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Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*)

Matthew J. Smith [a,*], Graham J. Forbes [c], Matthew G. Betts [b]

[a] Fundy National Park, P.O. Box 1601, Alma, NB E4H 1B4, Canada
[b] Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331, USA
[c] Faculty of Forestry and Environmental Management, University of New Brunswick, P.O. Box 4400, 28 Dineen Dr., Fredericton, NB E3B 5A3, Canada

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ABSTRACT

Reduced movement across a landscape due to habitat loss and fragmentation is considered one of the primary reasons for species' population declines. Gliding mammals, such as the northern flying squirrel (*Glaucomys sabrinus*), are expected to be particularly sensitive to large non-forested gaps and therefore have been used as umbrella species in planning for landscape connectivity. We tested the gap-crossing decisions of the northern flying squirrel in a forested landscape in southern New Brunswick, Canada. We translocated 35 flying squirrels across non-forested gaps (50–960 m) with varying detour efficiency (distance to return home across the gap divided by the forested detour distance) and recorded the individual movement paths to return home. We found that 69% of flying squirrels took the forested route home and avoided crossing gaps. Detour efficiency was the only significant landscape predictor of gap-crossing; for every 1% increase in detour efficiency the odds of flying squirrels returning were 15% higher. Northern flying squirrels were much more likely to take forested routes than to cross open canopy gaps, even when the direct distance was 6.8 times shorter. In addition, flying squirrels took substantially longer to return home if gaps in forest cover exceed a threshold of 335 m. Such threshold responses by flying squirrels could partly explain observed drops in flying squirrel occurrence in small, isolated patches of forest. Avoidance of gaps when detours are cheap suggests that there is a cost associated with crossing gaps. This provides support for the importance of maintaining functional connectivity in forested landscapes.

1. Introduction

Globally, forested landscapes have undergone dramatic changes due to anthropogenic habitat loss and degradation (Hansen et al., 2010). Half of the temperate broadleaf and mixed forest biome has been fragmented or deforested by human activity (Millennium Ecosystem Assessment, 2005). Although habitat amount is considered to have a dominating influence on population abundance (Fahrig, 2003; Swift and Hannon, 2010), habitat fragmentation is expected to impact some species, particularly when habitat amount is low (Betts et al., 2006). Fragmentation, independent of habitat amount, is predicted to negatively influence population viability due to the restriction of movement across non-habitat matrix or gaps, which may lower dispersal, restrict immigration, limit potential foraging area, increase competition to isolated patches, and increase predation rates (Andrén, 1994; Fahrig, 1998). Given the rapid loss in habitat area and associated fragmentation, there is an urgent need for species-specific movement models that realistically portray animal behaviour and movement ability in complex landscapes (Bélisle, 2005).

Unfortunately, describing the structural connectivity of habitat patches often is insufficient when explaining population numbers due to incorrect assumptions regarding species movement abilities and behaviour in fragmented landscapes (Kupfer et al., 2006; Taylor et al., 1993). Functional connectivity measures the permeability of different habitat types from the 'species point of view' using empirical data on how organisms perceive barriers and whether these match our assumptions (O'Brien, 2002; Taylor et al., 1993). Detailed understanding of animal movements is hampered by a lack of experimental studies controlling for the habitat amount and configuration (Stutchbury, 2007).

Previous studies have shown that an organism's gap-crossing decisions are often a function of two components: body size and behaviour (Mech and Zollner, 2002; Rizkalla and Swihart, 2007). Large-bodied species are predicted to have a greater perceptual range – the distance from which a species can detect patches or forest edge (Zollner and Lima, 1997). Less is known about what motivates a species to cross open areas if they detect habitat on the opposite side of the gap (Bélisle, 2005). These gap-crossing

* Corresponding author. Tel.: +1 (506) 887 6054; fax: +1 (506) 887 6071.
E-mail addresses: matthew.smith@pc.gc.ca (M.J. Smith), forbes@unb.ca (G.J. Forbes), matthew.betts@oregonstate.edu (M.G. Betts).

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movements are critical and may allow species to persist in fragmented landscapes through dispersal to isolated patches and by habitat supplementation – where an individual's territory expands to encompass several habitat patches (Dunning et al., 1992).

