary of key findings from multiple field studies of demography and multi-scale habitat relations of *Glaucomys sabrinus griseifrons*, an island endemic of Prince of Wales Island and barrier islands, Southeast Alaska.

Source Publication	Key findings
Smith and Nichols (2003). J. Mammal. 84:144–158.	Mean density, number of reproductive females, and summer survival of <i>Glaucomys sabrinus griseifrons</i> were significantly greater in upland-OG forest than in muskeg forest (peatland-MC).
Holloway and Smith (2011). J. Wild. Manage. 75:668–674.	Meta-analysis revealed <i>Glaucomys sabrinus</i> abundance was significantly reduced by forestry practices that influenced the structure or age of residual stands, both in the short and longer term.
Smith et al. (2004). J. Mammal. 85:663–674.	Four significant logistic regression models explained microhabitat use (Table S2): during spring and autumn, abundance of <i>Vaccinium</i> 0.3 – 1.5 m high and < 0.3 m high, respectively; density of large (>74 cm dbh) trees in peatland-MC; and during autumn, abundance of soft snags 10–49 cm dbh, hard snags 50–74 cm dbh, and paucity of herbaceous vegetation and small trees 10–49 cm dbh.
	<i>Glaucomys sabrinus griseifrons</i> density was positively correlated with density of large (>74 cm dbh) trees during spring and autumn in peatland-MC and density of hard snags 50–74 cm dbh in upland-OG. A significant positive relationship existed during spring with amount of down wood in decay class III in both habitats, and percentage cover of moss and down wood in decay classes I and IV explained 70% and 74% of the variation in spring flying squirrel density, respectively (Fig. 3).
Pyare et al. (2010). J. Mammal. 91:886–896.	Radio telemetry revealed 93% of 118 den locations were in cavities composed of snags (51%) or live trees that lacked external drays. Among significant regression models, dbh and prevalence of conks were positive correlates. Median dbh of dens were 20–30 cm greater than random samples in stand. Landscapes surrounding den trees had a greater proportion of high-volume forest, a smaller proportion of second-growth, and less fragmentation than randomly chosen areas within den neighborhoods.

conifer (MC). Number of reproductive females was higher in upland-OG (3.9/grid) than in peatland-MC (2.1/grid). Minimum summer (survival ranged from 16.7% during 1998 in peatland-MC to 65.7% during 2000 in upland-OG forest. Minimum winter survival rates were similar between habitats (Smith and Nichols, 2003). A loglikelihood ratio revealed that minimum summer survival, year, and habitat were not mutually independent. Moreover, neither year nor habitat was independent of survival rate with summer survival higher in upland-OG (55%) than in peatland-MC (46%; Smith and Nichols, 2003).

Variation in *G. s. griseifrons* density relative to stand-level conditions (Table S1, available in Supplemental Material) provided the first insights into the habitat relations of *G. sabrinus* in temperate rainforests of Southeast Alaska (Smith et al., 2004). They observed a positive relationship during spring with amount of down wood in decay class III (Sollins, 1982), which explained 77% of the variation in population density across 6 study sites (Fig. 3). Similarly, percentage cover of moss and down wood in decay classes I and IV explained 70% and 74% of the variation in spring density, respectively. During autumn (Fig. 3), density of trees > 74 cm dbh explained 65% of the variation among grids (Smith et al., 2004). Trees with dbh 10–49 cm and 5–10 cm were negatively correlated with trees > 74 cm and explained 73% and 72% of the variation in population density during autumn, respectively (Smith et al., 2004). T-test of stand-level means of habitat variables ($n = 26$) revealed all but three (Table S1) differed between upland-OG and peatland-MC (Smith et al., 2004). At the capture sites, they obtained 4 logistic regression models (Table S2). Density of live trees > 74 cm dbh was significant in both spring and autumn models of flying squirrel capture in peatland-MC (Fig. 3). The ecological impact of > 74 cm trees on flying squirrels was substantial, especially during autumn when an increase in mean density of 10 trees/ha increased the odds of capturing a squirrel by a factor of 17 (Smith et al., 2004). The autumn upland-OG model included 4 habitat variables. Only density of large (50–74 cm dbh) hard snags had a notable positive ecological impact on captures. An increase of 10 snags/ha of large hard snags increased the odds of capturing *G. s. griseifrons* by a factor of 2.3 (Smith et al., 2004).

To further understand the importance of large trees in the life history of *G. s. griseifrons*, Pyare et al. (2010) fitted juvenile (20 females, 12 males) and adults (10 females, 22 males) with radio-transmitters to study den use across North POW. They documented 118 den locations, 93% of which were in cavities composed of either snags (51%) or live trees that lacked signs of external drays (42%). Western hemlock was the predominant live tree used, but western redcedar (*Thuja plicata*) received much greater (250%) use than expected from its availability (Pyare et al., 2010). Presence of snags was not a significant selection variable among microhabitat regression models, but dbh was a positive correlate of den sites. Median dbh of den trees were 20–30 cm greater than a random sample

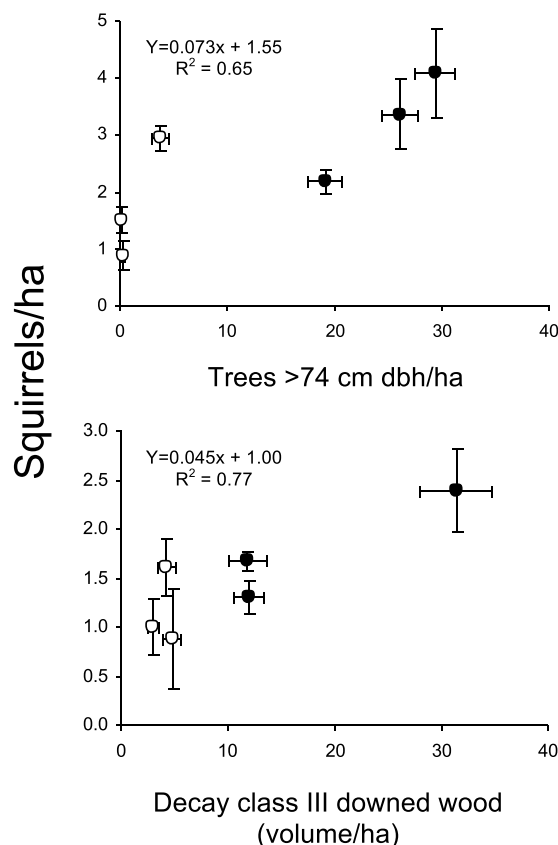


Fig. 3. Relationship between density of northern flying squirrels (*Glaucomys sabrinus griseifrons*) during autumn and a) density of large (>74 cm) trees, and b) flying squirrel density during spring and abundance of down wood in decay class III (Fig. 2 in Smith et al., 2004:669). Decay classes delineated according to Fogel et al. (1973), as modified by Sollins (1982). Data points constitute average values (mean $\pm$ SE) for upland-OG (o) and peatland-MC (•) habitats. Standard error bars denote variation in both the predictor (x) and response (Y) variables (Smith et al., 2004).

of trees in the same stands (Pyare et al., 2010).

At the broader scale, habitat composition around den trees differed from what was available in the surrounding neighborhood (Pyare et al., 2010). Landscapes surrounding den trees had a greater proportion of higher volume forest and a smaller proportion of young and older second-growth than randomly chosen areas within den neighborhoods. Furthermore, landscapes in which den sites occurred differed in degree of fragmentation than available areas in den neighborhoods. Mean patch size was greater and perimeter/area ratio of patches was lower in areas around den trees than randomly chosen areas (Pyare et al., 2010).

3.3. Persistence of *Glaucomys sabrinus griseifrons* in rainforest fragments

Glaucomys sabrinus was assigned a role as a viability indicator species in the 1997 TLMP Wildlife Conservation Strategy (WCS; Everest et al., 1997). Expectations of WCS in maintaining viable populations of endemic small mammals across the Tongass were founded in ecological theory (Smith et al., 2004). However, multiple inherent assumptions lacking empirical support (Smith and Flaherty, 2023) prompted a study to examine questions regarding the persistence of *G. s. griseifrons* in old-growth fragments of varying size and composition (Smith and Person, 2007). To meet biological objectives of an old-growth reserve (OGR) strategy, TLMP stipulated that $\geq 16\%$ of the total acreage ($\bar{x}$ = 4050 ha) in major watersheds be retained in undeveloped condition, which on the Tongass averaged ≈ 650 ha (USFS, 1997). If not fulfilled through other measures, then $\geq 16\%$ of the watershed (650 ha) must be designated a small OGR. The preferred biological objective was for each small OGR to contain ≥ 325 ha (50% of small OGR) of contiguous, productive old-growth (Smith and Person, 2007). In watersheds < 2025 ha, reserves should contain a minimum of 162.5 ha (0.5×325) of upland-OG (U.S. Forest Service, 1997, K-2). The remaining acreage for preferred or minimum options was unspecified (Smith and Person, 2007). Small OGRs were not spatially explicit and moved multiple times since implementation of the OGR network in 1997 to achieve other Tongass priorities (U.S. Forest Service, 2008, 2016, Smith et al., 2011a).

