Landscape Ecol
DOI 10.1007/s10980-011-9595-1

RESEARCH ARTICLE

Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic

**Matthew J. Smith · Matthew G. Betts ·
Graham J. Forbes · Daniel G. Kehler ·
Maryse C. Bourgeois · Stephen P. Flemming**

Received: 20 October 2010 / Accepted: 3 March 2011

Abstract Landscape composition and configuration, often termed as habitat loss and fragmentation, are predicted to reduce species population viability, partly due to the restriction of movement in the landscape. Unfortunately, measuring the effects of habitat loss and fragmentation on functional connectivity is challenging because these variables are confounded, and often the motivation for movement by target species is unknown. Our objective was to determine the independent effects of landscape connectivity from the perspective of a mature forest specialist—the northern flying squirrel (*Glaucomys sabrinus).* To standardize movement motivation, we translocated 119 squirrels, at varying distances (0.18–3.8 km) from their home range across landscapes representing gradients in both habitat loss and fragmentation. We measured the physical connectedness of mature forest using an index of connectivity (landscape coincidence probability). Patches were considered connected if they were within the mean gliding distance of a flying squirrel. Homing success increased in landscapes with a higher connectivity index. However, homing time was not strongly predicted by habitat amount, connectivity index, or mean nearest neighbour and was best explained as a simple function of sex and distance translocated. Our study shows support for the independent effects of landscape configuration on animal movement at a spatial scale that encompasses several home ranges. We conclude that connectivity of mature forest should be considered for the conservation of some mature forest specialists, even in forest mosaics where the distinction between habitat and movement corridors are less distinct.

Keywords Connectivity · Fragmentation · Configuration · Composition · Translocation · Animal movement · Mammalogy · Dispersal · *Glaucomys sabrinus* · Landscape

---

M. J. Smith (✉)
Fundy National Park, P.O. Box 1001, Alma,
NB E4H 1H7, Canada
e-mail: matthew.smith@pc.gc.ca

M. G. Betts
Department of Forest Ecosystems and Society, Oregon
State University, 321 Richardson Hall, Corvallis,
OR 97331, USA

G. J. Forbes
Faculty of Forestry and Environmental Management,
University of New Brunswick, P. O. Box 44555,
Fredericton, NB E3B 6C2, Canada

D. G. Kehler
Resource Conservation Section, Atlantic Service Centre,
Parks Canada, 1869 Upper Water St., Halifax,
NS B3J 1S9, Canada

M. C. Bourgeois
New Brunswick Department of Natural Resources,
Hugh John Flemming Forestry Centre, P.O. Box 6000,
Fredericton, NB E3B 5H1, Canada

S. P. Flemming
Kejimkujik National Park and Historic Site of Canada,
P.O. Box 236, Maitland Bridge, NS B0T 1B0, Canada

Introduction

Understanding a species' movement ability at the landscape scale is critical to predicting population persistence in human-dominated ecosystems (Hanski and Simberloff 1997). The functional connectivity of the landscape requires a species-specific perspective on the permeability of different habitat (Taylor et al. 1993), which may be very different from the physical connectedness of habitat. How best to define and validate connectivity metrics has proven difficult for many species (Calabrese and Fagan 2004) and hampered the accuracy of landscape planning and viability models (D'eon et al. 2002).

Movement is potentially influenced by both composition (i.e., habitat amount) and configuration (i.e., habitat fragmentation). Habitat loss reduces the total amount of habitat or habitat elements (e.g., size and number of habitat patches), whereas fragmentation specifically refers to the configuration of the remaining habitat elements (e.g., amount of edge, connectedness, and distance to next patch) (Fahrig 2003). Configuration and composition are highly correlated, making it problematic to determine the effects of one metric, independent from the other (Smith et al. 2009). Although some simulation studies have suggested important effects of configuration on animal demography at low habitat amounts (With and Crist 1995), the majority of empirical studies measuring the independent effects of configuration relative to habitat loss have found strong support for habitat loss and weak evidence for the independent effects of configuration (McGarigal and McComb 1995; Ritchie et al. 2009; but see Villard et al. 1999). These results have led researchers to conclude that landscape habitat loss explains most of the negative effects of fragmentation on wildlife populations (Trzcinski et al. 1999), although debate continues (Wiegand et al. 2005). Research on the relative importance of fragmentation and habitat loss is important because if fragmentation is a primary driver of species viability, managers may be able to design landscape configurations that minimize the negative impacts of habitat loss on biodiversity.

Due to the logistical difficulties of conducting landscape-scale experiments, most fragmentation studies are inferential or mensurative (McGarigal and Cushman 2002). Although these studies have often provided evidence for the effects of habitat loss, experimental studies may provide stronger inference to detect fragmentation effects while controlling for habitat amount (Debinski and Holt 2000). Experimentally testing the effects of configuration versus composition on critical ecological processes such as animal movement, has the potential to elucidate the mechanisms behind species distributions (McIntyre and Wiens 1999).

Homing or translocation experiments are increasingly being used to understand species-specific reactions to landscape pattern and scale. The main benefit is that translocation standardizes the motivation of territorial animals to move towards a known destination enabling the researcher to test hypotheses by manipulating the size and type of barrier between the displaced animal and its home range (Bélisle 2005). Previous movement studies have used homing experiments to assess species-specific movement abilities, including gap crossing ability, (Bowman and Fahrig 2002; Awade and Metzger 2009), movements in corridors (Castellón and Sieving 2006; Gillies and St. Clair 2008; Hadley and Betts 2009), and landscape permeability (Gobeil and Villard 2002; Desrochers et al. 2010); however few studies have tested for the effects of configuration while controlling for habitat amount (but see; Bélisle et al. 2001; Bélisle and St. Clair 2002; Gillies and St. Clair 2010).

