

Experimental trials of the northern flying squirrel (*Glaucomys sabrinus*) traversing managed rainforest landscapes: perceptual range and fine-scale movements

E.A. Flaherty, W.P. Smith, S. Pyare, and M. Ben-David

Abstract: Successful dispersal in many species may be a function of the distance at which animals can perceive a particular landscape feature (i.e., perceptual range), as well as energetic costs associated with traversing the distance towards that feature. We used a model, relating perceptual range to body size of mammals, to predict the perceptual range of the northern flying squirrel (*Glaucomys sabrinus* (Shaw, 1801)) in fragmented forests of Southeast Alaska. We hypothesized that the perceptual range of flying squirrels would be 325.5–356.5 m in clearcuts and 159.7–174.9 m in second-growth stands. The distance advantage in clearcuts may, however, be lost if the cost of transport in that habitat is higher. Our results suggest that as heuristically predicted by the model, the perceptual range of flying squirrels was greater in clearcut habitats than in second-growth stands. Nonetheless, for both habitats the actual perceptual range was significantly shorter than predicted by the model. We found that precipitation, and associated cloud cover and illumination, and wind speed, which affect olfaction capabilities, influenced orientation success. Although squirrels more often oriented towards the forest edge in clearcuts, they paused more often during their movements, which may lead to higher costs of dispersing through this habitat. The application of the mass-based model to nonagricultural landscapes should be done with caution, and variables such as wind and illumination be measured concurrently. Our data illustrate that dispersing squirrels likely will not venture into managed habitats because logging creates clearcuts larger than the perceptual range of these mammals.

Résumé : La réussite de la dispersion peut être fonction de la distance à laquelle les animaux peuvent percevoir un élément particulier du paysage (c'est-à-dire la portée de leur perception), ainsi que des coûts énergétiques associés à la distance à parcourir vers cet élément. Nous utilisons un modèle qui relie la portée de la perception à la taille corporelle chez les mammifères afin de prédire la portée de la perception chez le grand polatouche (*Glaucomys sabrinus* (Shaw, 1801)) dans des forêts fragmentées du sud-est de l'Alaska. Nous avons établi en hypothèse que la portée de la perception des polatouches serait de 325.5–356.5 m dans les zones de coupe à blanc et de 159.7–174.9 m dans les peuplements secondaires. L'avantage lié à la distance dans les zones de coupe à blanc peut, cependant, être perdu si les coûts du déplacement dans cet habitat sont plus élevés. Nos résultats indiquent que, comme le prédit de manière heuristique le modèle, la portée de la perception des polatouches est plus grande dans les habitats de coupe à blanc que dans les peuplements secondaires. Néanmoins, dans les deux habitats, la portée réelle de la perception est significativement inférieure aux prédictions du modèle. Les précipitations et la couverture nuageuse et l'éclairement qui les accompagnent, ainsi que la vitesse du vent qui affecte les capacités de l'olfaction, influencent le succès de l'orientation. Bien que les polatouches se dirigent plus fréquemment vers l'orée des forêts dans les zones de coupe à blanc, ils s'arrêtent plus souvent au cours de leurs déplacements, ce qui peut mener à des coûts plus élevés de la dispersion dans cet habitat. On doit utiliser avec prudence le modèle basé sur la masse dans les paysages non agricoles et il est nécessaire de mesurer concurremment les variables telles que le vent et l'éclairement. Nos données montrent que les polatouches durant leur dispersion ne vont vraisemblablement pas s'aventurer dans les habitats aménagés parce que la coupe forestière crée des zones de coupe à blanc plus étendues que la portée de la perception de ces mammifères.

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Introduction

In a fragmented landscape, movements between habitat patches during dispersal ensure population persistence and allow for recolonization of patches following localized extinction (Hanski and Gilpin 1991). Dispersing through a fragmented landscape might require an animal to cross a high-cost matrix (i.e., habitat with increased energetic costs, higher risk of predation, reduced foraging efficiency, etc.). The decision of an animal to venture into such a high-cost environment may be influenced by its ability to perceive features on the landscape towards which it can orient and move. Thus, perception and the propensity of an animal to initiate dispersal across a managed stand could be an important predictor of dispersal success (Lima and Zollner 1996; Zollner and Lima 1997; Selonen and Hanski 2003, 2004). Perceptual range, the distance at which an animal can perceive a particular habitat or landscape feature (Lima and Zollner 1996), must be important to the animal and is potentially species specific (Mech and Zollner 2002). For particular species, the lack of ability to perceive other suitable habitat patches may limit dispersal and reduce habitat connectivity (Lima and Zollner 1996). In addition, perceptual orientation, the ability to select the shortest distance towards a suitable habitat patch, may decrease the time an animal spends in high-cost habitats and reduce exposure to predators (Gruber and Henle 2004). Therefore, perceptual range and orientation ultimately may determine the probability of a successful dispersal.