Because gap-crossing events are rarely observed in nature, translocation experiments have been used to study gap-crossing behaviour; research on gap-crossing now exists for a number of taxa (e.g., insects (Pither and Taylor, 1998), fish (Turgeon et al., 2010), birds (Hadley and Betts, 2009), amphibians (Mazerolle and Desrochers, 2005) and mammals (Duggan et al., 2012)). This technique allows the researcher to test hypotheses by manipulating the size and type of barrier between the displaced animal and its home range (Bélisle, 2005). There is some evidence that species with long perceptual ranges are able to make cost/benefit decisions regarding whether or not to take a forested route or cross a gap (Bélisle and Desrochers, 2002; Desrochers and Hannon, 1997). Bakker and Van Vuren (2004) found that detour efficiency (distance to return home across the gap divided by the forested detour distance) was the most important predictor of red squirrel (*Tamiasciurus hudsonicus*) gap-crossing decisions. When the detour efficiency was below 60%, squirrels were more likely to cross the clearcut than use the forested route.

Gliding mammals, such as the northern flying squirrel (*Glaucomys sabrinus*), are expected to avoid large gaps because of their reliance on gliding from tall trees for movement across the landscape (Vernes, 2001). Movement studies of another temperate forest glider, the Siberian flying squirrel (*Pteromys volans*), indicate they will use woodland strips and non-habitat matrix for inter-patch movements, and will occasionally cross narrow open gaps (Desrochers et al., 2003; Selonen and Hanski, 2003). There is also evidence of dispersing juvenile *P. volans* crossing fields >300 m that were impossible to circumnavigate (Selonen and Hanksi, 2004). Although habitat isolation is predicted to negatively impact the viability of flying squirrel populations (Reunanen et al., 2000; Smith and Person, 2007) little is known about the cost-benefit factors influencing whether a glider will cross barriers. A glider's propensity to cross bare ground, recent clearcut- harvest area, or young plantations can be modeled to create different landscapes categorized in terms of a 'realistic cost surface' (Sawyer et al., 2011). Flying squirrels often are used as a model species for predicting the impacts of forest loss and fragmentation on biodiversity (Hurme et al., 2008; Smith, 2012). If an objective of landscape-scale forest management plans is to maintain functional connectivity (Betts and Forbes, 2005; Lindenmayer and Cunningham, 2013), information on movement behaviour is required in order to incorporate movement behaviour associated with different surfaces.

Two earlier studies have found lower occurrence of northern flying squirrels in patches surrounded by larger amounts of non-forest (Ritchie et al., 2009) and in smaller isolated patches (Patterson and Malcolm, 2010). Given the gliding ability of northern flying squirrels and their arboreal nature, we tested the hypothesis that flying squirrel occurrence is lower in these areas because they avoid crossing non-forested areas (clearcuts <10 years) if the gap exceeds their gliding ability (>30 m) (Vernes, 2001). In an earlier study (Smith et al., 2011), we found that the connectivity of mature forest (>60 years) was a strong predictor of flying squirrel homing success independent of mature forest amount. This study was conducted over a wide range of translocation distances (up to 3900 m) but individual movement paths were not recorded, so fine-scale mechanisms for variability in homing success are unknown. Also, models based on landscape-scale movements in previous translocation experiments may produce different results than those based on local-scale movements (Desrochers et al., 2011). In this study, we addressed these deficiencies by measuring the functional connectivity of non-forest gaps at the local-scale (<1 km) and collecting detailed movement data.

To determine the permeability of non-forested areas to flying squirrel movements we tested two predictions: (1) flying squirrels will not cross non-forested areas greater than their gliding distance if they can take an alternative forested route, or (2) flying squirrels will cross non-forest areas only if the detour distance is very long compared with the crossing distance (low detour efficiency). We also explored the relative importance of other variables, including sex and clearcut age, on the probability of gap-crossing and return time. Finally, we investigated the relative risk of gap-crossing by comparing the crossing rate and tortuosity of the movement paths in gap and forested return paths.

2. Materials and methods

2.1. Study area

We conducted our translocations within the Greater Fundy Ecosystem of southern New Brunswick, Canada. This area is composed of a mix of deciduous and coniferous species with 46% of the region covered in mature forest (>60 years), 36% by early seral stages (<20 years) and 18% is non-forested areas (clearcuts, wetlands, lakes). The average clearcut size on public land in New Brunswick is 35 ha, but the maximum permitted is 100 ha (Martin, 2003). Currently conifer (mainly *Picea*) plantations make up 10% of the landscape although that is expected to rise in the next 20 years to 28% of the landscape in an effort to increase wood fibre production (New Brunswick Department of Natural Resources, 2009).