Predictions from population viability models suggest that mature forest-associated species may be at risk if movement ability is constrained by a younger forest matrix (D'Eon et al. 2002; Betts and Forbes 2005; Smith and Person 2007). Northern flying squirrels are thought to move primarily via gliding between mature trees (Vernes 2001), which should make them particularly vulnerable to mature forest fragmentation. Indeed, the movements of Siberian flying squirrels (*Pteromys volans*) are constrained by landscape structure (Reunanen et al. 2000; Selonen and Hanski 2003) with lower occurrence in less connected mature forest patches (Reunanen et al. 2002).

We conducted experimental homing trials to test the hypothesis that movements of northern flying squirrels are not only impeded by a decrease in the amount of their primary habitat, mature forests, but also by a lack of connectedness among remnant primary habitat patches. Moreover, we tested the *landscape fragmentation hypothesis* that landscape configuration effects should be more prominent at low amounts of primary habitat cover (Andrén 1994;

Fahrig 1998). If configuration of mature forest is important to animals associated with this seral stage, the potential exists for forest managers to adapt harvesting plans in appropriate ways to maintain viable populations.

Methods

Study area

All translocations were conducted within the Greater Fundy Ecosystem (650 km^2) of southern New Brunswick, Canada, which includes Fundy National Park, a 202 km^2 protected area (Fig. 1). The forest is composed of a mix of hardwood: yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and American beech (*Fagus grandifolia*) and softwood species; balsam fir (*Abies balsamea*), red spruce (*Picea rubens*) and white spruce (*P. glauca*). Outside of Fundy National Park, the majority of the landscape is actively managed for forest production with ~47% of the region covered in mature forest (>60 years), 36% in early seral stages (10–60 years) and 15% in recent clearcuts (the remainder is comprised of non-forested, (2%) agricultural (1%) and lakes and wetlands (1%). Plantations comprise ~10% of the landscape. Within the national park, the majority (>88%) of the landscape is occupied by mature forest.

Trapping and translocations

Squirrels used in translocation trials were captured in mixed mature forest stands (>60 years) using Tomahawk 201 live traps (Tomahawk, Wisconsin, USA) according to sampling methods and recommendations by Carey (2000). Captured squirrels were sexed, weighed, and ear-tagged (Monel No. 1) on both ears. We radio collared (<4.5 g: Holohil MD-2C and PD-2C, Holohil Systems, Ontario, Canada and Biotrack SS1 transmitters) only adult squirrels, as identified by weight (>85 g), sexual condition and colouration of the pelage (Villa et al. 1999; Vernes 2004). Females lactating or visibly pregnant were immediately released, to prevent loss of the litter or undue stress to the pregnant female. Following release, squirrels were tracked during day and/or night to determine area of residence. The area of residence was used in calculating total homing distance. Night tracking positions were determined by triangulation from known stations or by actively tracking squirrels from a distance of 10–30 m over a period of 30 min. On average, 5 points were used to estimate area of

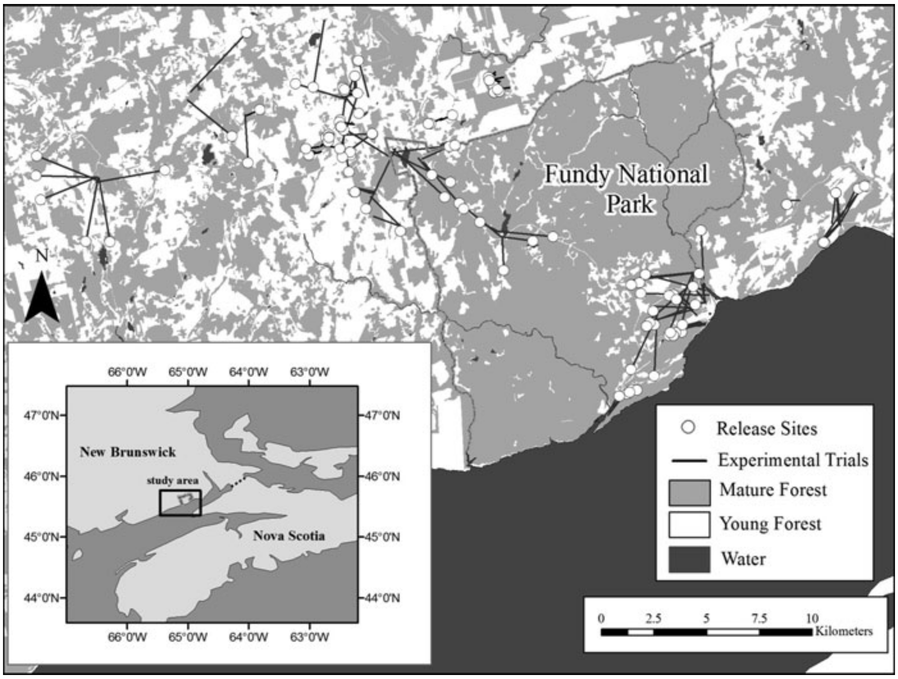

Fig. 1 Study area. Solid lines join capture and release sites

residence (range 1–30), while in a few cases ($n = 3$) flying squirrels were captured and released the following night without any previous tracking. From previous home range telemetry tracking (Gerrow 1996), we have strong evidence that adult flying squirrels moved short distances (<300 m) during the late summer and fall; hence we assumed that all squirrels were caught within their general area of residence.

Translocations occurred during the summer and fall of 1995–1996 (June 15–November 15, $n = 44$) and 2006–2008 (July 12–October 20, $n = 75$). The majority of translocations (76%) occurred between July and September. The translocations conducted in 1995 and 1996 were part of an earlier experiment which occurred in the same study area with similar methods (Bourgeois 1997). The night before translocations, flying squirrels were recaptured at their den trees and held in captivity at a research station. All squirrels were kept at a constant temperature and provided with unlimited food (peanut butter and apple) and water. Most squirrels were held for a period of 12 h (captured in the morning and released at dusk). On rare occasions ($n = 5$), squirrels were held for a longer period (max: 38 h) to avoid releasing individuals during heavy precipitation. The flying squirrels were transported to the release site in a covered trap to ensure no visual clues were given.