Mech and Zollner (2002) proposed a model that predicts the perceptual range of sciurids based on one of many potential predictors; height of the animal's eye from the ground estimated from body size:

$$S = 0.53839 - 0.00052M$$

where S is equal to the predicted slope of the perception line and M is equal to the mass of the species in grams. Perceptual range (D) in metres is estimated using the formula:

$$D = (AD_{\text{crit}}/S)(H/15.5)$$

where AD_{crit} is the critical angular divergence value for perceptual range (i.e., field of view of the eye and range of motion of the head, which among sciurids equals to 63° – 69°) and H is the height in metres of the given horizon. The value of 15.5 is a correction for the height of the horizon for grassland or other nonforest landscapes (Mech and Zollner 2002).

While this model was developed for use in agriculture habitats, we were interested in adapting it for use in a forested landscape. Typically, the surface of agricultural landscapes is relatively simple compared with that of a clearcut in forested landscapes, which has a greater amount of vertical structure. We used the model to predict the perceptual range of northern flying squirrels (*Glaucomys sabrinus* (Shaw, 1801)) in the fragmented, temperate rainforests of Southeast Alaska. During the past 40–50 years, Southeast Alaska has experienced considerable industrial-scale clearcut logging creating a mosaic of old-growth, young (<50 years old) second-growth, and clearcut habitats (USDA Forest Service 1997). Additional timber harvest will further fragment this habitat mosaic, potentially creating dispersal bar-

riers for flying squirrels and leading to isolation and localized extinction as successful immigration among remaining fragments across the managed landscape declines.

Old-growth is a low-cost habitat when considering energetic costs, risk of predation, and foraging efficiency of flying squirrels. Flying squirrels rely on old-growth habitat for both facilitation of their nightly long-distance movements (Vernes 2001; Scheibe et al. 2007) and for their diet (Carey et al. 1999). Habitat characteristics of old-growth forests include high canopies and relatively open under- and mid-story layers. For flying squirrels, this forest structure provides high launch points and unobstructed gliding space, which facilitates longer glide distances and increased energetic savings, especially when glides exceed 14 m (Scheibe et al. 2006). Clearcut logging eliminates these habitat features and necessitates that flying squirrels primarily use quadrupedal locomotion to move across managed landscapes (Selonen and Hanski 2003). Old-growth habitat also provides flying squirrels with a preferred diet item, hypogeous fungi (Maser et al. 1978; Gunther et al. 1983; Colgan 1997; Currah et al. 2000; Pyare and Longland 2001). Clearcut logging eliminates the tree hosts, removes the energy source for the fungi, and interrupts the fruiting of truffles (Amaranthus et al. 1994; Colgan 1997). Recovery time for these fungi in Southeast Alaska is unknown, but in other parts of the Pacific Northwest, it may take up to 100 years for these fungi to recover (Waters et al. 1997).

Given its life-history characteristics, specialized means of locomotion, and association with old-growth habitat (Carey 1989), the extensive logging throughout Southeast Alaska raises concerns regarding the ability of individual northern flying squirrels to disperse across the managed landscape. Dispersal of juveniles in early autumn may require flying squirrels to cross clearcut and second-growth habitats when moving between old-growth patches. The ability of these animals to perceive the forest edge beyond clearcut openings or young second-growth stands likely will determine whether they will choose to venture into this high-cost habitat, and ultimately the success of their dispersal (Zollner and Lima 1997).

Because old-growth habitats are most critical to this species' survival and reproduction (Smith and Nichols 2003; Smith and Person 2007), this is a landscape feature that individual flying squirrels should orient towards when moving through a disturbed landscape. Using the model developed by Mech and Zollner (2002), we hypothesized that the perceptual range of a northern flying squirrel in Southeast Alaska (mean mass \approx 130 g) in a clearcut facing a forest profile of 37.7 m (mean old-growth profile height from a clearcut) would be 325.5–356.5 m if the squirrel relies solely on vision. A flying squirrel traversing a young second-growth stand and facing a forest profile of 18.5 m should be able to perceive the forest edge at a distance of only 159.7–174.9 m. In this study, we tested whether the ability of squirrels to orient towards the forest edge conformed to these predictions.

While many mammals appear to use vision as the main sense for perceiving habitat features (Andreassen et al. 1998; Gillis and Nams 1998; Gruber and Henle 2004), others use additional senses such as olfaction. Several studies on small mammals and amphibians demonstrated that

these animals use orientation cues related to wind direction (Schooley and Weins 2003; Schooley and Branch 2005; Mazzerolle and Vos 2006). Therefore, we also investigated the effects of environmental conditions related to olfaction on the ability of squirrels to successfully orient towards the forest edge.