To evaluate the potential for small OGRs to sustain viable *G. s. griseifrons* populations in isolation, Smith and Person (2007) used demographic data from Smith and Nichols (2003). They estimated average per capita rates of increase (r) with 2 estimates of variance (v) in the absence of immigration or emigration in both upland-OG and peatland-MC habitats. Mean ($\pm$ SD) litter size was obtained from what are now *G. oregonensis* populations in the Puget Trough of Washington (Villa et al., 1999) and used in both habitats. Smith and Person (2007) simulated a birth–death model for *G. s. griseifrons* in upland-OG and peatland-MC forests using Monte Carlo techniques. Parameters were sampled with 4000 simulations from normal distributions defined by their means and standard deviations to estimate the value of r in each habitat. Substantial empirical evidence revealed that *G. sabrinus* exhibits density-dependent population growth (Fryxell et al., 1998; Lehmkuhl et al., 2006), so time to extinction estimates used density-dependent growth relative to

Table 3

Crisp summary of key findings from multiple field studies of persistence of *Glaucomys sabrinus griseifrons* in old-growth rainforest fragments of North Prince of Wales Island Biogeographic Province, Southeast Alaska.

Source Publication	Key findings
Smith and Person (2007). Biological Conservation 137:626–636.	Peatland-MC did not support viable breeding populations, as intrinsic rate of growth was zero. Source populations occurred only in upland-OG forests. Probability of persistence in small OGRs over 100 yrs. for the 50% upland-OG was 43% in peatland-MC and 73% in upland-OG (Table S3, S4). Minimum area of an isolated OGR with 100% upland-OG to achieve ≥ 0.95 persistence is 244,600 ha; minimum population ceiling of <i>G. s. griseifrons</i> is 684,880 (Table S5).
Pyare et al. (2010). J. Mammal. 91:886–896.	At the broader scale, <i>G. s. griseifrons</i> chose den locations in landscapes with higher-volume forests, lower levels of fragmentation, and less young and older second-growth. Mean patch size was greater and perimeter/area ratio of patches was lower in areas around den trees than randomly chosen areas.
Shanley et al. (2013). Ecological Indicators 24:68–74.	Across landscapes, <i>G. s. griseifrons</i> occupied habitat patches with higher-volume forests. Fragments required a minimum area of 73 ha of upland-OG to be occupied by <i>G. s. griseifrons</i> and second-growth ≤ 40 yrs. old were avoided.
Smith and Flaherty (2023). J. Wild. Manage. 87:1–23.	<i>Glaucomys sabrinus griseifrons</i> was extirpated from a 40-ha fragment of upland-OG that was surrounded by ≤ 40 -year-old unmanaged second-growth stands.
Smith et al. (2011a). Source-sinks, metapopulations, and forest reserves: conserving northern flying squirrels in the temperate rainforests of Southeast Alaska. P. 399–422 in J. Liu, V. Hull, A. T. Morzillo, and J. Wiens, editors. Sources, sinks, and sustainability across landscapes. Cambridge University Press, New York, New York, USA.	Effective dispersal distance of moving through clearcuts was $16 \times$ greater than moving a similar distance through contiguous old-growth forest (Table S6). At least 50% of small OGRs in North POW are not functionally connected. Annual dispersers required to prevent <i>G. s. griseifrons</i> extirpation for ≥ 100 years in small OGRs with 25% upland-OG is 162; 30 dispersers for 50% upland-OG and 10 for 100% upland-OG (Table S7). Maximum effective distances for 0.95 probability of persistence over 100 years was 844 m for small OGRs with 25% primary habitat and 1151 m for OGRs with 100% upland-OG (Table S8). Conclusions inferred from demographic analyses and experimental translocations of <i>G. s. griseifrons</i> are that existing habitat OGRs have a low probability of supporting viable breeding populations of flying squirrels over the planning horizon. Expectations that viable metapopulations of <i>G. s. griseifrons</i> will exist through dispersal among fragments with existing populations seem unrealistic because North POW landscapes are not functionally connected.

habitat carrying capacity (Smith and Person, 2007).

The findings of Smith and Person (2007) challenged the expectations of the OGR network (Table 3), demonstrating that the WCS assumptions were untenable (Smith and Flaherty, 2023). Moreover, demographic analyses revealed that peatland-MC did not support viable breeding populations of *G. s. griseifrons*. The only source populations occurred in upland-OG (Smith and Person, 2007). In upland-OG components of OGRs, persistence probabilities for 25 years ranged 90–95% (Table S3). For 50-year and 100-year time horizons, values ranged 81–91% and 66–82%, respectively (Table S3). For populations in peatland-MC, probabilities of persistence for 25 years ranged 81–87% (Table S4). For 50-year and 100-year time horizons, values ranged 65–75% and 43–56%, respectively (Table S4). Smith and Person (2007) only estimated minimum areas for OGRs comprised of 100% upland-OG because the density of reproductive females in peatland-MC was substantially lower than in upland-OG, and because r for populations in peatland-MC was effectively zero, with most simulations generating negative per capita rates of increase.

The minimum area of an isolated OGR to achieve a specified P_t for 25, 50, and 100 years ranged widely (Table S5). For populations with a lower variance of r , a 41-ha patch of upland-OG had an 85% probability of sustaining *G. s. griseifrons* for 25 years. Populations with greater variance required 63 ha of upland-OG to achieve the same level of certainty. To achieve $P_{25} = 95\%$, 578–1127 ha of upland-OG was needed in small OGRs (Table S5), whereas 1136–2354 ha achieved $P_{100} = 85\%$ for 100 years (planning horizon; U.S. Forest Service, 1997). To achieve $P_{100} = 95\%$, 78,935–244,600 ha was needed, depending on v (Smith and Person, 2007).

3.4. Movement limitations: landscape resistance, functional connectivity, movement capability, and probability of dispersal

Another assumption of the WCS was that the OGR network is effective in facilitating the persistence of *G. s. griseifrons* among small OGRs as demes of viable metapopulations (U.S. Forest Service, 1997, Smith and Flaherty, 2023) relying on emigration from source populations (Fahrig and Merriam, 1985, Smith et al., 2011b, Trapp et al., 2019). Smith et al. (2011a) evaluated the efficacy of small OGRs as a functionally connected network of reserves that provide temporary functional habitat for animals dispersing between large and medium OGRs. Their specific objectives were: 1) to determine the number of immigrants required for *G. s. griseifrons* populations in small OGRs to persist for 25 and 100 years; and 2) to determine the maximum landscape resistance that could exist between small and larger reserves and still ensure the required number of immigrants (Smith et al., 2011a). They assumed source populations were supported solely by primary habitat (upland-OG). Peatland-MC forests depended on immigrants to sustain flying squirrel populations and likely produced few, if any emigrants (Smith and Person, 2007), and second-growth was unsuitable (Smith and Nichols, 2003, Smith et al., 2004, Flaherty et al., 2008, Holloway and Smith, 2011).

Smith et al. (2011a) used the proportion of radio-marked *G. sabrinus* juveniles that left their natal area during autumn to estimate emigration rate. The mean $\pm 95\%$ confidence interval (CI) of Euclidian distances between natal dens and all subsequent den locations was used to estimate dispersal distance (Pyare et al., 2010). Permanent relocations with a displacement distance greater than the upper 95% CI were classified as emigrations (Smith et al., 2011a). The probability of a successful juvenile dispersal was estimated as a function of distance and habitat type (Pyare and Smith, 2005). Smith et al. (2011a) used experimental translocations to measure the elapsed time and distance moved by *G. s. griseifrons* coursing through different habitats. The ratio of distance traveled to elapsed time

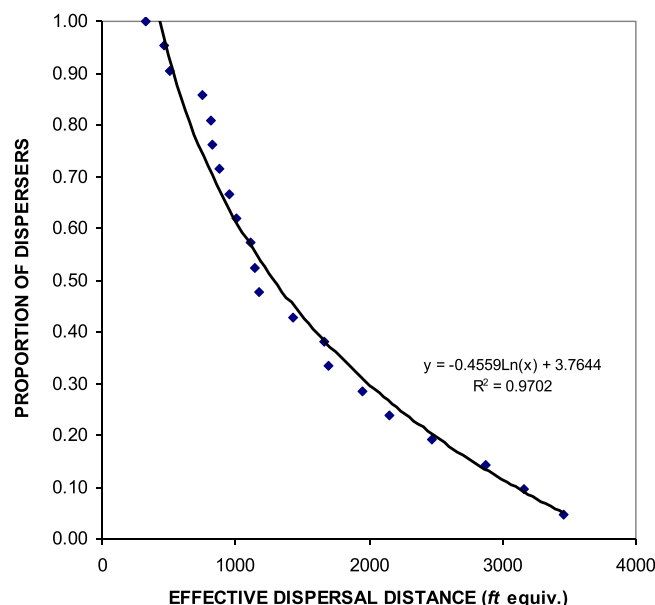


Fig. 4. Proportion of juvenile flying squirrels (*Glaucous griseifrons*) that dispersed in managed matrix of Southeast Alaska relative to effective distance, which was calculated by adding effective distance (permeability) of different landscape elements (Figure 19.2 in Smith et al., 2011a:409).

(effective movement rate) became a surrogate for landscape resistance. Habitat-specific effective distance estimates (Table S6) represented the distance an animal can effectively move through a patch after explicitly considering its resistance (Smith et al., 2011a). The resulting proportions of radio-marked juveniles that dispersed over a range of observed effective distances was used to derive dispersal probability (Fig. 4).