2.2. Selection of translocation study sites

We selected 15 clearcuts < 400 m from flying squirrel capture transects (Fig. 1). These clearcuts represented a range of shapes and gap required to test the effects of gap size and detour efficiency on flying squirrel movement behaviour. To meet our selection criteria, all clearcuts needed to be <10 years old and surrounded by mature forest with tree heights >10 m (clearcut vegetation characteristics are shown in Supplementary Material A, Table 1A). We chose a minimum tree regeneration height of 10 m to ensure a well-defined 'hard' edge between the clearcut and surrounding forest. All clearcuts had been planted with conifer seedlings within a year after harvesting, and subsequently treated with herbicide to remove most broadleaved trees and shrubs. The older clearcuts (i.e., plantations) contained conifer trees up to 2.6 m tall. Previous studies have found that flying squirrels tend to use mature forest more frequently than other age classes for denning and foraging (Holloway and Smith, 2011) and avoid young forests (*P. volans*; Selonen and Hanski, 2003).

Flying squirrel gliding distance is <30 m (Vernes, 2001) so we chose a minimum gap size of 50 m to ensure flying squirrels could not glide across clearcuts.

2.3. Translocation methods

In addition to the 30 squirrels translocated in 2007–2008 we used five squirrels translocated during a previous study in the same study area in 1994–1995 (Bourgeois, 1997). This study used similar trapping and translocation methods and occurred across two clearcuts (Fig. 1F and H). We selected only those squirrels from Bourgeois (1997) that met these criteria: (1) they were translocated across recent clearcuts (<10 years), (2) gaps consisted of a conifer plantation (not deciduous regeneration), and (3) they had a well-defined gap and forested detour route. Bourgeois (1997) did not collect vegetation data for these two clearcuts and we assumed similar vegetation characteristics to clearcuts of the same age in our samples.

standard deviation = 0.99, $n = 29$). Of the remaining squirrels ($n = 6$), one did not return home (the signal was lost after 8 days) and the others took between 7 and 26 days to return. Based on subsequent den tree locations, those squirrels that did not return home in one night ($n = 5$) were assumed not to have crossed the clearcut. For more information on the squirrels translocated see: Supplementary Material A, Table 3A.

3.2. Predictors of crossing probability

The probability of gap-crossing was best explained by sex, clearcut age, squirrel mass and detour efficiency ($w_i = 0.54$; Supplementary Material A, Table A4). The same model including mass was equally supported ($w_i = 0.45$). The 95% confidence intervals (CI) estimated for detour efficiency did not bound zero (Table 1) and the odds ratio indicated that flying squirrels were 15.63% less likely to cross the clearcut for every 1% increase in detour efficiency (Table 1). There was much less support for including gap distance ($w_i = 0.006$) (Fig. 2), total distance ($w_i = 0.003$), or direct distance ($w_i = 0.003$). The model including detour efficiency was also better supported than the base model ($w_i = 0.002$) (Fig. 2).

Although males were more likely than females to detour around clearcuts rather than cross (50% of females crossed versus 19% of males), the 95% CI just bounded zero (Table 1). In the model that did not include mass (i.e., probability of crossing ~ sex + clearcut age + detour efficiency|site), the 95% CI for sex did not bound zero (Table 1).

Older clearcuts appeared to be more permeable to flying squirrels, but again the 95% confidence interval bounded zero indicating poor precision of the estimate (Table 1).

3.3. Predictors of time to home

Flying squirrels took between 0.75 and 624 h to return home. All squirrels translocated across gaps 331 m or less returned in one night ($n = 25$). Total distance translocated was the most influential variable in determining time to home ($w_i = 0.32$; Supplementary Material A, Table A.5). Several other predictor variables that were correlated with total distance translocated (clearcut size, detour distance, and gap distance) were also supported in the model set (Table 2). Gap distance was less supported in the model ($w_i = 0.094$), although the parameter estimate did not bound zero (Table 2). A model incorporating only clearcut size had less support in the model set ($w_i = 0.062$). Detour efficiency was not well supported with weights of 0.008 and 0.006. The effect size of sex was quite large; however, similar to mass there was a large amount of uncertainty around the parameter estimate (Table 2). The CART threshold model indicted that flying squirrels take much longer to return home if a gap is >335 m and if the total distance to return is >677 m (Fig. 3).

3.4. Crossing speed and path sinuosity

Once released on the opposite side of the clearcut, most flying squirrels remained near the release site for 10–30 min before attempting to return home. For those squirrels that homed and had known movement paths ($n = 28$), the mean time to return home was 118 min (stdev ± 59.57); females tended to return more slowly on average (123.2 min) than males (113 min).