The distance advantage associated with correct orientation towards the forest edge in clearcuts as predicted by the Mech and Zollner (2002) model may, however, be lost if the cost of transport in that habitat is larger than that in second-growth stands. Studies of gray squirrels (*Sciurus carolinensis* Gmelin, 1788) suggest that increased vigilance behavior and associated tortuous movement paths (i.e., short vector lengths and high sinuosity) result in an increase in travel time and cost of transport (Kramer and McLaughlin 2001; Zollner and Lima 2005). Therefore, because successful dispersal in fragmented landscapes will emerge from the ability of squirrels to orient towards the forest edge combined with the costs of transport in each habitat, we also estimated and compared these characteristics of the squirrels' movement paths (Lima and Zollner 1996; Zollner and Lima 1999a, 2005).

Materials and methods

We investigated the perceptual range of northern flying squirrels by recording the azimuth and length of each vector along the movement path (Zollner and Lima 1997, 1999a; Zollner 2000) of individuals fitted with a tracking spool released in clearcuts ($n = 42$) or second-growth stands ($n = 14$) at varying distances from the edge of adjacent old-growth forest (Zollner and Lima 1997). This approach assumes that orientation and movement toward an old-growth forest edge are empirical correlates of perceptual capability (Zollner 2000); thus, the maximum distance at which flying squirrels orient and move toward forest habitat is their perceptual range (Zollner and Lima 1997). We assumed that once placed in clearcuts or second-growth stands, flying squirrels will move towards the forest edge to avoid higher predation risk and absence of gliding opportunities (Vernes 2001; Scheibe et al. 2007). To provide a context for movement patterns and the associated cost of transport in clearcuts and second-growth stands, we also released squirrels fitted with a tracking spool in old-growth habitats (the flying squirrel primary habitat; $n = 8$) and open-forest muskeg (habitat occasionally used by flying squirrels in Southeast Alaska, but where survival of individuals is low (Smith and Person 2007); $n = 14$). For a detailed description of these two habitats see Smith and Nichols (2003).

We trapped northern flying squirrels in old-growth Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands in the northwestern portion of Prince of Wales Island ($55^{\circ}53'28.44''\text{N}$, $133^{\circ}9'57.83''\text{W}$). Trapping took place during the autumn months of 2003–2005 and the spring months of 2004–2005. Squirrels were captured with Tomahawk no. 201 ($41\text{ cm} \times 13\text{ cm} \times 13\text{ cm}$) live traps (Tomahawk Live Trap, Tomahawk, Wisconsin) placed approximately 1.5 m above the ground on the bole of a tree and baited with a mixture of peanut butter, oatmeal, and molasses (Smith and Nichols 2003). Traps were checked at sunrise and males, juveniles

(young of the year), and nonreproductive females were kept in polyvinylchloride (PVC) canisters ($35\text{ cm} \times 7\text{ cm}$) provisioned with apple and a small amount of bait until approximately 30 min before sunset. Our trials were male-biased because they occurred when females had young in the nest. Therefore, we immediately released all trapped females that appeared to be nursing to minimize the time they were separated from their dependent offspring. Because of the small number of females in our trials, we present results from pooled analyses of male and female observations. Our protocols followed guidelines for live-trapping and handling small mammals published by the American Society of Mammalogists' Animal Care and Use Committee (1998), and were approved by an Institutional Animal Care and Use Committee at the University of Wyoming.

We released squirrels in clearcuts or second-growth stands within 2 km of capture sites to limit travel time for squirrels returning to home ranges after the release. Within clearcuts, release stations were 100, 150, and 180 m ($\pm 1\text{ m}$ horizontal distance estimated with a Bushnell Yardage Pro 1000 laser rangefinder; Bushnell, Overland Park, Kansas) from the edge of old-growth forest; in second-growth stands, releases occurred at distances of 25, 50, and 100 m from the edge of old-growth forest. We had no opportunity to test greater distances because of the sizes and shapes of clearcuts in our study area. No releases occurred within 200 m of a second release in a single stand on the same night, and squirrels were not released at the same station on consecutive nights to ensure that they were not using olfactory cues that could have remained from releases during the preceding night.

At the release site, squirrels were fitted with a tracking spool (180 m cocoon bobbin; Barbour Threads Inc., Anniston, Alabama) that was placed inside an uninflated rubber balloon (Zollner 2000). The balloon was glued to the hair on the squirrel's nape and the free end of the thread was tied to a stake placed near the release canister. Following handling, squirrels were returned to the canister for a few minutes; the canister was placed on the ground in a randomly pre-chosen direction relative to the forest edge. We then removed the lid of the canister and quickly and quietly left the area in the opposite direction of the canister's open end. We did not return to the release site until the following day. On only one occasion did a squirrel exit the canister before we departed and no animals remained inside the release canister the entire night.

On the following day, we returned to the release stations and measured the tracking spool thread left by the animal as it exited the release canister and moved through a clearcut or second-growth stand. We modified Zollner's (2000) protocol for measuring spools because microtopography and downed logs and slash (in clearcuts) prevented us from using flags as markers. Beginning at the canister, we used a Brunton compass (model no. 8099; Brunton, Riverton, Wyoming) and field tape to record the azimuth and length of each vector measured to the nearest centimetre. A vector was defined a priori as a segment of the movement path with less than a 5° change in azimuth (Zollner 2000). We measured the movement path of squirrels until the end of a tracking spool was located, or the animal entered an old-growth stand (Fig. 1). Eight squirrels broke the thread or removed the spool before reaching its end.