For example, travel times were $16 \times$ greater in recent clearcuts than in intact old-growth (Pyare and Smith, 2005). Thus, the effective dispersal distance of a clearcut crossing was $16 \times$ greater than moving a similar distance through contiguous old-growth forest. Consequently, dispersing through 1 km of old-growth forest was equivalent to dispersing through 62.5 m of a clearcut. Intermediate effective dispersal distances result from *G. sabrinus* moving across a combination of habitats (Table S6). Smith et al. (2011a) derived effective distance estimates experimentally for a subset of common habitats in the study area and subsequently modeled each as a function of vertical forest height. The ability of *G. sabrinus* to move through managed landscapes is significantly influenced by forest structure (Scheibe et al., 2006). The mean length of straight-line movement increases and cost of transport decreases as forest canopy height increases and stem density decreases (Smith et al., 2011a).

Applying the procedures of Smith and Person (2007), Smith et al. (2011a) determined number of annual dispersers needed to achieve an average intrinsic rate of population growth (r) sufficient to achieve time to extinction for time horizons of 25 and 100 years (Smith and Person, 2007). These estimates of r were applied to OGRs with 3 different carrying capacities (K) and populations with ≥ 1 breeding pair relative to K (Table S7). Number of annual dispersers needed to prevent *G. s. griseifrons* from becoming extirpated for ≥ 25 years averaged 1 every 5 years for small OGRs with 100% primary habitat. Small OGRs with minimum prescriptions required ≥ 1 disperser every year; 162 dispersers per year were needed to sustain populations for 100 years in small OGRs with 25% primary habitat (Table S7). For small OGRs in which *G. s. griseifrons* populations are extirpated, ≥ 6 juvenile dispersers per year were needed for $P_t = 0.95$ that a breeding pair would reach the patch (Smith et al., 2011a).

Similarly, Smith et al. (2011a) employed the dispersal probability function of Pyare and Smith (2005) to estimate maximum effective distances for varying scenarios of habitat composition and time horizons (Table S8). Maximum effective distances for persistence ($P_t = 0.95$) over 100 years ranged from 844 m for small OGRs with 25% primary habitat to 1151 m for small OGRs comprised of 100% primary habitat (Table S8). Corresponding values for small OGRs over a 25-year time horizon were 1172 m and 1174 m. Maximum effective distance to establish a breeding pair in vacant small OGRs was 0.1% less than in circumstances when immigrants supplemented local intrinsic rate of growth during 25-year time horizons (Table S8). For 100 years, the maximum effective distance to establish a breeding pair in a vacant small OGR was 38% greater than when dispersal augmented local populations in small OGRs composed of 25% primary habitat. The difference was $< 0.1\%$ for small OGRs composed of 100% primary habitat (Table S8).

Thus, conclusions inferred from demographic analyses (Smith and Person, 2007) and experimental translocations (Smith et al., 2011a) of *G. s. griseifrons* are that existing OGRs have a low probability of supporting viable breeding populations of flying squirrels over the planning horizon (Smith and Flaherty, 2023). Furthermore, expectations that viable metapopulations of *G. s. griseifrons* will exist through dispersal among fragments with existing populations seem unrealistic because POW landscapes are not functionally connected (Smith et al., 2011a). Landscape resistance across managed landscapes, habitat composition of available unmanaged fragments, and dispersers needed for demographic rescue depict circumstances under which successful dispersal is unlikely (Smith and Flaherty, 2023).

Table 4

Crisp summary of key findings from multiple field and laboratory studies of energetic, food resource, and risk to predation limitations of *Glaucomys sabrinus griseifrons* dispersal among old-growth rainforest fragments of North Prince of Wales Island Biogeographic Province, Southeast Alaska.

Source Publication	Key findings
Flaherty et al. (2008). Can. J. Zool. 86:1050–1058.	In experimental trials of quantifying perceptual range of <i>Glaucomys sabrinus griseifrons</i> , the proportion of squirrels successfully orienting towards a forest edge decreased with increasing distance in clearcuts ($r = 0.986$, $P = 0.014$). Although all squirrels released at 25 m in second-growth reached the forest edge within the 180 m spool length, there was no relationship between distance and orientation ($r = 0.879$, $P = 0.317$). Unthinned second growth (Fig. 5) obstructs visual perception and prevents orientation. Successful orientation was positively influenced by wind speed and negatively affected by precipitation. Although habitat was statistically insignificant ($P = 0.382$), its exclusion from the model reduced correct classification of cases. <i>Glaucomys sabrinus griseifrons</i> released in muskegs (peatland-MC) had the longest mean vector lengths, whereas animals released in clearcuts had the shortest mean vector length (Table S9, Fig. 6). Mean vector length in upland-OG forest was greater than in muskegs (peatland-MC) for 3 of 6 spools (Table S9, Fig. 6). Both muskegs and upland-OG vector lengths were greater than clearcuts or second-growth.
Flaherty et al. (2010a). J. of Compar. Physiol. B. 1080:1067–1078.	Net energetic cost of quadrupedal locomotion for <i>G. s. griseifrons</i> was significantly greater than values predicted from allometric equations relative to body mass (two-way ANOVA $F_{2,216} = 264.466$, $P < 0.001$; Table S10). As velocity increased, net cost of transport increased exponentially ($F_{0.05(1),1105} = 10.300$, $P = 0.002$, $r^2 = 0.089$) and excess oxygen consumed above resting increased significantly ($F_{0.05(1),1106} = 158$, $P < 0.001$, $r^2 = 0.644$; Table S10).
Flaherty et al. (2010b). J. Mammal. 91:79–91.	Hemlock and spruce cones were approximately 2.5 and 2.9 times more available during spring in upland-OG, respectively. <i>Vaccinium</i> was more available in autumn (Table S11). Transects in old-growth forest stands had 30 times more spruce cones than managed habitats (Table S11). Hemlock cones were 20 times more abundant in old-growth forest compared with second-growth stands and 9 times more abundant than in clearcuts. <i>Vaccinium</i> spp. were 2–3 times more common in old growth than in managed habitats. No truffles were found in second-growth stands, whereas truffles were about 2.5 times more abundant in old-growth plots than in clearcuts ($P = 0.034$). There was twice as much lichen in old-growth stands than in clearcuts and 9 times more than in second-growth stands ($P = 0.002$; Table S11).

3.5. Movement limitations: Perceptual range, locomotor performance, foraging efficiency, and risk to predation

There are numerous factors that affect the movement capability of *G. sabrinus* (Scheibe et al., 2006, Flaherty et al., 2008, 2010a, Flaherty et al., 2010b, Smith et al., 2011a; Table 4). Moving through a fragmented landscape requires crossing an energetically demanding matrix (Flaherty et al., 2010a, Smith et al., 2011a) and experiencing higher risks of predation (Smith, 2012a) and reduced foraging efficiency (Flaherty et al., 2010b). A necessary prerequisite in moving across nonhabitat within fragmented landscapes is the ability to perceive structural elements and features of habitat (Flaherty et al., 2010a, Trapp et al., 2019). Thus, perception and the inclination of an animal to initiate movement across managed stands could ultimately determine whether *G. sabrinus* successfully disperses across varying landscapes (Flaherty et al., 2008, Trapp et al., 2019). Perceptual range is the distance animals can perceive landscape features (Zollner and Lima, 1997); perceptual orientation, the ability to select the shortest distance toward a landscape feature, can reduce time flying squirrels spend in high-cost habitats and reduce exposure to predators (Flaherty et al., 2008).

Flaherty et al. (2008) investigated the perceptual range of *G. s. griseifrons* on POW by recording the azimuth and length of each vector along movement paths (Zollner and Lima, 1997) of live-captured individuals fitted with a tracking spool in recent clearcuts or unthinned second-growth. This approach assumes that orientation and movement towards an old-growth forest edge are empirical correlates of perceptual capability (Zollner, 2000). Of all the squirrels released in this experiment > 80% returned to the forest patch in which each was captured within 6–7 days after the experiment (Flaherty et al., 2008). The logistic regression model that best distinguished successful squirrels included the variables precipitation, wind speed, and habitat type. The model correctly classified 71.4% of unsuccessful orientations and 61.9% of successful ones (Flaherty et al., 2008). The proportion of individuals successfully orienting towards a forest edge decreased with increasing distance in clearcuts. Although all squirrels released at 25 m in second-growth reached the forest edge, there was no relationship between distance and orientation. According to each's thread-spool path, individuals released in second-growth climbed a tree, returned to the forest floor, and proceeded in an increasingly larger circular path until it intersected the edge of old-growth forest (Flaherty et al., 2008). Unthinned second-growth (Fig. 5) obstructs visual perception and orientation. Second-growth is also energetically costly because *G. sabrinus* uses quadrupedal locomotion to move across branches within dense stands rather than gliding (Scheibe et al., 2006, Flaherty et al., 2010a).

Flaherty et al. (2008) also observed a significant difference in mean vector lengths of squirrel movement among habitats (Table S9, Fig. 6). *Glaucomys s. griseifrons* released in peatland-MC had the longest mean vector lengths, whereas animals released in clearcuts had the shortest mean vector length (Fig. 6). Variation among habitats remained significant when vector length was analyzed in 25-m segments. Mean vector length in old-growth was greater than in peatland-MC for 3 of 6 spools (Table S9, Fig. 6); both were greater than either clearcuts or second-growth (Flaherty et al., 2008). Moreover, there was a positive Spearman rank correlation in both clearcuts and second-growth between mean vector length and cumulative spool segment length (Fig. 6).