The movement rates across clearcuts tended to be faster (16.3 ± 9.8 m/min, $n = 11$) than through the forest (11.8 ± 4.4 m/min, $n = 17$), but support for a model with cover type included was not supported when compared to an intercept-only model (ΔAIC = 0.41). Flying squirrels that crossed clearcuts appeared to use residual trees and stumps on their path home (Smith, pers. observation).

Flying squirrel movement paths across clearcuts were significantly straighter (sinuosity: 1.13 ± 0.023) than those individuals that returned through the forest (sinuosity: 1.30 ± 0.0092; ΔAIC = 9.51), suggesting a strong motivation to cross open areas via the shortest path (Fig. 1).

4. Discussion

Gap-crossing movements by adults and dispersing juveniles are vitally important for the maintenance of isolated populations in fragmented landscapes (Hanski and Simberloff, 1997). However, these rare movements are difficult to capture in observational studies. As a result, population viability models often rely on expert opinion or intuition as a proxy for actual movement data, which may incorrectly estimate the functional connectivity of the landscape (Castellon and Sieving, 2006). In this study, we addressed this deficiency by measuring the functional connectivity of recent clearcuts by varying the gap distance home versus the detour distance and collecting detailed movement data. Ours is one of the few experimental studies to use actual movement paths to demonstrate how gap-crossing events are influenced by gap configuration (but see: Bakker and Van Vuren, 2004; Duggan et al., 2012; Turgeon et al., 2010).

4.1. Clearcut configuration influences flying squirrel movements

Northern flying squirrels were much more likely to take forested routes than to cross open canopy gaps even when the direct distance was 6.8 times shorter (threshold ratio of direct distance home versus detour distance). Gap distance, detour distance and total distance were much less important than detour efficiency in predicting probability of gap-crossing. Flying squirrels began to cross clearcuts once the detour efficiency dropped below 55% and crossed gaps up to 436 m; this is much further than the maximum recorded gliding distance of 30 m. This suggests that flying squirrels are making cost-benefit decisions regarding predation risks or assessing the energetic costs of moving across versus

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Table 1
Model-averaged coefficients and unconditional standard errors for GLMM predicting crossing probability controlling for sex, clearcut age, and mass with clearcut site as a random effect. The odds ratio is shown for only those parameters which have 95% CI which do not include zero.

Parameter estimates	β	SE	# of models	L (95% CI)	U (95% CI)	ODDS ratio (%)
Intercept	−8.516	10.124	6			
Sex (Male)	−4.34	2.39	6	−9.02	0.33	
Clearcut age (Years)	0.43	0.38	6	−0.32	1.18	
Squirrel mass (g)	−0.088	0.17	6	−0.42	0.25	
Gap distance (m)	−0.0088	0.0085	1	−0.0255	0.0079	
Detour efficiency (%)	−0.17	0.076	2	−0.32	−0.021	**15.63**
Detour distance (m)	0.0019	0.0027	1	−0.0035	0.0072	
Total distance (m)	−0.0024	0.0035	1	−0.0092	0.0045	

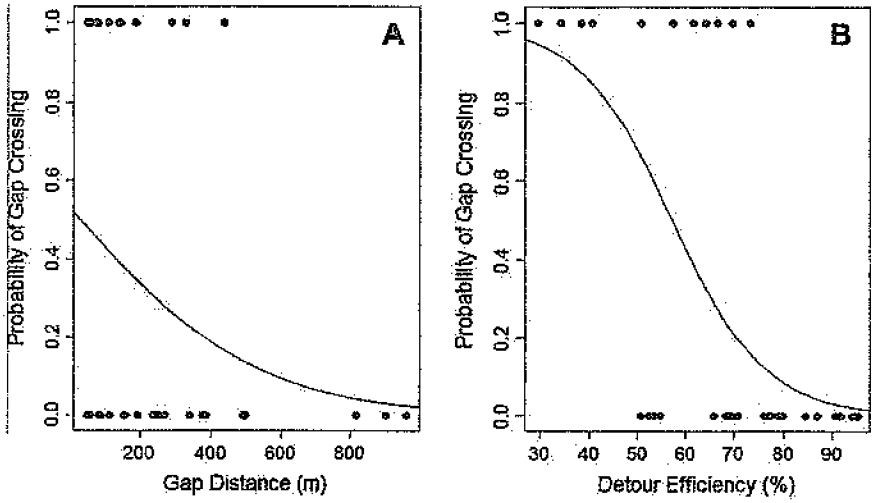

Fig. 2. Gap-crossing decisions of flying squirrels translocated across clearcuts in relation to (A) gap distance (m); and (B) detour efficiency (%). 1-crossed the gap, 0-detoured around the gap ($n = 35$).