Individuals were released between an hour after sunset and midnight, at distances ranging from 0.18 to 3.9 km (mean: 1.5, St. Dev.: 0.97) from capture locations. A majority of flying squirrels (70%) were translocated less than 2 km (0.18–1 km, $n = 45$; 1–2 km, $n = 38$; 2–3 km, $n = 24$; 3–3.9 km, $n = 12$). The maximum distance translocated was based on the mean dispersal distance of Siberian flying squirrels (4.53 ± 2.05 km) (Selonen and Hanski 2006). The shortest distances were based on the minimum width of a flying squirrel home range size (female, range (2.2–6.9 ha $n = 14$; male, 3.1–24 ha, $n = 10$) (Gerrow 1996). Release locations were chosen, a priori, using a stratified random design, based on the amount of mature forest in rectangle sections between capture and release sites (see "Methods" below). To avoid the possible problem of confounding landscape effects with stand-level variability, we controlled for local habitat quality by capturing and releasing all individuals in mixed mature forest, which was the strongest variable in stand-level flying squirrel habitat models (Ritchie et al. 2009). In the few cases ($n = 5$) where more than one squirrel was released at the same site (from different captured sites), each squirrel was released in 30-min intervals to prevent one squirrel from following the other. To maintain statistical independence, no individuals were captured and translocated at the same location and no individuals were translocated more than once. To assess potential loss of data independence due to the proximity of translocations, we dropped data for squirrels which were translocated in similar landscape sections (<200 m between capture and release points, $n = 28$). The results were qualitatively similar (i.e., AIC ranks and parameter estimates did not change substantively), so we report the results of only the full dataset here.

Each translocated flying squirrel was re-located daily for the first 3 weeks, then weekly until the animal homed, or the transmitter failed. Flying squirrels were considered homed if they returned to the area of where they had been observed prior to translocation. If the transmitter signal was lost, or no movement was recently detected, we searched the home site and last known location. Animals which did not home, but were still alive were tracked a period of 30 days or longer (August 4 to December 9).

Landscape characterisation

We determined the spatial distribution of mature forest (MF) (forest >60 years) using 1993 and 2003 provincial forest inventory data derived from aerial photographs (1 m resolution) (NBDNR 1993, 2003). Non-forest (NF) included water, non-treed wetlands, roads, agricultural land, clearcuts, and regenerating clearcuts (<10 years). Most of the non-forest category was regenerating clearcuts (~94%). Given our limited sample size we were unable to test for differences in cover types at finer resolutions. We updated recent clearcuts on the forest inventory using 2007 Landsat5 imagery within ArcGIS 9.3 (Environmental Systems Research Institute (ESRI) Inc., Redlands, USA). The final mature forest and non-forest data layers were exported as a raster with each pixel measuring 10 × 10 m (100 m^2).

We measured landscape composition and configuration for each flying squirrel translocation, using an ellipse-based approach (Bélisle et al. 2001; Gobeil and Villard 2002; Selonen et al. 2010). A rectangle landscape section was defined for each squirrel using two foci (based on the capture and release points) and a constant eccentricity of 0.67, which defines the shape of the ellipse. The final landscape section for each squirrel was defined as the smallest rectangle possible that would enclose the ellipse (Fig. 2).

The landscape variables calculated for each rectangle section were: MF; % of mature forest, NF; % of non-forest, and MNN; mean nearest neighbour distance (measured edge to edge in kilometres). MNN distance provides information on the mean size of gaps between mature habitat patches that squirrels would encounter on their path home, (Bélisle et al. 2001); however, MNN distance has been criticised as being too simple a measure to detect connectivity effects (Moilanen and Nieminen 2002). For this reason, we used a graph theory approach (Urban and Keitt 2001) to calculate an index of connectivity (CON) (termed landscape coincidence probability (LCP) by Pascual-Hortal and Saura (2006)):

$$\mathrm{CON} = \sum_{i=1}^{\mathrm{NC}}\sum_{j=1}^{\mathrm{NC}}\left(\frac{\mathrm{a}_i\mathrm{a}_j\mathrm{c}_{ij}}{\mathrm{A}_L^2}\right) \times 100 \qquad (1)$$

where NC is the total number of mature habitat patches, a_i and a_j are areas of patches i and j respectively, c_{ij} is a passibility value which is 0 or 1, and A_L is the total landscape area (including non-forest and habitat patches). Patches were considered the same patch ($\mathrm{c}_{ij} = 1$, fully connected) if they were within the maximum gliding distance of a flying squirrel (<30 m) (Vernes 2001), otherwise they were considered unconnected ($\mathrm{c}_{ij} = 0$). This metric is defined as the probability that any two random points will be connected (0% indicating no connections to 100% indicating fully connected (one patch)). For a given habitat amount, maximal connectivity is achieved if the entire available habitat is in one patch.