Energetic costs and efficiency of locomotion by *G. s. griseifrons* coursing through various habitats are significant factors determining whether individuals can successfully disperse across managed landscapes (Vernes, 2001, Scheibe et al., 2006, Flaherty et al., 2010a, Byrnes and Spence, 2011). Gliding allows *G. sabrinus* to exploit canopy habitats of contiguous old-growth forests (Fig. 7a) as a means to save energy (Scheibe et al., 2006, Byrnes and Spence, 2011). The age, size, and density of trees within second-growth (Fig. 5) require flying squirrels to use quadrupedal locomotion (Flaherty et al., 2008). Moreover, the composition and structure of managed landscapes impose multiple impediments and deficiencies to *G. sabrinus* (Fig. 7b), which rely on late seral forests with large trees, open midstories, diverse understories with vegetative cover and available food resources, and abundant, secure nest sites (Smith 2007a, 2012a; Minns et al., 2024).

To further understand the likely impacts of clearcut logging on movement capability of flying squirrels across Southeast Alaska, Flaherty et al. (2010a) measured quadrupedal locomotor performance of *G. s. griseifrons*. Animals were trained to run inside a Plexiglas chamber on a treadmill while flow-through respirometry methods were used to measure energetic costs of locomotion. The observed net energetic cost of quadrupedal locomotion for *G. s. griseifrons* was significantly greater than values predicted from the allometric equations related to body mass. Furthermore, as velocity increased, the net cost of transport increased exponentially and excess oxygen consumed above resting increased (Table S10). Thus, quadrupedal locomotion in flying squirrels is energetically inefficient, further supporting a conclusion that *G. s. griseifrons* is poorly adapted for a running mode of locomotion and dispersing through clearcuts and

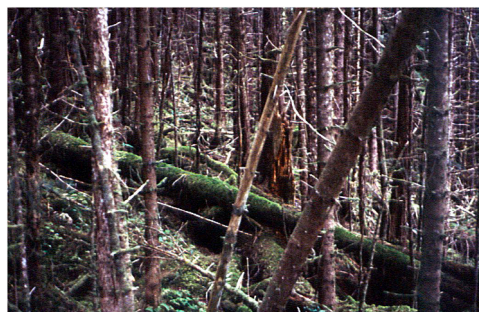


Fig. 5. Unmanaged, previously clearcut logged, second-growth stand of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) in Southeast Alaska.

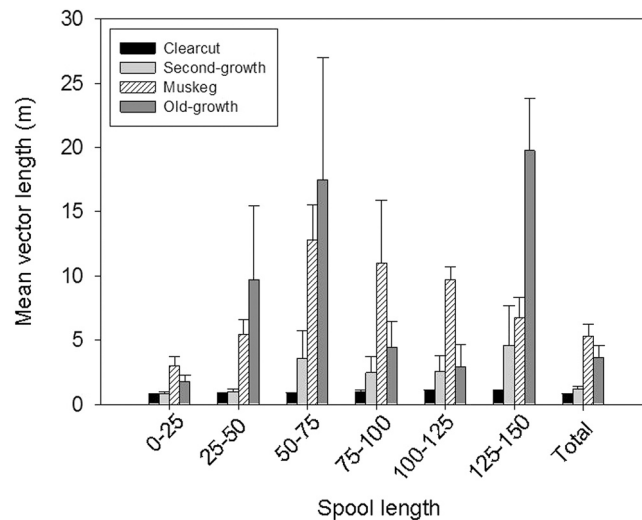


Fig. 6. Mean vector lengths in meters for each 25 m segment of the spool, as well as the entire spool trail, of flying squirrels (*Glaucomys sabrinus griseifrons*) released in clearcuts, second-growth stands, muskegs (peatland-scrub/mixed-conifer forests; sensu Smith and Nichols, 2003) and old-growth forests in Southeast Alaska during 2003–2005 (Fig. 3 in Flaherty et al., 2008:1055). Reliable measurements of 150–160 m were available for most trials. An increase in vector length in distal portions of the spool indicates squirrels became more directional traversing managed habitats (Flaherty et al., 2008).

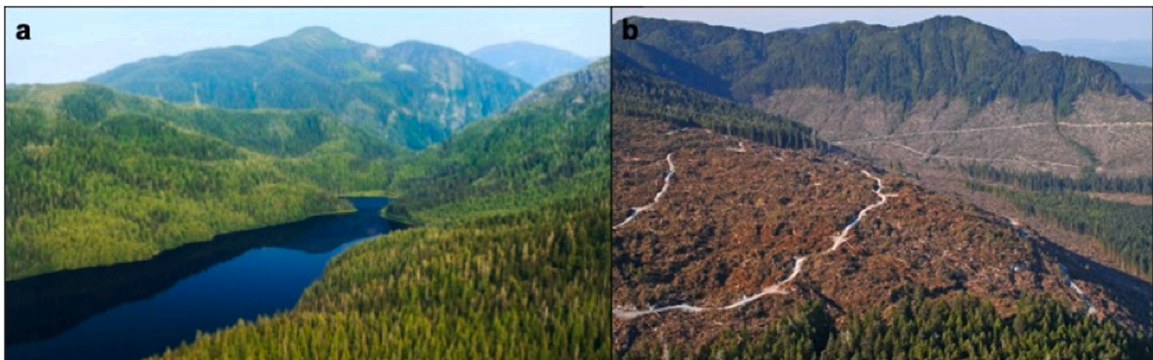


Fig. 7. Forest management of the Tongass National Forest in Southeast Alaska was dichotomous, producing sharply contrasting unmanaged and managed landscapes of (a) intact old-growth temperate rainforests (Photo: Alan Wu/Flickr Creative Commons) and (b) extensive clearcuts (Photo: John Schoen) (Fig. 2 in Smith and Flaherty, 2023:4). Although 12% of the entire Tongass National Forest was logged (Smith and Flaherty, 2023), 67% of the highest volume forests were harvested (Albert and Schoen, 2012). Some smaller islands experienced disturbance across a significant proportion of the entire distribution of resident endemic mammals (Smith et al. 2011a, Smith and Fox, 2017).

unmanaged second-growth stands (Flaherty et al., 2010a).

When locomotion is energetically expensive, food availability and foraging efficiency are essential to facilitate dispersal across managed landscapes (Flaherty et al., 2010b). In the Pacific Northwest, extensive clearcut logging changes the structure and microclimate of old-growth forests (Colgan, 1997), removes the energy sources (trees) for fungi (Amaranthus et al., 1994, Colgan, 1997), and damages the hyphal mat during logging operations (Carey et al., 2002). Consequently, resulting clearcuts and second-growth exhibited lower fungal biomass and diversity than old-growth forests (Amaranthus et al., 1994, Waters et al., 1994, Carey et al., 2002). Thus, Flaherty et al. (2010b) used stable isotopes and fecal analyses to estimate the relative importance of fungal fruiting bodies and other food items in the diet of *G. s. griseifrons*. They used this information to determine if the abundance of diet items varies between old-growth and managed forests, and to evaluate whether dispersers would be expected to encounter adequate food resources while traversing managed landscapes (Flaherty et al., 2010b).

Generally, availability of potential food items did not differ seasonally, except for hemlock and spruce seeds and *Vaccinium* spp. (Table S11). Hemlock and spruce cones were approximately $2.5 \times$ and $2.9 \times$ more available during spring in upland-OG, respectively. *Vaccinium* was more available in autumn (Table S11). Transects in old-growth forest had $30 \times$ more spruce cones than managed habitats (Table S11). Hemlock cones were $20 \times$ more abundant in old-growth forest compared with second-growth and $9 \times$ more abundant than in clearcuts (Table S11). Similarly, *Vaccinium* was $2\text{--}3 \times$ more common in old-growth forest than in managed habitats

(Table S11). No truffles were found in second-growth, whereas truffles were about $2.5 \times$ more abundant in old-growth plots than in clearcuts. Likewise, there was $2 \times$ as much lichen in old-growth forest than in clearcuts and $9 \times$ more than in second-growth (Table S11). However, the abundance of epigeous fungi was similar among habitats (Flaherty et al., 2010b).

4. Discussion

4.1. Demography, habitat use, and ecological correlates of abundance

Smith and Nichols (2003) observed that *G. s. griseifrons* was consistently more abundant in upland-OG than peatland-MC forests. Reproductive females during spring and juveniles during autumn were more abundant in upland-OG than in peatland-MC; summer survival was also higher in upland-OG (Smith and Nichols, 2003). Smith and Person (2007) reported that although flying squirrels occurred in peatland-MC, it was unable to sustain viable populations of *G. s. griseifrons*, relying largely on emigration from source populations in upland-OG (Smith and Person, 2007). More juvenile males were captured in peatland-MC (Smith and Nichols, 2003) and higher densities invariably occurred on peatland-MC grids that were closest to upland-OG (Smith and Person, 2007). Also, simulations in peatland-MC produced a negative intrinsic rate of growth with a mean near zero despite having obtained data to estimate r during a period of rapid population increase (Smith and Person, 2007).