Perceptual range was evaluated using two statistics (Zollner 2000). The first assesses the linearity of movement trajectories by estimating the sinuosity of the paths using a discretization of travel paths of 1 m (Bovet and Benhamou 1988). This parameter is a unitless numerical description of the convolution (i.e., departure from linearity) of the path. The second test uses angular regression to determine if the mean azimuth traveled by a squirrel was significantly oriented toward the nearest forest edge. In this analysis, the 95% confidence angular intervals are compared with the predicted angle (Batschelet 1981; Zollner 2000). We chose V tests over Raleigh tests because of increased power when a predicted direction is known a priori (Batschelet 1981). For this analysis we used the default α of 0.05 because we wanted to ensure that our results are comparable with those of other studies. To compare orientation success between animals that were released in clearcuts and those released in second-growth stands, we used a one-tailed Z test of two proportions (Zar 1999). Because release distances differed in the two habitats, we only compared the orientation success for animals that were released at 50 m in second-growth stands with those that reached that distance from the forest edge in clearcuts.

In all other analyses, we accepted a probability of <0.10 as indicating statistical significance. We used a type I error of 0.10 to reduce the chance of a type II error, given our small sample sizes and the expected amount of variability in habitat structure that exists in rainforest habitats in Southeast Alaska (Smith et al. 2004).

To explore what variables in addition to vision might affect the ability of squirrels to perceive the forest edge, we compiled data on temperature, precipitation, wind speed, and wind direction from the Weather Underground weather history Web site (<http://wunderground.com>; accessed 18 November 2007) for the town of Klawock, the nearest weather station to our field site. We used data for the night of release for each squirrel. We then introduced these variables together with habitat type (clearcut or second growth) and release distance into a logistic regression model with successful orientation (coded 1) and unsuccessful orientation (coded 0) towards the forest edge as the dependent variable. We chose the top model among several candidate models with a best subset approach based on correct classification of animals and the significance of variables (Hosmer and Lemeshow 2000). We then evaluated the fit of the data to the two top candidate models with Akaike's information criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002).

To evaluate effects of habitat type and distance to forest edge on sinuosity, we used analysis of variance (ANOVA; Zar 1999). In that analysis, sinuosity of the entire path of each squirrel was used as the response variable. We also used ANOVA to compare mean vector lengths among habitats and distances for the entire spool. In that analysis, we included data from squirrels released in open-forest muskeg and old-growth habitats. To determine whether differences in mean vector length among habitats changed as the squirrels moved away from the release canister, we also re-evaluated these data in 25 m segments. For each spool, mean vector length was calculated for each consecutive 25 m from the canister to the most distal point of that spool.

We then compared the results for mean vector length separately for each 25 m segment among the four different habitat types. We treated each 25 m segment as if it was independent of the ones before and after because total spool lengths varied among individuals. Such independent treatment of segments is comparable to multiple comparisons following an ANOVA (Zar 1999), and avoid problems associated with pseudoreplication.

Results

We released a total of 42 northern flying squirrels in clearcuts ($n = 41$ males; $n = 1$ female). Of these, 13 were released at distances of 100 m from the nearest old-growth edge, 17 at distances of 150 m, and 11 at distances of 180 m from an old-growth forest edge. We released a total of 14 squirrels in young (20–25 years old) second-growth habitats ($n = 13$ males; $n = 1$ female). Of these, 7 were released at 25 m from the nearest old-growth edge, 5 were 50 m from the edge, and 2 were 100 m from the edge. We did not release any additional squirrels at 100 m in the second-growth stands because of the difficulties associated with measuring the spool in this habitat and concerns regarding the high risk of mortality in this habitat from American martens (*Martes americana* (Turton, 1806)) and ermines (*Mustela erminea* L., 1758). Of all the squirrels in this experiment, $>80\%$ were recaptured in the old-growth stand where they were originally captured within a mean of 6–7 days after the experiment.

The proportion of animals successfully orienting towards the forest edge (i.e., observed and predicted direction are not significantly different from each other; V test) declined with increasing distance in clearcuts (Table 1, Fig. 1; $r = 0.986$, $p = 0.014$). No such relation between orientation and distance occurred in second-growth stands ($r = 0.879$, $p = 0.317$), although all animals released at 25 m successfully reached the forest edge within the 180 m spool length. When comparing orientation success between these two habitats for animals that were either released at or reached 50 m from the forest edge, animals in clearcuts showed greater ability to orient towards the forest edge (Table 1, Fig. 1; one-tailed Z test of two proportions, $Z = 7.836$, $p = 0.0026$).