Table 2
Model-averaged coefficients using weighted Cox estimation to predict time to return home with unconditional standard errors (Se). The parameters for which the 95% CIs exclude one are shown in bold.

Parameter estimates	Coef	SE	Exp (coef)	# of models	L (95% CI)	U (95% CI)
Sex (Male)	−0.575	0.67	1.952	7	0.152	2.087
Squirrel mass (g)	−0.084	0.051	1.053	4	0.831	1.017
Clearcut age (Years)	0.031	0.084	1.087	7	0.875	1.215
Clearcut size (ha)	**−0.026**	**0.011**	**1.011**	**1**	**0.955**	**0.995**
Gap distance (m)	**−0.004**	**0.014**	**1.001**	**1**	**0.993**	**0.999**
Detour efficiency (%)	−0.17	0.014	1.014	2	0.964	1.017
Detour distance (m)	**−0.002**	**0.001**	**1.001**	**1**	**0.997**	**0.999**
Total distance (m)	**−0.003**	**0.001**	**1.001**	**2**	**0.996**	**0.999**

circumnavigating clearcuts. Our results are similar to Bakker and Van Vuren (2004) who found that red squirrels were more likely to detour around clearcuts when detour efficiencies exceeded 60%. Chickadees (*Poecile atricapillus*) and red-breasted nuthatches (*Sitta canadensis*) were more likely to detour at detour efficiencies of 50% and 80%, respectively (Desrochers and Hannon, 1997). In contrast, gap-crossing decisions by Franklin's ground squirrels were not influenced by detour efficiency, which may be due to their preference for dense vegetation cover and ground burrows; they may also be unfamiliar or unable to use visual information to compare movement paths (Duggan et al., 2012).

Flying squirrel movement paths were substantially straighter across clearcuts than movements in surrounding forest, indicating that they moved in a more directed travel mode (Lima and Zollner, 1996). Straight movement paths occur when moving between habitat patches whereas more tortuous paths often indicate foraging or searching (Schick et al., 2008). Although we have no data to indicate lower survival while crossing clearcuts, the directed movement paths and short clearcut crossing times suggest they were trying to minimise time spent in a potentially risky or resource-poor habitat.

4.2. Thresholds in flying squirrel gap-crossing

Detour efficiency was not an important predictor of homing time, which was better explained by total distance from home, detour distance, and gap distance. There was a high amount of variability in the homing time data at short distances (range = 1–5 h, mean = 1.8 h, stdev. = 0.77). At distances >335 m we generally observed much longer homing times (range = 1.6–624 h, mean = 185 h, stdev = 216 h). One possible explanation for longer homing times for squirrels translocated >335 m is that the animals were unable to detect distant habitat across the clearcut. Flaherty

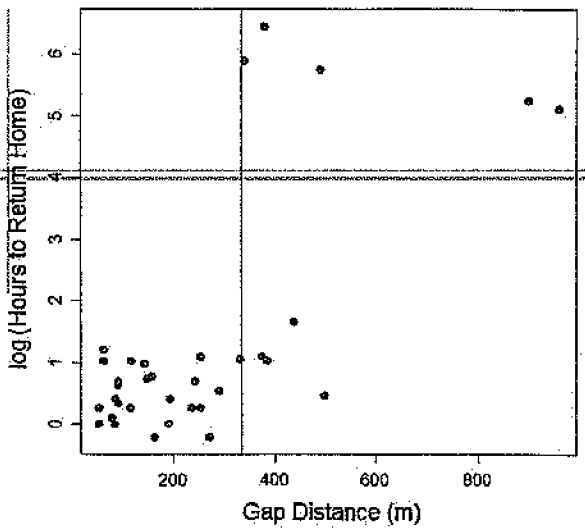

Fig. 3. Time to return home for all flying squirrels in relation to gap distance (m) ($n = 34$). Line indicates a threshold at 335 m in time to return identified using a regression tree.

et al. (2008) estimated the perceptual range of flying squirrels as 100–150 m in clearcuts and 25–50 m in second growth stands, a distance 250–300 m shorter than predicted by Mech and Zollner (2002). In our experiment, four flying squirrels crossed gaps >150 m (150–436 m), which suggests that flying squirrels are able to perceive mature forest across gaps from further distances than previously thought. Alternatively, the squirrels we translocated may have used previous gap-crossing experience and crossed following known movement paths across the gap. However, this is not likely as most flying squirrels spent 0.5–2 h exploring the area before returning, indicating less familiarity with the location. Also we released squirrels in areas outside of their predetermined area of residence.