Despite the widely documented association of flying squirrel populations with old-growth forest characteristics (Carey, 1995, Carey et al., 1999, Smith et al., 2003, Holloway and Smith, 2011), conclusions of previous research varied regarding the impacts of forest management on *G. sabrinus* (Smith 2007b, Smith 2012a). Several studies reported no difference in abundance between late seral forests and various treatments among managed stands (Holloway and Smith, 2011). However, a regression of sample size against effect size revealed that studies reporting no difference in abundance had insufficient statistical power to discern significant differences (Holloway and Smith, 2011). When studies were incorporated in a meta-analysis, it became obvious that flying squirrel abundance was reduced by forestry practices that affected structure or age of residual stands, both in the short and longer term (Holloway and Smith, 2011). Immediate impacts occurred under partial harvesting practices such as shelterwood logging, whereas long-term effects were evident in the reduced suitability of stands that regenerate following clearcut logging (Smith and Nichols, 2003, Smith et al., 2004, Sullivan and Sullivan, 2024). Western coniferous forests require $\geq 75\%$ basal area retention to sustain flying squirrel populations (Holloway et al., 2012). Throughout North POW, *G. s. griseifrons* avoided regenerating forests (≤ 40 yrs. old) and 1-km^2 fragments required $> 70\%$ productive old-growth to approach an $\geq 50\%$ expectation of occupancy (Shanley et al., 2013).

Clearly, *Glaucomys sabrinus* is sensitive to logging at both local and broader landscape scales, (Pyare et al., 2010, Holloway and Smith, 2011, Holloway et al., 2012, Shanley et al., 2013). Indeed, the abundance of sciurids has consistently been correlated with micro- and macro-habitat attributes that are common among mature forest types across several locations in western North America (Carey et al., 1999, Smith et al., 2003). Stand attributes such as snag and large tree density, understory plant diversity, and truffle biomass are essential habitat features of *G. sabrinus* populations (Lehmkuhl et al., 2006, Smith 2012a), all of which have been severely impacted by extensive clearcut logging (Smith, 2007b, Sullivan and Sullivan, 2024).

Still, the composition and diversity of arboreal rodent communities likely have shaped habitat relations and demography of *G. sabrinus* populations (Smith et al., 2003, Smith 2007b, 2012a). Smith et al. (2005) reasoned that the higher densities of *G. sabrinus* observed on POW were likely a consequence of the depauperate small mammal fauna in Southeast Alaska (MacDonald and Cook, 1996, Smith, 2005). The semiarboreal Keen's mouse (*Peromyscus keeni*) is the only other arboreal rodent on POW (MacDonald and Cook, 1996), whereas ecological communities across the Pacific Northwest contain several arboreal rodent species (Carey, 1995, Carey et al., 1999, Smith et al., 2003). In Southeast Alaska, den use and demography of *G. sabrinus* differs between islands with and without red squirrels (*Tamiasciurus hudsonicus*). Home ranges were larger, whereas population density, female density, and juvenile recruitment of *G. sabrinus* were all lower on Mitkof Island in sympatry with red squirrels (Smith, 2012b). Flying squirrels on POW exclusively used cavities as maternal dens, whereas females sympatric with *T. hudsonicus* were displaced by red squirrels and forced to use external maternal nests that were less secure against predators (Bakker and Hastings, 2002, Smith 2012b).

The availability of secure cavities for maternal dens appears to be a primary habitat feature explaining variation in *G. sabrinus* densities among old-growth and younger forests (Pyare et al., 2010, Smith 2012b). *Glaucomys sabrinus* prefers large, old trees as den sites (Bakker and Hastings, 2002, Smith 2007b, 2012a, b). On POW, Pyare et al. (2010) reported that *G. s. griseifrons* selected dens in the largest diameter live trees and snags. At the broader scale, *G. s. griseifrons* occupied habitat patches and chose den locations in landscapes with higher-volume forests, lower levels of fragmentation, and less second-growth (Pyare et al., 2010, Shanley et al., 2013). Fragmentation and isolation have increased substantially because of clearcut logging (Smith and Person, 2007, Smith et al., 2011a). Smaller fragments have increased and the mean patch size of primary habitat that exceeds the occupancy threshold has decreased by 58% (Table 1).

Another consistent predictor of *G. sabrinus* presence or abundance is the availability of hypogeous fungi (Loeb et al., 2000, Flaherty et al., 2010b, Trapp et al., 2017, Persad et al., 2025). Truffles are an essential resource influencing occupancy and dispersal success in fragmented forests throughout the range of northern flying squirrels (Loeb et al., 2000, Flaherty et al., 2010b, Trapp et al., 2017, Persad et al., 2025), especially the vulnerable or imperiled populations in West Virginia (Trapp et al., 2017), North Carolina (Loeb et al., 2000, and Alaska (Flaherty et al., 2010b). Thus, factors affecting the distribution or abundance of truffles are likely significant determinants of habitat use and ultimately influence *G. sabrinus* demographics (Flaherty et al., 2010b Trapp et al., 2017). On POW, the limited availability of truffles throughout the managed matrix likely limits occupancy of second-growth, reduces functional connectivity, and restricts dispersal by *G. s. griseifrons* across managed landscapes (Flaherty et al., 2010b).

Older managed forests can support *G. sabrinus* (Smith et al., 2003, Holloway and Smith, 2011) if stands have been thinned and

succession has progressed sufficiently toward mature forest structure (Sullivan et al., 2021), or sufficient green tree retention of older trees occurs (Holloway et al., 2012). Younger, or older unthinned second-growth lack the vegetative diversity and structural attributes and complexity of late-seral forests (Carey, 1995; Carey et al., 1999, 2002; Holloway et al., 2012). Mature forests not only provide large old trees with cavities, older regenerating forests facilitate gliding, develop understories with abundant down, decaying material that create micro- and macro-habitats with hypogeous fungal communities (Carey et al., 2002; Flaherty et al., 2010a, b) to support breeding *G. sabrinus* populations (Smith et al., 2003, Holloway and Smith, 2011). Thus, managed landscapes in Southeast Alaska will require sufficiently large, well-distributed, productive old-growth fragments to sustain viable, widely-distributed *G. sabrinus* populations in isolation, or as metapopulations, to prevent additional local extirpations and extinction (Smith and Person, 2007, Smith et al., 2011a, Smith 2012a).

4.2. Persistence of *Glaucomys sabrinus griseifrons* in old-growth reserves or as a metapopulation

Smith and Nichols (2003) recorded some of the highest *G. sabrinus* densities among forested habitats of western North America (Smith 2007b, Holloway and Smith, 2011, Smith 2012a). Unexpectedly, the relatively high densities reported in peatland-MC were not evidence of viable breeding populations. Further demographic analyses revealed negative intrinsic rates of growth, and that peatland-MC populations were sustained by emigration from nearby upland-OG (Smith and Person, 2007). The density of reproductive females and the large trees females depend on were an order of magnitude lower in peatland-MC than upland-OG (Smith and Person, 2007). Consequently, peatland-MC should not be considered in determining the habitat composition of OGRs. Small OGRs with the preferred prescription that includes peatland-MC do not have a high probability of supporting *G. sabrinus* in isolation for long periods. In the best scenario (100% upland-OG), > 90% persistence in small OGRs was only realized for a time horizon of 50-years (Smith and Person, 2007). Thus, the likelihood that small OGRs will contribute to sustaining *G. sabrinus* will largely depend on the degree of isolation and functional connectivity with other OGRs and sufficiently large productive old-growth fragments (Smith and Person, 2007, Smith et al., 2011a).

Functional connectivity on POW depends on the ability of *G. s. griseifrons* to occupy old-growth forest remnants and reliably disperse through and among diverse habitats of the landscape mosaic with varied landscape resistances (Fahrig and Merriam 2005, Pyare and Smith, 2005, Smith et al., 2011a). Successful dispersal is a function of the distance at which an animal can perceive a specific landscape feature, as well as the energetic costs and risks of predation traversing that distance towards the feature (With and Crist, 1995, Flaherty et al., 2008, Smith 2012a). Flaherty et al. (2008) demonstrated that dispersing *G. s. griseifrons* are unlikely to venture into managed habitats because logging on POW created clearcuts larger than the perceptual range of these mammals. Young second-growth prevented flying squirrels from detecting old-growth forest edges at a distance of 25 m (Flaherty et al., 2008). The shortest vector lengths were in clearcuts, which had few saplings and an abundance of logs and woody debris. Tracking spool paths indicated that *G. s. griseifrons* likely perceived risks of predation in clearcuts as they remained close to structure and increased vigilance behavior as evidenced by frequent shorter, more torturous movements within dense woody debris (Flaherty et al. (2008). Smith (2012a) reported corroborating evidence from an experiment on POW that revealed *G. s. griseifrons* experienced greater predation risk in clearcuts than in second-growth or old-growth.

Typically, straighter dispersal paths are more efficient because straighter paths reduce time, energy consumption, and risk to predation (Flaherty et al., 2008). Although vector length data revealed that *G. sabrinus* will more likely venture into second-growth than clearcuts, orientation data revealed they will spend more time and energy in second-growth in search of the nearest old-growth forest edge (Flaherty et al., 2008). Still, the intermittent locomotion and torturous movement paths in clearcuts likely result in substantial energy expenditure because of associated variation in acceleration and deceleration compared with continuous locomotion (Flaherty et al., 2008, Flaherty et al., 2010a). Regardless, flying squirrels need to access sufficient food resources while dispersing (Flaherty et al., 2010b).

Therefore, to evaluate the dispersal of *G. s. griseifrons* it is necessary to consider both the cost of locomotor transport and availability of food resources for each habitat type (Flaherty et al., 2008, Trapp et al., 2017). Movements, population density, survival, and recruitment (Lehmkuhl et al., 2006) of *G. sabrinus* are correlated directly with truffle availability. Surveys of commonly used food resources on POW revealed that conifer seeds, lichens, and fungi were more prevalent in old-growth than second-growth or clearcuts (Flaherty et al., 2010b). Thus, the availability of food resources on POW not only influences foraging success but also dispersal movements of *G. s. griseifrons* across the managed matrix because of limited food resources in clearcuts and second-growth (Flaherty et al., 2010b).