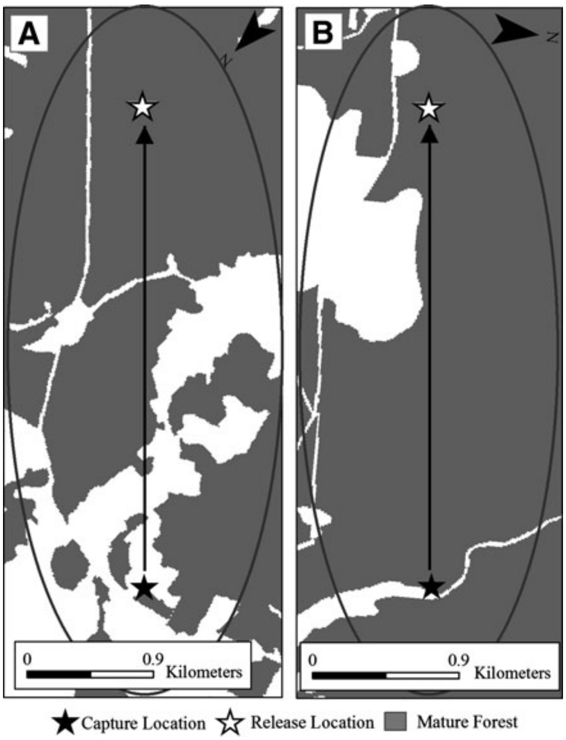

Fig. 2 Landscapes sections and ellipses of individuals translocated in landscapes with similar amounts of mature forest (MF: A & B = 71%) but with different connectivity (CON: A = 12.6%, B = 26%, MNN: A = 0.041 km, B = 0.029 km). Connectivity is measured based on the whole rectangle landscape section not just between the capture and release points

We used the patch output file generated by Patch Analyst (Elkie et al. 1999) and ArcGIS 9.3 (ESRI) to calculate the habitat patch area for each landscape section. Flying squirrels were released in mature patches of varying sizes; mean 84 ha ± 122.9 (0.02–549). The median and range of landscape parameters for all landscape sections were as follows; DIS: 1.3 km (0.18–3.9); MNN: 0.034 km (0.001–0.95), CON: 20.06% (0.06–70.47), MF: 60.39% (3–91); and NF: 22.17% (2–76).

Statistical analysis

Confounding variables

Predictor variables were quite strongly correlated in some cases (CON ∼ MF: ($r = 0.79$,), MF ∼ NF: ($r = -0.67$), CON ∼ NF ($r = 0.48$,), MNN ∼ NF ($r = 0.48$,), DIS (Distance Translocated) ∼ NF ($r = -0.35$,), and MNN ∼ CON ($r = -0.22$,). As suggested by Smith et al. (2009), we calculated variance inflation factor (VIF) by regressing each continuous predictor variable against all others ($1/(1 - R^2)$). Calculated VIF indicated moderate collinearly for some variables; MF = 3.70, MNN = 1.19, DIS = 1.61, NF = 2.39, and CON = 3.20. Usually, VIF > 10 suggest "severe" collinearity (Neter et al. 1990).

A number of statistical solutions have been used to address collinearity in landscape variables, the two most common being, residual regression (McGarigal and McComb 1995; Villard et al. 1999; Bélisle et al. 2001) and variance partitioning (MacNally 2000). Based on simulation modeling, Smith et al. (2009) indicated that standardized partial regression coefficients were the most unbiased in their estimates of the relative importance of the predictor variables.

Homing success

Logistic regression models were used to assess the influence of covariates on the homing probability. We started with a base model that included distance and sex, which have previously been found to influence rodent homing ability (Bovet 1984), and a term to control for study period (0 (1995–1996)) and (1 (2006–2008)).

Following methods recommended by Smith et al. (2009), we statistically controlled for the influence of composition variables (mature forest or non-forest) by including these terms in all models which included our configuration variables (connectivity or mean nearest neighbour). In this way we investigated configuration effects (MNN and CON), independent of habitat amount (%MF and %NF). We also tested a base model which included no landscape measures in order to better understand the effect of non-landscape variables (distance translocated, sex and study) on homing success and homing time. We compared the AIC value of MF × CON to MF + CON and NF × CON to NF + CON in order to assess the fragmentation threshold hypothesis (after Andrén 1994); this hypothesis (tested here with the statistical interaction MF × CON and NH × CON) states that configuration effects should only be evident when habitat amount drops below some threshold. All models with interaction terms also include the main effects.

Model fit was evaluated with the global model (base model + composition + configuration), which showed no signs of overdispersion ($\hat{c} > 1$). We assessed the strength of evidence for the landscape metrics against the base model using Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson 2002). We calculated unconditional parameter estimates and unconditional standard errors using model averaging techniques to incorporate model uncertainty (Burnham and Anderson 2002). Model accuracy was tested by calculating Area under the Receiver Operating Characteristic Curve (AUC) within R (R Development Core Team 2005) (Sing et al. 2005; Fawcett 2006).

Time to home

To investigate which variables were the most important in predicting homing time, we used Cox regression, which compares survival curves (survival = time elapsed before some terminal event) among treatment groups. In this study, the terminal event was returning home. Those squirrels which did not return home were treated as censored data. We used a similar modelling approach as probability to home when assessing the importance of landscape variables on time to home.

We used the weighted estimation of the Cox hazards model (R package coxphw) (Schemper 1992; Schemper et al. 2009) because a Cox proportional hazards model failed the assumption of constant hazards over time (Schofield residuals $\chi^2 = 27.51$, $P < 0.01$). We assigned weights to the risk sets according to the survival function estimates (Prentice weights). Because of the weighting, the weighted Cox hazards model is not a true likelihood approach; therefore, we used the Wald χ^2 statistic as a large sample approximation to the likelihood, and used $-\chi^2 + 2 *$ (number of parameters) of the model, as an approximation of AIC (Chou and Bentler 1996). Model goodness-of-fit was assessed using the Wald Statistic for the global model.

Results

Most of the 119 flying squirrels translocated (81; 68%) were able to return home within 40 days from release. Return rate was lower (44%; $n = 36$) from distances beyond 2 km, with none of the 10 females translocated returning when released >1.5 km from their area of residence. A total of 38 individuals were censored because they died ($n = 8$, 4 females/4 males), lost collar or signal ($n = 10$), or did not return home after the last day of the study ($n = 20$). Three flying squirrels died from weasel (*Mustela* sp.) predation, 3 from unknown predators, and 2 from unknown causes.