The logistic regression model that best distinguished squirrels that successfully oriented towards the forest edge from those that failed, included the variables precipitation, wind speed, and habitat type (logistic regression, $p = 0.015$). This model correctly classified 71.4% of unsuccessful orientation cases and 61.9% of successful ones (overall 67.3%). Ability of squirrels to orient towards the forest edge was positively influenced by wind ($\beta = 0.169$, $p = 0.093$; odds ratio 1.184) and negatively affected by precipitation ($\beta = -1.168$, $p = 0.045$; odds ratio 0.311). Although the effect of habitat was statistically insignificant ($p = 0.382$), exclusion of this variable from the model resulted in lower correct classification of cases (overall 61.2%; unsuccessful orientation cases 75%; successful 42.9%; Hosmer and Lemeshow 2000). The models including and excluding the habitat variable were within 2 AIC_c scores of each other (65.37 including habitat and 63.78 excluding habitat), suggesting strong support for both (Burnham and Anderson 2002). AIC_c weights also suggested that both models had

Fig. 1. Angular divergence plot between predicted and observed direction of orientation towards the forest edge for northern flying squirrels (*Glaucomys sabrinus*) released in clearcuts (A) and second-growth stands (B) of temperate rainforest on northwestern Prince of Wales Island, Southeast Alaska, during 2003–2005. Open circles represent animals released at 100 m, open diamonds represent animals released at 150 m, and open triangles represent animals released at 180 m. Closed circles represent animals released at 25 m, closed diamonds represent animals released at 50 m, and closed triangles represent animals released at 100 m.

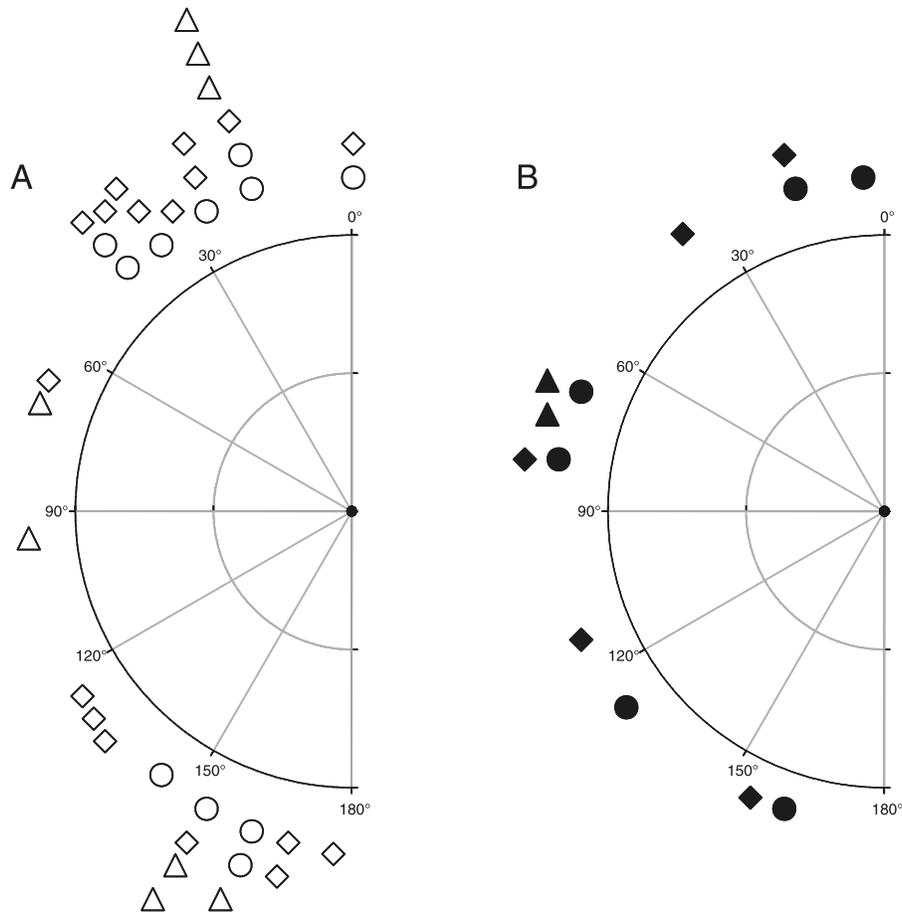


Table 1. Number and proportion (in parentheses) of northern flying squirrels (*Glaucomys sabrinus*) released in clearcuts and second-growth stands in Southeast Alaska during 2003–2005 that successfully oriented toward the forest edge (angular divergence not significant).