Smith et al. (2011a) calculated the maximum effective distance between larger reserves and a small OGR that would achieve an immigration rate sufficient to persist, or for a breeding pair to successfully colonize. Maximum effective dispersal distance for supplementing populations or establishing a breeding pair was essentially the same for $P_t = 25$ years (Smith et al., 2011a). Thus, spacing small OGRs at an effective distance of 1 km across old-growth would probably facilitate both recolonization of vacant reserves and supplementation of existing populations and its genetic diversity (Smith et al., 2011a). For $P_t = 100$ years, the maximum effective dispersal distance for supplementing populations was less than the effective distance for recolonization. Small OGRs with minimum prescriptions (25%) should probably be < 850 m from other reserves; small OGRs comprised of $\geq 50\%$ upland-OG can probably be spaced at 1-km intervals in landscapes containing sufficiently large fragments of contiguous upland-OG forests (Smith et al. (2011a). The 1997 TLMP implementation guidelines produced landscapes in which distances among small OGRs averaged 3 km, were spatially inexplicit, and were moved without consideration of landscape context or implications (U.S. Forest Service, 1997, Smith et al., 2011a).

4.3. Additional considerations for wildlife viability across an archipelagos

The Tongass is comprised of thousands of islands (DellaSala et al., 2011). For an island endemic, a significant portion of its range often is a relatively small area. The entire distribution of the Suemez Island ermine (*Mustela erminea seclusa*) is < 160 km² (MacDonald and Cook, 1996). This review illustrates the susceptibility of island endemics to extinction with an example that exemplifies the consequences of intensive, broad-scale removal of habitat with elimination of indispensable resources and interruption of life-sustaining activities. There are numerous other examples (Cook and MacDonald, 2001, Smith, 2005, Arbogast, 2007, Smith, 2013, Smith and Fox, 2017), but only a few have been investigated.

Smith and Fox (2017) detailed the consequences of clearcut logging on the Wrangell Island endemic red-backed vole (*Clethrionomys gapperi wrangeli*), an old-growth habitat specialist. Wrangell Island is 544 km²; 85% of the island is in the Tongass, 72% of which is available for timber harvest (Smith and Flaherty, 2023). Clearcut logging of $\cong$ 15% of old-growth habitat extirpated multiple local vole populations, fragmented remaining vole populations, facilitated increases in local populations of *Peromyscus keeni*, a habitat generalist, and increased interspecific competition between voles and mice in old-growth fragments across managed landscapes (Smith and Fox, 2017). The Tongass has proposed to harvest an additional 16.8 km² (U.S. Forest Service, 2019). Moreover, there are no explicit conservation guidelines or actions to protect this island endemic from further local extirpations (U.S. Forest Service, 2019:4–87).

Threats of extinction are not limited to endemic small mammals. The Queen Charlotte goshawk (*Accipiter gentilis laingi*) is an endemic forest raptor of Southeast Alaska that was designated a sensitive species and underwent viability assessment during the 1997 TLMP revision (Smith and Flaherty, 2023). Formally designated as a metapopulation, the U.S. Fish and Wildlife Service listed all areas with nests as threatened subpopulations in 2012 except Prince of Wales Island (Smith and Flaherty, 2023). Smith (2013) conducted a spatially explicit analysis of contributions of the Tongass toward sustaining goshawk habitat and reported that only 50% of the old-growth habitat required for successful breeding was available. Moreover, only 50% of that habitat was protected and not available for timber harvests (Smith and Flaherty, 2023).

5. Conclusions, conservation implications, and recommendations

The vulnerability of *G. s. griseifrons* stems from 4 well-documented realities: 1) *G. s. griseifrons* has the lowest mitochondrial (Bidlack and Cook, 2001) and nuclear (Bidlack and Cook, 2002) genetic diversity of all populations throughout this species' entire geographic range; 2) its distribution is limited to Prince of Wales Island and a few barrier islands; 3) viable, breeding populations occur only in high-volume old-growth dominated by western hemlock and Sitka spruce; and 4) $\geq$ 40% of its primary habitat and 58% of fragments that exceed the occupancy threshold (Shanley et al., 2013) have been reduced by clearcut logging. Furthermore, because of an increasingly fragmented distribution and limited dispersal capability in managed landscapes, local *G. s. griseifrons* populations are at risk of continued decline and diminishing genetic diversity due to further isolation and inbreeding (Bidlack and Cook, 2001).

Population viability is a contemporary scientific concept referring to a state of low extinction risk over a long period of time (Vucetich et al., 2006). In the 1997 TLMP, the planning horizon of 100 years was specified as the temporal context within which maintaining viable, widely distributed populations was delineated (U.S. Forest Service, 1997, 2008, 2016). The Endangered Species Act of 1973 specified unacceptable risks of extinction by defining threatened or endangered species in terms of a significant portion of a species' range over which a species is in danger of extinction. Recently, the legal definition of extinction was expanded to include species in danger of extinction in any portion of its geographic range (Vucetich et al., 2006). A primary criterion of IUCN's definition of species endangerment includes range occupation (IUCN, 2001).

I conclude that a significant portion of this endemic's entire geographic range is unable to support viable populations. The evidence compiled from numerous field and laboratory studies indicate that in addition to the vacant young clearcuts, unmanaged second-growth, and managed younger (<100 yr. old) second-growth, *G. s. griseifrons* will continue to become extirpated from smaller old-growth remnants in the matrix. Furthermore, there is little evidence to support the assumption that metapopulations exist given the paucity of source populations among old-growth fragments and the landscape resistance that disrupts functional connectivity and impedes dispersal. Consequently, the risk of extinction of *G. s. griseifrons* has not been mitigated by the 1997 TLMP Wildlife Conservation Strategy, corroborating previous conclusions that the status of this endemic subspecies needs immediate formal review (Demboski et al., 1998b, MacDonald and Cook, 1996, Bidlack and Cook, 2001, 2002; Arbogast, 2007). Therefore, I recommend 4 TLMP policy adjustments: 1) discontinue logging of all remaining old-growth forests; 2) restore forests through intermediate management of second-growth stands; 3) conduct a formal review of TLMP conservation elements and assumptions; 4) and implement a comprehensive monitoring plan.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The research summarized in this review was conducted on the Tongass National Forest while the author was employed as a Principal Wildlife Scientist with the U.S. Forest Service, Pacific Northwest Research Station. I thank E. A. Flaherty for her assistance

with a Web of Science literature search and published research contributions to this review article. I thank C. Shanley for help with completing a spatially-explicit GIS analysis to estimate existing and historical landscape conditions on Prince of Wales Island. Brian Arbogast and John Scheibe reviewed an early draft of this manuscript and provided helpful comments. Friends of Blackwater and Alaska Defenders of Wildlife provided financial support to cover the cost of publishing this article.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2026.e04393](https://doi.org/10.1016/j.gecco.2026.e04393).

Data availability

No data was used for the research described in the article.