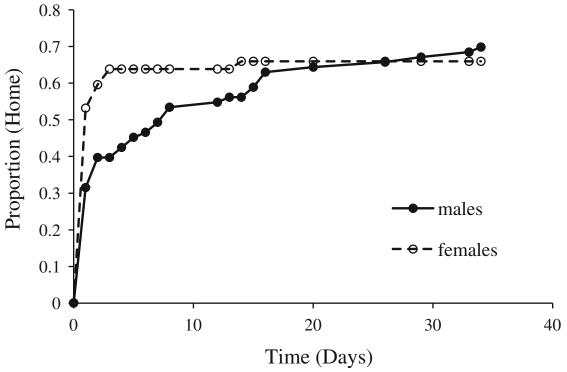

Fig. 3 Cumulative proportions of males ($n = 72$) and females ($n = 47$) homing over time

The time to return to area of residence ranged from 1 to 34 days. The majority (85%) of those squirrels that returned, came back within the first 10 days. Those squirrels that did not return home were tracked an average of 50 days after release (range = 30–75 - days). Squirrels that did not return home selected a new home range (as evidenced by reduced movements within a contained area) after 10–30 days. Of those females that returned home, most returned within the first 3 days (97% $n = 30$), whereas 42% males returned home after 3 days, with 5 returning 20 days after translocation (Fig. 3).

Homing success

We found strong effects of connectivity on homing success by flying squirrels. Models including the effect of connectivity (controlling for amounts of mature and non-mature forest) ranked as the top models (ΔAICc ≤ 2 (Table 1)). Unconditional 95% confidence intervals for connectivity did not bound zero (Table 2, Fig. 4). The odds ratio for the model-averaged coefficient indicated that each percentage increase in connectivity increased the odds of homing by 7.8% (Table 2). The top model had strong discriminatory power (AUC: 0.85) and showed no signs of lack of fit.

In contrast, we found less support for mature forest amount in predicting probability to home; >2 AIC units from the top model (Table 1), a small effect size (1.68% decrease in the odds of homing for every 1% increase in mature forest) and the 95% confidence interval was wide and bounded zero indicating poor precision (Table 2). Similarly, there was less support for including only amount of non-forest in the model (Table 1).

We found equal support for the fragmentation threshold hypothesis: (MF × CON, ΔAICc < 2, Table 1) and the top model, although the effect size for the parameter estimates were small with large standard errors (Table 2). We found similar results for amount of non-forest and connectivity (NF x CON, ΔAICc < 2).

Flying squirrels appeared to be negatively impacted by increases in mean nearest neighbour distance when we controlled for both mature forest and non-forest (ΔAICc = 2.71; Table 1). The effect size for MNN was large, however, unconditional standard errors around the parameter estimates were quite broad (Table 2).

There was also some support for the base model that lacked landscape variables; this model exhibited

Table 1 Comparison of models for homing probability, number of parameters (K), Akaike's Information Criterion (AICc), weights (w_i), and evidence ratios (ER) for models of northern flying squirrel (*G. sabrinus*) based on logistic regression

Rank	Models	K	AICc	ΔAICc	w_i	ER
1	Distance × Sex, Study, Mature Forest, Connectivity	7	113.10	0	0.23	1.00
2	Distance × Sex, Study, Non-Forest, Connectivity	7	113.10	0	0.23	1.00
3	Distance × Sex, Study, Non-Forest × Connectivity	8	114.11	1.01	0.14	1.65
4	Distance × Sex, Study, Mature Forest × Connectivity	8	114.47	1.37	0.12	1.99
5	Distance × Sex, Study	5	115.16	2.07	0.081	2.81
6	Distance × Sex, Study, Mature Forest, Mean Nearest Neighbour	7	115.65	2.55	0.0064	3.59
7	Distance × Sex, Study, Non-Forest, Mean Nearest Neighbour	7	115.81	2.71	0.059	3.89
8	Distance × Sex, Study, Mature Forest	6	115.86	2.76	0.057	3.98
9	Distance × Sex, Study, Non-Forest	6	117.22	4.12	0.029	7.86

The evidence ratio is computed based on the top ranking model

Table 2 Model-averaged coefficients and unconditional standard errors for logistic regression model predicting homing probability with 95% upper confidence level: L (95% CL) and upper confidence level: U (95% CL)

Parameter	β^{a}	SE	# of models	L (95% CL)	U (95% CL)	Odds ratio
Distance (km)	**−4.528**	**1.745**	**9**	**−7.948**	**−1.107**	**0.0115**
Sex (males)	−2.771	1.961	9	−6.614	1.072	
Sex × Distance	**3.668**	**1.815**	**9**	**0.111**	**7.225**	**39.177**
Study	−0.263	0.573	9	−1.386	0.861	
% Mature forest	−0.017	0.030	3	−0.076	0.041	
% Non-forest	0.021	0.023	3	−0.023	0.066	
% Connectivity (CON)	**0.075**	**0.037**	**2**	**0.0015**	**0.148**	**1.0778**
Mean nearest neighbour (km)	−5.93	5.08	2	−15.88	4.032	
% Non-Forest × CON	0.002	0.0018	1	−0.0020	0.0056	
% Mature Forest × CON	0.001	0.0015	1	−0.0016	0.0045	

[a] Estimate in bold face type indicates that 0 is excluded from the 95% confidence interval and that the variable influences homing success