Distance from forest edge	Clearcuts		Second-growth stands	
	<i>n</i>	Successful orientation	<i>n</i>	Successful orientation
25			6	2 (0.33)
50	11*	10 (0.91)	5	2 (0.40)
100	11	7 (0.64)	2	0 (0.0)
150	17	9 (0.53)		
180	8	3 (0.38)		

*No squirrels were released at 50 m from the forest edge in clearcuts, but of those that reached that distance (italic type) during their travels in this habitat, 91% oriented towards the forest edge. Several of the animals that were released in the clearcut and oriented successfully towards the forest edge, including the three animals released at 180 m, did not reach 50 m from the forest edge at the end of their spool.

similar fit to the data (excluding habitat 0.689, including habitat 0.311). Despite the strong support for both models with AIC_c, the superior classification of successful orientation cases by the model that included habitat suggests that

the model including habitat provides better representation of the performance of flying squirrels. This logistic regression model indicated that animals released in clearcuts were more likely to orient successfully toward the forest edge. Because release distances differed between the two habitat types, the two variables could not be included in the same model (as one provided the same information as the other). In a model substituting distance for habitat, correct classification of sites was lower and therefore not reported here.

Analysis of sinuosity yielded values that ranged from 0.401 to 1.53, with no significant effect (two-way ANOVA, $F_{[2,54]} = 0.82$, $p = 0.574$; Fig. 2) attributable to distance from release site to forest edge or the habitat type. A one-way ANOVA comparing sinuosity of paths for animals that successfully oriented towards the forest edge with those that did not (Zollner and Lima 1999a) was significant in second-growth stands ($F_{[2,11]} = 4.73$, $p = 0.058$) but not in clearcuts ($F_{[2,41]} = 0.29$, $p = 0.592$).

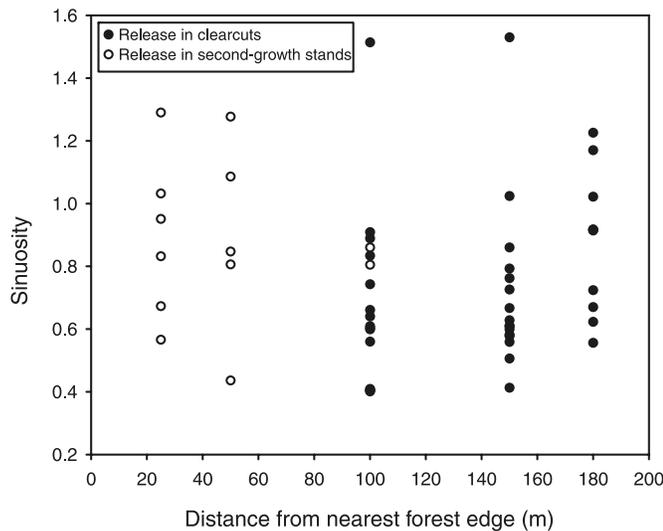
There was a significant difference in mean vector lengths of squirrel movements among habitats (Table 2, Fig. 3; ANOVA, $F_{[2,48]} = 7.35$, $p < 0.05$). Flying squirrels released in muskegs had the largest mean vector lengths, whereas animals released in clearcuts had the lowest mean vector length (Fig. 3). The variation among habitats remained significant

Table 2. Sample sizes for vector length measurements of spool trails of northern flying squirrels (*Glaucomys sabrinus*) released in clearcuts, second-growth stands, muskegs, and old-growth stands in Southeast Alaska during 2003–2005.

Spool length (m)	Clearcuts		Second-growth stands		Muskegs		Old-growth stands	
	<i>n</i>	Significance	<i>n</i>	Significance	<i>n</i>	Significance	<i>n</i>	Significance
0–25	36	a	13	b	12	c	8	c
25–50	33	a	9	a	11	b	7	b
50–75	31	a	9	b	8	c	5	c
75–100	30	a	6	b	7	c	5	bc
100–125	24	a	6	b	6	c	5	b
125–150	21	a	5	b	5	b	4	c
Total spool	42	a	14	b	14	c	8	d

Note: Data are presented in Fig. 3. Letters indicate significant differences (post hoc multiple comparisons at $\alpha = 0.05$) among habitat types for each 25 m segment. Reliable measurements up to approximately 150–160 m were available for most trials.

Fig. 2. Sinuosity of the movement paths of northern flying squirrels (*Glaucomys sabrinus*) following releases in both clearcuts and second-growth stands of temperate rainforest at 25, 50, 100, 150, and 180 m in Southeast Alaska during 2003–2005.