References

- Alaback, P.B., 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. *Ecology* 63, 1932–1948.
- Albert, D.M., Schoen, J.W., 2012. Use of historical logging patterns to identify disproportionately logged ecosystems within temperate rainforests of southeastern Alaska. *Conserv. Biol.* 27, 774–784.
- Amaranthus, M., Trappe, J.M., Bednat, L., Arthur, D., 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Can. J. For. Res.* 24, 2157–2165.
- Androski, A., Wiens, B.J., Cook, J.A., Dawson, N.G., Colella, J.P., 2024. Phylogeography of mammals in Southeast Alaska and implications for the management of the Tongass National Forest. *J. Wildl. Manag.* 88, 1–26. <https://doi.org/10.1002/jwmg.22627>.
- Arbogast, B., Schumacher, K.I., Kerhoulas, N.J., Bidlack, A.L., Cook, J.A., Kenagy, G.J., 2017. Genetic data reveal a cryptic species of New World flying squirrel: *Glaucmys oregonensis*. *J. Mammal.* 98, 1027–1041. <https://doi.org/10.1093/jmammal/gyx055>.
- Arbogast, B.S., 2007. A brief history of the New World flying squirrels: phylogeny, biogeography, and conservation genetics. *J. Mammal.* 88, 840–849.
- Bakker, V.J., Hastings, K., 2002. Den trees used by northern flying squirrels (*Glaucmys sabrinus*) in southeastern Alaska. *Can. J. Zool.* 80, 1623–1633.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
- Beier, C.M., Lovecraft, A.L., Chapin III, F.S., 2009. Growth and collapse of a resource system: an adaptive cycle of change in public lands governance and forest management in Alaska. *Ecol. Soc.* <http://www.ecologyandsociety.org/vol14/iss2/art5/>.
- Bellante, G., Foss, J., Homan, K., et al., 2025. Tongass National Forest Existing Vegetation Data Products. GO-10300-RPT1. Salt Lake City Ut. U. S. Dep. Agric. For. Serv. Geospatial Off. <https://www.arcgis.com/home/item.html?id=6e0478716240483b9476aee53110037f>.
- Bidlack, A.L., Cook, J.A., 2001. Reduced genetic variation in insular northern flying squirrels (*Glaucmys sabrinus*) along the North Pacific Coast. *Anim. Conserv.* 4, 283–290.
- Bidlack, A.L., Cook, J.A., 2002. A nuclear perspective on endemism in northern flying squirrels (*Glaucmys sabrinus*) of the Alexander Archipelago, Alaska. *Conserv. Genet.* 3, 247–259.
- Brodie, J.F., Redford, K.H., Doak, D.F., 2018. Ecological function analysis: incorporating species roles into conservation. *Trends Ecol. Evol.* 33, 840–850.
- Burkey, T.V., 1995. Extinction rates in archipelagos: implications for populations in fragmented habitats. *Conserv. Biol.* 9, 527–541.
- Byrnes, G., Spence, A.J., 2011. Ecological and biomechanical insights into the evolution of gliding in mammals. *Integr. Comp. Biol.* 51, 991–1001.
- Caouette, J.P., DeGayner, E.J., 2005. Predicting mapping for tree sizes and densities in Southeast Alaska. *Landsc. Urban. Plan.* 72, 49–63.
- Carey, A.B., 1995. Sciurids in Pacific Northwest managed and old-growth forests. *Ecol. Appl.* 5, 648–661.
- Carey, A.B., Colgan III, W., Trappe, J.M., Molina, R., 2002. Effects of forest management on truffle abundance and squirrel diets. *Northwest. Sci.* 76, 148–157.
- Carey, A.B., Kershner, J., Biswell, B., Dominguez De Toledo, L., 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildl. Monogr.* 142, 1–71.
- Cole, K.L., Davis, M.B., Stearns, F., Guntenspergen, G., Walker, K., 2003. Historical landcover changes in the Great Lakes Region. U.S. Geological Survey Landuse History of North America. U.S. Department of Interior (<http://biology.usgs.gov/luhna/contents.html>).
- Colgan, W., 1997. Diversity, productivity, and mycophagy of hypogeous mycorrhizal fungi in a variably thinned Douglas-fir forest. Ph.D. Dissertation, Oregon State University, Corvallis, USA.
- Conroy, C.J., Demboski, J.R., Cook, J.A., 1999. Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. *J. Biogeogr.* 26, 343–352.
- Cook, J.A., Bidlack, A.L., Conroy, C.J., et al., 2001. A phylogeographic perspective on endemism in the Alexander Archipelago of southeast Alaska. *Biol. Conserv.* 97, 215–227.
- Cook, J.A., Dawson, N.G., MacDonald, S.O., 2006. Conservation of highly fragmented systems: the north temperate Alexander Archipelago. *Biol. Conserv.* 3 1–15.
- Cook, J.A., MacDonald, S.O., 2001. Should endemism be a focus of conservation efforts along the north Pacific coast of North America? *Biol. Conserv.* 97, 207–213.
- Crooks, K.R., Burdett, C.L., Theobald, C.M., et al., 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *PNAS* (29), 7635–7640.
- Crutzen, P.J., 2002. Geology of mankind. *Nature* 415, 23. <https://doi.org/10.1038/415023a>.
- DellaSala, D.A., Alaback, P.A., Craighead, L., et al., 2011. Temperate and Boreal Rainforests of the World: Ecology and Conservation (editors). Island Press, Washington, D.C., USA.
- DellaSala, D.A., Gorelik, S.R., Walker, W.S., 2022. The Tongass National Forest, Southeast Alaska, USA: a natural climate solution of global significance. *Land* 11, 1–18.
- Demboski, J.R., Jacobsen, B.K., Cook, J.A., 1998a. Implications of cytochrome b sequence variation for biogeography and conservation of the northern flying squirrels (*Glaucmys sabrinus*) of the Alexander Archipelago, Alaska. *Can. J. Zool.* 76, 1771–1777.
- Demboski, J.R., Kirkland, G., Cook, J.A. 1998b. *Glaucmys sabrinus*. Pp. 37–39 In North American Rodents: Status Survey and Conservation Action Plan. Edited by D. J. Hafner, E. Yensen, and G. L. Kirkland, Jr., 37–39. IUCN/SSC Rodent Specialist Group, Gland, Switzerland.
- Everest, F.H., Swanston, D.N., Shaw III, G.C., Smith, W.P., Julin, K.R., Allen, S.D., 1997. Evaluation of the use of scientific information in developing the 1997 Forest Plan for the Tongass National Forest. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-415, Portland, Oregon, USA.
- Fahrig, L., Arroyo-Rodríguez, V., Cazetta, E., Ford, A., Lancaster, J., Ranius, T., 2021. Landscape Connectivity (Edited by). In: Francis, R.A., Millington, J.D.A., Perry, G.L.W., Minor, E.S. (Eds.), The Routledge handbook of landscape ecology. Taylor and Francis, New York, New York, USA, pp. 67–88 (Edited by).
- Fahrig, L., Merriam, G., 1985. Habitat patch connectivity and population survival. *Ecology* 66, 1762–1768.
- Flaherty, E.A., Ben-David, M., Smith, W.P., 2010a. Quadrupedal locomotor performance in two species of arboreal squirrels: predicting energy savings of gliding. *J. Comp. Physiol. B* 180, 1067–1078.