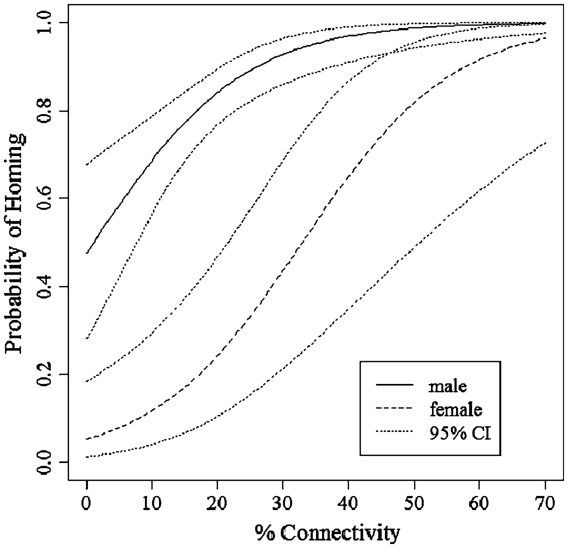

Fig. 4 Predicted probability to home (with 95% confidence intervals) as a function of connectivity for male and female flying squirrels (model: Distance × Sex + Study + MF + CON). For the purposes of plotting, fitted lines are for mean values of distance (1.5 km) and mature forest (57%)

high discriminatory power (AUC = 0.82) and was ranked near the top of the model set (ΔAICc = 2.06). As expected, distance translocated had a strong effect on the ability of flying squirrels to return home. For every 1 km of distance translocated flying squirrels had a 98.9% ((1 – 0.011) × 100) decrease in the odds of returning home. The interaction between sex and distance was also supported, with males more likely than females to return home from longer distances (Table 2, Fig. 4).

Time to home

The top model included mean nearest neighbour distance in the model, and although the effect size of mean nearest neighbour distance was large the 95% confidence interval bounded 1 (Table 3). There was less support for including only habitat amount (MF and NF) (Table 3) in the model. There was no support for including connectivity or the interactions (CON × MF or CON × NF) (Table 3). The fit of the global model was strong (Wald Statistic = 109.76 on 5 df, $P < 0.001$).

The base model, which included no landscape variables, performed better than a model including connectivity (CON) and habitat amount (MF and NF), but had less support than a model including MNN (ΔAICc = 7.70). The interaction between distance and sex were strong predictors of homing time (Table 3); at 500 m, females were 67% faster than males at returning home, whereas at the average translocation distance (1.52 km) males returned 5 times more quickly.

Maximum homing distance

The proportion of males (16/43) who returned home when moved 1.5 km or greater was significantly higher than females (0/10) ($\chi^2 = 9.57$, df = 1,

Table 3 Comparison of models predicting time to home using weighted Cox estimation. Akaike's Information Criterion (AICc), weights (w_i), and evidence ratios (ER) for models of time to home for the northern flying squirrel (*G. sabrinus*) given different landscape metrics

Rank	Variables	K	AICc	ΔAICc	w_i	ER
1	Distance × Sex, Study, Non-Forest, Mean Nearest Neighbour	6	−120.65	0.00	0.79	1.00
2	Distance × Sex, Study, Mature Forest, Mean Nearest Neighbour	6	−117.75	2.90	0.18	4.26
3	Distance × Sex, Study	4	−112.95	7.70	0.02	46.82
4	Distance × Sex, Study, Mature Forest	5	−111.76	8.89	0.01	85.08
5	Distance × Sex, Study, Non-Forest	5	−110.14	10.51	0.00	191.16
6	Distance × Sex, Study, Mature Forest, Connectivity	6	−107.06	13.59	0.00	893.50
7	Distance × Sex, Study, Non-Forest, Connectivity	6	−105.83	14.82	0.00	1652.67
8	Distance × Sex, Study, Mature Forest × Connectivity	7	−104.69	15.96	0.00	2909.41
9	Distance × Sex, Study, Non-Forest × Connectivity	7	−103.45	17.20	0.00	5408.11

$P = 0.001$). When we incorporated the uncertainty associated with animals which did not home (censored animals), our best model predicted that males had a 50% homing probability at 3 km, while females had a 20% homing probability from 1.5 km.

Discussion

We found strong support for our hypothesis that connectivity influences dispersal-scale movements of a mature forest specialist even after accounting for amount of mature forest. In contrast, the amount of mature forest in landscapes alone had little effect. To date, the majority of observational studies on species distributions have found weak independent effects of configuration (see Prugh et al. 2008 for review). However, only two existing studies have considered the independent effects of habitat loss and configuration on animal movement (Tewksbury et al. 2002; Gillies and St. Clair 2010), both of which found fragmentation effects. However, both of these studies occurred in systems with a nearly dichotomous landscape: patches and corridors were well-defined. It is commonly hypothesized that forest landscapes should be more permeable than agricultural landscapes. (Tewksbury et al. 2002; Brotons et al. 2003; but see Hurme et al. 2007). However, our results do not support this notion. Previous work also suggests that fragmentation effects on animal distributions are most likely to occur when habitat amount is low (Andrén 1994, 1996; Betts et al. 2006). We found equal support for fragmentation threshold hypothesis (an interaction of MF and CON), but the most parsimonious model included only CON. Squirrel movements appear to be disrupted even with moderate amounts of habitat disturbance in landscapes dominated by forest.

We propose two reasons for our detection of fragmentation effects. First, habitat specialists, with fidelity to a particular cover type are more likely than generalists to respond to configuration. For instance, flying squirrels rarely travel on the forest floor, and use large trees for gliding to cover larger distances more rapidly and efficiently (Vernes 2001). Mature forest maximizes the benefits of gliding behaviour, as stated by the Ecological Cost of Transport Hypothesis (Garland 1983); climbing up a tree and gliding to the next is more energetically efficient compared to running along the ground over the same distance.

Second, we tested for independent effects of configuration using an experimental approach which directly measured the effects of pattern on process (Turner 1989). This approach likely provides more power to detect differences that may not be apparent with passive home range tracking studies (Selonen and Hanski 2003) or mensurative experiments (McGarigal and Cushman 2002).