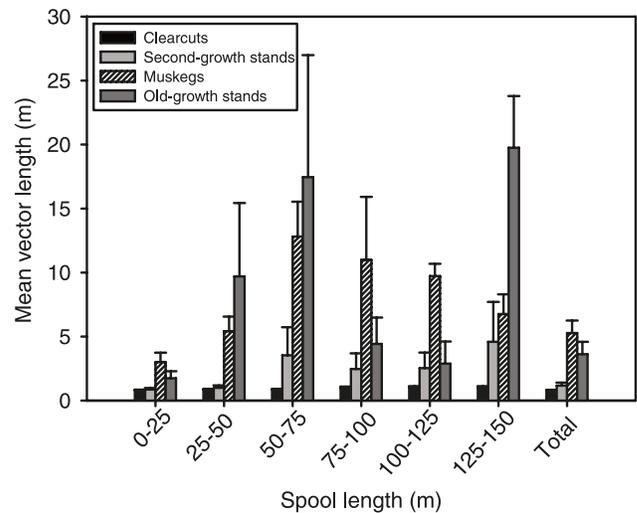


($p < 0.05$) even when vector length was analyzed in 25 m segments (beginning at the release canister). Mean vector length in old-growth forest was greater than in muskegs for three of the six spool segments (Table 2, Fig. 3), but both were greater than either clearcuts or second-growth stands (Table 2, Fig. 3). In both clearcuts and second-growth stands, as distance from release site increased, there was a positive correlation (clearcuts: Spearman rank correlation, $r_s = 0.933$, $n = 6$, $p < 0.05$; second-growth stands: Spearman rank correlation, $r_s = 0.823$, $n = 6$, $p < 0.05$; Zar 1999) between mean vector length and cumulative spool segment length (Fig. 3).

Discussion

Our results suggest that as heuristically predicted by the model developed by Mech and Zollner (2002), the perceptual range of northern flying squirrels is greater in clearcut habitats than in second-growth stands. Nonetheless, for both habitats the actual perceptual range was significantly shorter than predicted by the model (100–150 vs. 325–357 m for clearcuts, 25–50 vs. 159–175 m for second-growth stands).

Fig. 3. Mean vector lengths in metres for each 25 m segment of the spool, as well as for the entire spool trail, of northern flying squirrels (*Glaucomys sabrinus*) released in clearcuts, second-growth stands, muskegs, and old-growth stands in Southeast Alaska during 2003–2005. Reliable measurements up to approximately 150–160 m were available for most trials. The increase in vector lengths in the distal portions of the spool suggests that animals became more directional traveling the managed habitats.



This difference suggests that in forested landscapes predicting perceptual range based on vision as determined by body mass and height of horizon alone may be inappropriate. Indeed, our data suggest that olfaction may also play an important role in determining the ability of flying squirrels to orient towards the forest edge. One of the two variables that best separated successful orientation from unsuccessful cases was wind speed, which can affect the ability of squirrels to smell the forest edge. More importantly, our results demonstrate that determination of the perceptual range of flying squirrels may be only one step in evaluating the success of dispersal. Our data indicate that although squirrels more often oriented towards the forest edge in clearcuts, they were more tentative in their movements (shorter vector lengths) likely because of perceived high risk of predation in that habitat. In contrast, although squirrels were less able to orient toward the forest edge in second-growth stands, they were more deliberate in their movements (less sinuous

and longer vector lengths), supposedly because of higher confidence.

Several factors could explain the departure of our estimates of perceptual range from the predictions of the model based on body mass (Mech and Zollner 2002). As noted by the authors their model is best used in open agricultural landscapes. Small mammals in such landscapes seem to use the visible vertical profile of an edge as a cue in discerning their target habitat (Zollner and Lima 1997; Mech and Zollner 2002). Unlike most midwestern agricultural landscapes, which are relatively homogenous, the forest habitats of Southeast Alaska are spatially heterogeneous at multiple spatial scales (Smith and Nichols 2003). The extent to which the perceptual abilities of northern flying squirrels are affected by downed woody debris and logs (clearcuts) or microtopography (clearcuts and second-growth stands) is unclear. We noticed that flying squirrels in our study immediately climbed a tree (second-growth stand) or a nearby stump (clearcut) following release, presumably to scan the horizon. We expected that this behavior would increase the perceptual range relative to that predicted because squirrels had the residual forest structure to aid in scanning for preferred habitat. However, following a climb, the squirrel usually moved back to the ground and it is likely that the variation in microtopography and large debris obscured the view of the old-growth forest profile. Unfortunately, in this study we were unable to control for effects of variation in microtopography and proportion of the forest edge that was visible, or standardize sampling where the visible horizon is similar among release stations. This should be the goal of future studies.

In animals that rely on vision, perceptual range may be decreased with lower ambient illumination (Zollner and Lima 1999b). For example, overcast days negatively affected the success rate of turtles orienting toward aquatic habitats (Yeomans 1995). Similarly, we found that precipitation negatively influenced the ability of northern flying squirrels to orient towards the forest edge. Precipitation is associated with greater cloud cover, and therefore low illumination, and may also obscure the horizon. This result suggests that indeed flying squirrels do rely on vision to orient towards the forest edge but that, similar to other species which are affected by environmental conditions (Olden et al. 2004), their ability to do so is lowered on overcast, rainy nights.

Our analyses also indicate that northern flying squirrels may not rely solely on vision for perceiving their preferred habitat. Similar to other small mammals and amphibians that use wind direction for orientation (Schooley and Weins 2003; Schooley and Branch 2005; Mazerolle and Vos 2006), we found squirrels better able to orient towards the forest edge on windy nights. Flying squirrels have a well-developed sense of smell to locate subterranean fungi (Pyare and Longland 2001), and likely use olfactory cues to orient towards old-growth habitats. Interestingly, we found no effect of wind direction on the ability of squirrels to detect the forest edge. Unfortunately, we cannot conclude that wind direction was not an important factor because we only had data on mean wind direction. From experience we know that wind direction can change within minutes in that environment. Therefore, to fully address

this issue one will need more fine-scale data on wind direction.