- Flaherty, E.A., Ben-David, M., Smith, W.P., 2010b. Diet and food availability of the endemic Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons*) in Southeast Alaska: implications for dispersal across managed landscapes. *J. Mammal.* 91, 79–91.
- Flaherty, E.A., Smith, W.P., Pyare, S., Ben-David, M., 2008. Experimental trials of the northern flying squirrel (*Glaucomys sabrinus*) traversing managed rainforest landscapes: perceptual range and fine-scale movements. *Can. J. Zool.* 86, 1050–1058.
- Fogel, R.M., Ogawa, M., Trappe, J.M., 1973. Terrestrial decomposition: a synopsis. Coniferous Forest Biome Internal Report 135. In: College of Forest Resources. University of Washington, Seattle, USA.
- Forsman, E.D., Meslow, E.C., Wight, H.M., 1984. Distribution and biology of the spotted owl in Oregon. *Wildl. Monogr.* 87, 1–64.
- Frankham, R., 1998. Inbreeding and extinction: island populations. *Conserv. Biol.* 12, 665–675.
- Fryxell, J.M., Falls, J.B., Falls, E.A., Brooks, R.J., 1998. Long-term dynamics of small-mammal populations in Ontario. *Ecology* 79, 213–225.
- Hafner, D., Yensen, E., Kirkland, G., 1998. Jr., editors. North American Rodents: Status Survey and Conservation Action Plan. IUCN Rodent Specialist Group, Gland, Switzerland.
- Hansen, M.C., Wang, L., Song, L., et al., 2020. The fate of tropical forest fragments. *Sci. Adv.* 6 (11), eaax8574. <https://doi.org/10.1126/sciadv.aax8574>.
- Holloway, G.L., Smith, W.P., 2011. Forest age, stand structure, and northern flying squirrel densities: a meta-analysis. *J. Wildl. Manag.* 75, 668–674.
- Holloway, G.L., Smith, W.P., Halpern, C.B., Gitzen, R.A., Maguire, C.C., West, S.D., 2012. Influence of forest structure and experimental green-tree retention on northern flying squirrel (*Glaucomys sabrinus*) abundance. *For. Ecol. Manag.* 285, 187–194.
- IUCN, 2001. IUCN Red List Categories and Criteria: Version 3.1. Species Survival Commission. IUCN, Cambridge, United Kingdom.
- Kelt, D.A., Heske, E.J., Lambin, X., et al., 2019. Advances in population ecology and species interactions in mammals. *J. Mammal.* 100, 965–1007.
- Laurance, W.F., 1991. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv. Biol.* 5, 79–89.
- Lehmkuhl, J.F., Kistler, K.D., Begley, J.S., Boulanger, J., 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. *Ecol. Appl.* 16, 584–600.
- Lewis, S.B., Titus, K., Fuller, M.R., 2006. Northern goshawk diet during the nesting season in Southeast Alaska. *J. Wildl. Manag.* 70, 1151–1160.
- Loeb, S.C., Tainter, F.H., Cázares, E., 2000. Habitat associations of hypogeous fungi in the Southern Appalachians: implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). *Am. Midl. Nat.* 144, 286–296.
- MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. *Monogr. Popul. Biol.* 1, 1–203.
- MacDonald, S.O., Cook, J.A., 1996. The land mammal fauna of southeast Alaska. *Can. Field Nat.* 110, 571–598.
- Maser, C., Maser, Z., 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. *Gt. Basin Nat.* 48, 358–369.
- Maxwell, S.L., Cazalis, V., Dudley, N., et al., 2020. Area-based conservation in the twenty-first century. *Nature* 586 (7828), 217–227. <https://doi.org/10.1038/s41586-020-2773-z>.
- Minns, R., Persad, R., Menelon, L., Newar, S.L., O'Brien, P.P., Stead, S.M., Bowman, J., 2024. Seasonal nest use of sympatric North American flying squirrels. *Wildl. Res.* 51, WR23041.
- Nowacki, G.J., Kramer, M.G., 1998. The Effects of Wind Disturbance on Temperate Rainforest Structure and Dynamics of Southeast Alaska. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-421, Portland, Oregon, USA.
- Persad, R., Stead, S.M., Stephens, R.B., Bowman, J., 2025. Home range size, habitat selection, and mycophagy of sympatric North American flying squirrels. *Ecosphere* (7), e70333. <https://doi.org/10.1002/ecs2.70333>.
- Püttker, T., Crouzeilles, R., Almeida-Gomes, M., et al., 2020. Indirect effects of habitat loss via habitat fragmentation: a cross-taxa analysis of forest-dependent species. *Biol. Conserv.* 241, 1–10.
- Pyare, S., Smith, W.P., 2005. Functional connectivity of Tongass old-growth reserves: an assessment based on flying squirrel movement capability. U.S. Fish and Wildlife Service, Juneau Fish and Wildlife Field Office, Ecological Services, Juneau, Alaska, USA.
- Pyare, S., Smith, W.P., Shanley, C., 2010. Den use and selection by northern flying squirrels in fragmented landscapes. *J. Mammal.* 91, 886–896.
- Rosenberg, D.K., Swindle, K.A., Anthony, R.G., 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Can. J. Zool.* 81, 1715–1725.
- Scheibe, J.S., Smith, W.P., Basham, J., Magness, D., 2006. Locomotor performance and cost of transport in the northern flying squirrel, *Glaucomys sabrinus*. *Acta Theriol.* 51, 169–178.
- Shanley, C.S., Pyare, S., Smith, W.P., 2013. Response of an ecological indicator to landscape composition and structure: implications for functional units of temperate rainforest ecosystems. *Ecol. Indic.* 24, 68–74.
- Smith, M.J., Betts, M.G., Forbes, G.J., Kehler, D.G., Bourgeois, M.C., Fleming, S.P., 2011b. Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landsc. Ecol.* <https://doi.org/10.1007/s10980-011-9595-1>.
- Smith, W.P., 2005. Evolutionary diversity and ecology of endemic small mammals of southeastern Alaska with implications for land management planning. *Landsc. Urban. Plan.* 72, 135–155.
- Smith, W.P., 2007a. The northern flying squirrel: a biological portrait of a forest specialist in post-European North America. *J. Mammal.* 88, 837–839.
- Smith, W.P., 2007b. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. *J. Mammal.* 88, 862–881.
- Smith, W.P., 2012a. Sentinels of ecological processes: the case for the northern flying squirrel. *BioScience* 62, 950–961.
- Smith, W.P., 2012b. Flying squirrel demography varies between island communities with and without red squirrels. *Northwest. Sci.* 86, 27–38.
- Smith, W.P., 2013. Spatially explicit analysis of contributions of a regional conservation strategy toward sustaining essential wildlife habitat. *Wildl. Soc. Bull.* 37 (3), 649–658. <https://doi.org/10.1002/wsb.271>.
- Smith, W.P., Anthony, R.G., Waters, J., Zabel, C.J., 2003. Ecology and Conservation of Arboreal Rodents of the Pacific Northwest. In: Mammal Community Dynamics in Western Coniferous Forests (Edited by). In: Zabel, C.J., Anthony, R.G. (Eds.), Management and Conservation. Cambridge University Press, United Kingdom, pp. 157–206 (Edited by).
- Smith, W.P., Flaherty, E.A., 2023. Wildlife studies on the Tongass National Forest challenge essential assumptions of its wildlife conservation strategy. *J. Wildl. Manag.* 87, 1–23. <https://doi.org/10.1002/jwmg.22450>.
- Smith, W.P., Fox, B.J., 2017. Interspecific competition, habitat selection, and coexistence between a generalist (*Peromyscus keeni*) and specialist (*Myodes gapperi*) in rainforest of Southeast Alaska. *Northwest. Sci.* 91, 103–123.
- Smith, W.P., Nichols, J.V., 2003. Demography of the Prince of Wales flying squirrel: an endemic of southeastern Alaska temperate rain forest. *J. Mammal.* 84, 144–158.
- Smith, W.P., Nichols, J.V., Gende, S.M., 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforest of southeastern Alaska. *J. Mammal.* 85, 663–674.
- Smith, W.P., Nichols, J.V., Gende, S.M., 2005. The northern flying squirrel as a management indicator species of north temperate rainforest: test of a hypothesis. *Ecol. Appl.* 15, 689–700.
- Smith, W.P., Person, D.K., 2007. Estimated persistence of northern flying squirrels populations in old-growth rain forest fragments. *Biol. Conserv.* 137, 626–636.
- Smith, W.P., Person, D.K., Pyare, S., 2011a. Source-sinks, Metapopulations, and Forest Reserves: Conserving Northern Flying Squirrels in the Temperate Rainforests of Southeast Alaska (Edited by). In: Liu, J., Hull, V., Morzillo, A.T., Wiens, J. (Eds.), Sources, Sinks, and Sustainability Across Landscapes, 399–422. Cambridge University Press, New York, New York, USA.
- Sollins, P., 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12, 18–28.
- Steiner, M., Huettmann, F., 2023a. Big Data for Small Tree Squirrels in Old-growth Forests? Landscape Metrics, Open Access Field Data, Machine Learning, and GIS Models from Remotely-sensed Imagery in the Tanana Valley State Forest Wilderness of Alaska. Sustainable Squirrel Conservation: A modern reassessment of Family Sciuridae. Edited by M. Steiner and F. Huettmann. Springer Nature, Cham, Switzerland, pp. 251–264. https://doi.org/10.1007/978-3-031-23547-4_8.
- Steiner, M., Huettmann, F., 2023b. Can Squirrels Be Used as Indicators to Identify and Protect Old-Growth Forest Reserves? A Worked Strategic Conservation Planning Workflow with Several Optimization Methods for Environmental Impacts and Climate Change, Involving Indigenous Land. Sustainable squirrel conservation: A

- modern reassessment of Family Sciuridae. Edited by M. Steiner and F. Huettmann. Springer Nature, Cham, Switzerland, pp. 265–278. https://doi.org/10.1007/978-3-031-23547-4_9.
- Steiner, M., Huettmann, F., 2025. Moving beyond the physical impervious surface impact and urban habitat fragmentation of Alaska: quantitative human footprint inference from the first large scale 30 m high-resolution landscape metrics big data quantification in R and the cloud. *Peer J. Life Environ.* 13, e18894. <https://doi.org/10.7717/peerj.18894>.
- Sullivan, T.P., Sullivan, D.S., 2024. Influence of stand thinning on wildlife in managed second-growth forests: tree squirrels, small mustelids, and mammalian species richness. *Wildl. Res.* 51, WR24063.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M., Ransome, D.B., Klenner, W., 2021. Acceleration of forest structural development for large trees and mammals: Restoration in decades or centuries. *Forest.* <https://doi.org/10.1071/WR24063>.
- Toussaint, A., Brosse, S., Bueno, C.G., Pärtel, M., Tamme, R., Carmona, C.P., 2021. Extinction of threatened vertebrates will lead to idiosyncratic changes in functional diversity across the world. *Nat. Commun.* 12, 5162. <https://doi.org/10.1038/s41467-021-25293-0>.
- Trapp, S.E., Flaherty, E.A., Zollner, P.A., Day, C.C., Smith, W.P., 2019. Modeling the influence of landscape connectivity on dispersal movements of the northern flying squirrel (*Glaucomys sabrinus griseifrons*). *Ecol. Model.* 394, 44–52.
- Trapp, S.E., Smith, W.P., Flaherty, E.A., 2017. Diet and food availability of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*): implications for dispersal in a fragmented forest. *J. Mammal.* 98, 1688–1696. <https://doi.org/10.1093/jmammal/gyx115>.
- U.S. Forest Service, 1997. Tongass Land and Resource Management Plan. United States Department of Agriculture, Forest Service R10-MB-338b, Juneau, Alaska, USA.
- U.S. Forest Service, 2008. Tongass Land and Resource Management Plan. United States Department of Agriculture, Forest Service Volume I, II, R10-MB 603a,c,d, Juneau, Alaska, USA.
- U.S. Forest Service, 2016. Tongass Land and Resource Management Plan. R10-MB-769j. United States Department of Agriculture, Forest Service, Juneau, Alaska, USA.
- U.S. Forest Service, 2019. Central Tongass Project. Central Tongass Draft Environmental Impact Statement. USFS R10-MB-832a, Juneau, Alaska, USA. USFS R10-MB-832a, Juneau, Alaska, USA.
- Vernes, K., 2001. Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forests of eastern Canada. *J. Mammal.* 82, 1026–1033.
- Villa, L.J., Carey, A.B., Wilson, T.M., Glos, K.E., 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-444, Portland, Oregon, USA.
- Vucetich, J.A., Nelson, M.P., Phillips, M.K., 2006. The normative dimension and legal meaning of endangered and recovery in the U.S. *Endangered Species Act. Conserv. Biol.* 20, 1383–1390.
- Waters, J.R., McKelvey, K.S., Zabel, C.J., Oliver, W.W., 1994. The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi. *Can. J. For. Res.* 24, 1516–1522.
- Wells-Gosling, N., Heaney, L.R., 1984. *Glaucomys sabrinus*. *Mamm. Species* (229), 1–8.
- WildEarth Guardians, 2011. Petition to list the Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons*) under the U.S. Endangered Species Act. https://ecosystem-documents-production-public.s3.amazonaws.com/sams/public_docs/petition/474.pdf.
- With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76, 2446–2459.
- Zollner, P.A., 2000. Comparing the landscape perceptual abilities of forest sciurids in fragmented agricultural landscape. *Landsc. Ecol.* 15, 523–533. <https://doi.org/10.1023/A:1008154532512>.
- Zollner, P.A., Lima, S.L., 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* 80, 51–60. <https://doi.org/10.2307/3546515>.