Why did we not detect a stronger effect of mature forest composition? There is a possibility that we may have detected a stronger effect of composition if we had higher-resolution data on the amount of flying squirrel habitat at the landscape scale. An 'organism-centered' approach which incorporates fine-scale habitat data (e.g., number of snags, truffle biomass) and landscape cover might make it more likely to detect effects of both configuration and composition (Wiens 1976). Further, we emphasize that our study landscapes contained relatively high proportions of mature forest (mean: 57% range: 5–90%). We predict that as the amount of mature forest continues to decline, evidence of the fragmentation threshold hypothesis will become stronger and the apparent importance of the remaining mature forest and its configuration will intensify.

Though connectivity was important to homing success, we found little support for configuration variables in predicting homing times. Unfortunately, our statistical power to detect differences was low because the majority of squirrels that returned home did so in the first 2 days (70%, $n = 81$); this left little variation for models to explain. Though there was massive variability in male homing time (e.g., 3 vs. 40 days for two different individuals to return from 3 km), little of this variation could be explained by landscape variables. Homing time may be inherently more difficult to predict due to possible stochasticity in initial search direction, presence of predators, or individual variability in search pattern tendencies and individual 'personality' traits which may make some individuals bolder than others in crossing non-forest areas (Dingemanse and Reale 2005). This individual variation in homing ability may be critical for understanding how populations respond to habitat fragmentation.

The most influential predictors of time to return and probability of homing for flying squirrels were sex and distance, respectively. It is well known that mammals are less successful and take longer to return home as translocation distance increases (Bovet 1984). But we also observed large differences in the ability of females to home from longer distances, with females reaching a critical homing distance near 1.4 km. This result reflects observations of dispersing Siberian flying squirrel wherein females settled faster than males, a behaviour attributed to females being more time-limited because females have to locate a suitable nesting site to raise young in the spring and summer (Selonen and Hanski 2010). Differences in dispersal behaviour may have important consequences for how populations respond to lower connectivity, females may be less able to find quality habitat patches as the landscape becomes more fragmented. Although this seems a likely hypothesis we found no evidence for an interaction between sex and connectivity ($\Delta\text{AIC} < 1$; $P = 0.33$) in our study.

Although it is still uncertain whether the behavior of translocated animals is similar to that of dispersers, our results have implications for flying squirrel population dynamics in landscapes that are becoming increasingly fragmented by forest management. Restricted landscape-scale movements of adults will likely reduce the opportunities for habitat supplementation (i.e., the ability to take advantage of nearby habitat by expanding their home range) (Dunning et al. 1992). The Siberian flying squirrel, an indicator of diverse mature forest structure (Hurme et al. 2008; Vierikko et al. 2010), underwent steep population declines in Finland over the past 30 years, primarily due to intensive forest management (Hokkanen et al. 1982; Rassi et al. 2000). Studies have also shown that isolation of mature patches appears to reduce Siberian flying squirrel survival (Lampila et al. 2009b) and genetic diversity (Lampila et al. 2009a). Further, if the behaviour of translocated adults reflects dispersal movements of juveniles, we predict that unconnected patches of mature forest are less likely to be colonized over time, potentially reducing the long-term stability of squirrel populations (Hanski and Ovaskainen 2000).

In conclusion, our study tested the ability of flying squirrels to return home in landscapes with varying amounts of mature forest and connectivity. We revealed that configuration of mature forest can affect movements of a mature forest associate, independent of the effects of landscape composition. To sustain viable populations of flying squirrels in industrial forests, we recommend that forest managers consider not only the amount of mature forest, but also landscape connectivity. However, creation of movement corridors between patches should not be a substitute for the conservation value of large patches. In landscapes with long distances between mature patches, we predict that leaving movement corridors is likely to enhance population persistence.

Acknowledgments We would like to thank the following funders; Parks Canada, New Brunswick Wildlife Trust Fund, Province of New Brunswick (Department of Natural Resources), and Fundy Model Forest. This work would not have been possible without the hard work of these field technicians; Michael Avery, Blair Cabot, Angela Freeman, Luke Fryer, Shawn Gerrow, Mathieu McCann, Shavonne Meyer, Paul Morris, Carolyn Richardson, Trina Rytwinski, Eric Shaffer, and Jane Watts. We gratefully acknowledge the helpful comments and suggestions made by the coordinating editor and two anonymous reviewers. Live trapping, handling

and housing procedures were approved by the Institutional Animal Care and Use Committee of Acadia University and University of New Brunswick and followed the guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998).

References

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366

Andrén H (1996) Population responses to habitat fragmentation: statistical power and the random sample hypothesis. Oikos 76:235–242

Awade M, Metzger JP (2009) Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral Ecol 33:863–871

Bélisle MA (2005) Measuring landscape connectivity: the challenge of behavioural landscape ecology. Ecology 86:1988–1995

Bélisle MA, St. Clair CC (2002) Cumulative effects of barriers on the movements of forest birds. Conserv Ecol 5:9 (accessed online: http://www.ecologyandsociety.org/vol5/iss2/art9/)

Bélisle MA, Desrochers A, Fortin MJ (2001) Influence of forest cover on the movements of forest birds: a homing experiment. Ecology 82:1893–1904

Betts MG, Forbes G (eds) (2005) Forest management guidelines to protect native biodiversity in the Greater Fundy Ecosystem. Cooperative Fish and Wildlife Research Unit, Fredericton, NB

Betts MG, Forbes GJ, Diamond AW, Taylor PD (2006) Independent effects of habitat amount and fragmentation on songbirds in a forest mosaic: an organism-based approach. Ecol Appl 16:1076–1089

Bourgeois MC (1997) An examination of two unconventional methods to assess resource use by two New Brunswick forest mammals: the marten and the northern flying squirrel. MSc Thesis, Acadia University, Wolfville, NS, Canada