4.3. Influence of gender on gap-crossing

We found substantial differences in the way that male and female flying squirrels responded to gaps. Males were more likely than females to detour around clearcuts. This contrasts with a non-experimental movement study (Selonen and Hanski, 2003), where male Siberian flying squirrels were more likely than females to cross non-habitat matrix and moved faster and more directly in the matrix. In fact, female Siberian flying squirrels rarely leave their habitat patch and use the matrix only for foraging (Selonen and Hanski, 2003). Females may have smaller perceptual ranges compared with males hampering their ability to choose less costly movement paths. An alternative explanation is that females that crossed gaps were avoiding confrontations with other territorial females found along the forested detour. Unlike males, female northern flying squirrels do not have overlapping home ranges and defend their territory from other females (Gerrow, 1996). Understanding sex-specific gap-crossing behaviours may be important for the persistence of forest specialists in fragmented landscapes.

4.4. Conservation implications

Determining the permeability of different types of matrix is essential for the conservation of habitat specialists (Lindenmayer et al., 2008). Forest stands are expected to become younger as more intensive forestry practices are employed and harvest rotations are shortened (Betts et al., 2007). Biomass harvesting and short rotations in high yield plantations may therefore restrict movements of forest species (Villard and Haché, 2012). In our study we found that post-clearcut conifer plantations >7 years old with trees >1.8 m still presented at least partial barriers to flying squirrel movements. There was some evidence that propensity to cross increased with clearcut age; however the error around the estimate was high. Future work should investigate the influence of older (>10 years) conifer plantations on flying squirrel movements.

Our research quantifies important parameters (probability of gap-crossing) that can be used readily in forest management and the development of metapopulation and cost-distance models. Based on the time to return home we suggest that recent clearcuts and young conifer plantations >300 m may be substantial barriers to flying squirrels. As habitat loss progresses, the emergence of such barriers could partly explain the frequently identified occupancy and abundance thresholds exhibited by species in response to habitat loss and fragmentation (Andrén, 1994; Fahrig, 2003). Landscape patterns that minimize the negative effects of habitat loss may be critical for some species at a given level of habitat amount (Mortelliti et al., 2011). For instance, in our system, the strong influence of detour efficiency on gap-crossing suggests that irregularly shaped clearcuts should be favoured over square harvest blocks. Irregular shaped clearcuts with several gap distances (<100 m) should provide adequate gap crossing and therefore higher functional connectivity for flying squirrels. However, we note that mitigation of isolation through connectivity does not supplant the primary objective of maintaining contiguous habitat. Indeed, a study conducted in the same landscape indicated that mature forest amount was the primary predictor of patch occupancy by flying squirrels (Ritchie et al., 2009). Forest managers should therefore be careful not to implement management plans that reduce the overall habitat amount in the effort to enhance forest connectivity. Finally, flying squirrels were able to cross larger gaps than several forest birds in a similar gap-crossing experiment (Desrochers and Hannon, 1997). This highlights the importance of considering habitat amount and connectivity requirements for a suite of species when maintaining overall forest biodiversity.

Our work indicates that animal movement patterns can be influenced by relatively 'soft' fragmentation (i.e., conifer plantations) even when motivation to move is high. Such movement limitation is likely to be one of the mechanisms for reduced occupancy of flying squirrels in isolated patches of mature forest (Ritchie et al., 2009). Reduced movement may have important ramifications for forest productivity in new conifer plantations and forest fragments considering their key role in the dispersal of beneficial mycorrhizal fungi (Maser and Maser, 1988; Smith, 2012). Our conclusions may also applicable to other similar sized forest gliders in temperate forests, for example *P. volans*, which has declining populations linked to forestry (Rassi et al., 2010; Reunanen et al., 2002). Given expected continued loss and fragmentation of mature forest in eastern Canada (Betts et al., 2007) and worldwide (Hansen et al., 2010), managers should consider landscape designs that minimize travel costs to mature-forest dependent species such as the northern flying squirrel.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.10.008.

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