The shortest mean vector length was recorded in clearcuts, which had few saplings and an abundance of logs and coarse woody debris. We speculate that because flying squirrels were probably more vulnerable (or perceived greater risk) in clearcuts to avian and mammalian predators (Pyare and Longland 2002), they remained close to structure (evident from tracking spools) and increased vigilance behavior, the consequences of which were shorter, more tortuous movement paths likely leading to an increase in travel time (Kramer and McLaughlin 2001; Zollner and Lima 2005). Red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)) move more slowly across clearcuts than through habitat with forest cover (Bakker and Van Vuren 2004), and gray squirrels foraging in unforested landscapes pause more often than those moving in forested ones (Kramer and McLaughlin 2001). Thus, although flying squirrels more often oriented towards the forest edge in clearcuts, they were more tentative in their movements when compared with movement patterns in old-growth stands, muskegs, and second-growth stands (Table 2). The shorter vector lengths we observed suggest that squirrels moving through clearcuts likely paused more often during their movement forays. Such intermittent locomotion may result in increased energy expenditure because of the associated variation in acceleration and deceleration compared with continuous locomotion (Alexander 1989; Kramer and McLaughlin 2001). In general, straighter dispersal paths are more efficient than tortuous ones during landscape-level dispersal because straighter paths minimize redundant search, minimize energy consumption, and minimize potential predation on the disperser (Lima and Zollner 1996; Zollner and Lima 1999a; Zollner and Lima 2005). Therefore, dispersal success of flying squirrels through clearcuts may be compromised because of increased energetic costs and higher risk of predation.

Although high sinuosity has been correlated with low crossing or homing success (McDonald and St. Clair 2004), some sinuosity could allow for increased chance of detection of preferable patches in landscapes with clumped habitat distributions (Duvall et al. 1994). This may explain our observation that although a small proportion of animals successfully oriented towards the forest edge in second growth, all those released at a distance of 25 m were able to reach the forest edge within the length of their spool. Thus, these squirrels “diffused” back to the old-growth in second-growth stands. The vector length data suggest that flying squirrels will be more likely to venture into second-growth stands than clearcuts, but the orientation data indicate that they will likely spend more time diffusing through this habitat in search of the nearest forest edge. Therefore, to assess the dispersal costs of squirrels in this landscape mosaic, it will be necessary to model the cost of transport, evaluate food availability, and estimate risk of predation separately for each habitat type. It is interesting, however, that in both habitats squirrels appeared less tentative the longer they spent moving through the managed landscape. How such acclimation may affect subsequent dispersal behavior and cost of transport is unclear and merits further investigation.

In conclusion, our observations suggest that in addition to considering body mass in the estimation of perceptual range

of small mammals (Mech and Zollner 2002), more information than body mass and the height of the horizon may be needed to accurately estimate this variable in complex habitats. Furthermore, we suggest that perceptual range in mammals may deviate from body mass predictions not only because of horizontal relief and microtopography but also because of varying life-history requirements. We suspect that flying squirrels and other mammals may rely on multiple cues (visual, olfactory, and auditory) and are affected by environmental conditions. Therefore, we suggest that application of the model proposed by Mech and Zollner (2002) to nonagricultural landscapes be done with caution as suggested by the authors and that other factors and variables such as wind, temperature, humidity, and illumination be measured concurrently.

Finally, dispersal success of flying squirrels in Southeast Alaska will largely depend on the configuration of the habitat mosaic. Because our estimated distances of perceptual range in both habitats were much lower than the distances across most existing clearcuts and second-growth stands on Prince of Wales Island (on average ≥ 360 m; USDA Forest Service 1997), it is unlikely that dispersing squirrels will venture into either of these high-cost habitats, especially into clearcuts. Siberian flying squirrels (*Pteromys volans* (L., 1758)) were willing to cross open habitat only when the opening could have been crossed with a single glide (Selonen and Hanski 2003). Northern flying squirrels will glide across a distance that is twice as long as the height of their launch (Vernes 2001). Given that the mean tree height of old-growth Sitka spruce and western hemlock is 37.7 m, dispersing squirrels will be unable to glide across existing clearcuts. Indeed, results of a companion study using radio telemetry suggests that squirrels released in clearcuts used stream buffers as movement corridors to return to their home range once they found the nearest forest edge (S. Pyare and W.P. Smith, unpublished data). Similar observations were made by Bakker and Van Vuren (2004) for red squirrels. Therefore, our findings illustrate that further fragmentation of old-growth forests with large-scale clear-cutting in Southeast Alaska may create barriers to flying squirrel dispersal, unless viable corridors are maintained.

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