Bovet J (1984) Strategies of homing behaviour in the red squirrel, *Tamiasciurus hudsonicus*. Behav Ecol and Sociobiol 16:81–88

Bowman J, Fahrig L (2002) Gap crossing by chipmunks: an experimental test of landscape connectivity. Can J Zool 80:1556–1561

Brotons L, Mönkkönen M, Martin JL (2003) Are fragments islands? Landscape context and density-area relationships in boreal forest birds. Am Nat 162:353–357

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, USA

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Front Ecol Environ 2:529–536

Carey AB (2000) Effects of new forest management strategies on squirrel populations. Ecol Appl 10:248–257

Castellón T, Sieving K (2006) An experimental test of matrix permeability and corridor use by an endemic understory bird. Conserv Biol 20:135–145

Chou C-P, Bentler PM (1996) Application of AIC to Wald and Lagrange multiplier tests in covariance structure analysis. Multivar Behav Res 31:352–370

D'Eon RG, Glenn SM, Parfitt I, Fortin M-J (2002) Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conserv Ecol 6:10 [online] URL: http://www.consecol.org/vol6/iss2/art10

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14:342–355

Desrochers A, Bélisle M, Morand-Ferron J, Bourque J (2010) Integrating GIS and homing experiments to study avian movement costs. Landscape Ecol. doi:10.1007s10980-010-9532-8

Dingemanse NJ, Reale D (2005) Natural selection and animal personality. Behaviour 142:1159–1184

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175

Elkie P, Rempel R, Carr A (1999) Patch analyst users manual Ontario Ministry of Natural Resources. Northwest Science and Technology, Thunder Bay, ON, TM-002

Fahrig L (1998) When does fragmentation of breeding habitat affect population survival? Ecol Model 105:273–292

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fawcett T (2006) An introduction to ROC analysis. Pattern Recogn Lett 27:861–874

Garland T Jr (1983) Scaling the ecological cost of transport to body mass in terrestrial mammals. Am Nat 121:571–587

Gerrow S (1996) Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. MSc Thesis, Acadia University, Wolfville, NS, Canada

Gillies CS, St. Clair CC (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. Proc Natl Acad Sci USA 105:19774–19779

Gillies CS, St. Clair CC (2010) Functional responses in habitat selection by tropical birds moving through fragmented forest. J Appl Ecol 47:182–190

Gobeil J-F, Villard M-A (2002) Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. Oikos 98:447–458

Hadley AS, Betts MG (2009) Tropical deforestation alters hummingbird movement patterns. Biol Lett 5:1–4

Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. Nature 404:755–758

Hanski I, Simberloff D (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanski I, Gilpin ME (eds) Metapopulation biology. Academic Press, San Diego, CA, USA, pp 5–26

Hokkanen H, Törmälä T, Vuorinen H (1982) Decline of the flying squirrel *Pteromys volans* L. populations in Finland. Biol Conserv 23:273–284

Hurme E, Reunanen P, Mönkkönen M, Nikula A, Nivala V, Oksanen J (2007) Local habitat patch pattern of the Siberian flying squirrel in a managed boreal forest landscape. Ecography 30:277–287

Hurme E, Mönkkönen M, Sippola A-L, Ylinen H, Pentinsaari M (2008) Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. Ecol Indicators 8:246–255

Lampila S, Kvist L, Wistbacka R, Orell M (2009a) Genetic diversity and population differentiation in the endangered Siberian flying squirrel (*Ptermys volans*) in a fragmented landscape. Eur J Wild Res 55:397–406

Lampila S, Wistbacka R, Makela A, Orell M (2009b) Survival and population growth rate of the threatened Siberian flying squirrel (*Pteromys volans*) in a fragmented forest landscape. Ecoscience 16:66–74

MacNally R (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—'predictive' and 'explanatory' models. Biodivers Conserv 9:655–671

McGarigal K, Cushman S (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345

McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon Coast range. Ecol Monogr 65:235–260

McIntyre NE, Wiens JA (1999) Interactions between habitat abundance and configuration: experimental validation of some predictions from percolation theory. Oikos 86:129–137

Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. Ecology 83:1131–1145

NBDNR(New Brunswick Department of Natural Resources) (1993) New Brunswick forest inventory. New Brunswick Department of Natural Resources, Fredericton, NB, Canada

NBDNR(New Brunswick Department of Natural Resources) (2003) New Brunswick forest inventory. New Brunswick Department of Natural Resources, Fredericton, NB, Canada

Neter J, Wasserman W, Kutner MH (1990) Applied linear statistical models, 3rd edn. Irwin, Chicago, IL, USA

Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecol 21:959–967

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci USA 105:20770–20775

Rassi P, Alanen A, Kanerva T, Mannerkoski I (eds) (2000) Threatened species in Finland 2000. [Website in Finnish with an English summary.] Ympäristö ministeriö, Helsinki, Uhanalaisten lajien II seurantatyöryhmä, esipainos. [Online], URL: http://www.vyh.fi/luosuo/lumo/lasu/uhanal/uhanalhtm

Reunanen P, Mönkkönen M, Nikula A (2000) Managing boreal forest landscapes for the flying squirrel. Conserv Biol 14:218–226

Reunanen P, Nikula A, Mönkkönen M, Hurme E, Nikula V (2002) Predicting occupancy for the Siberian flying squirrels in old-growth forest patches. Ecol Appl 12:1188–1198

Ritchie LE, Betts MG, Forbes G, Vernes K (2009) Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. For Ecol Manage 257:1920–1929

Schemper M (1992) Cox analysis of survival data with non-proportional hazards. Statistician 41:455–465

Schemper M, Wakounig S, Heinze G (2009) The estimation of average hazard ratios by weighted Cox regression. Stat Med 28:2473–2489

Selonen V, Hanski IK (2003) Movements of the flying squirrel *Pteromys volans* in corridors and in matix habitat. Ecography 26:641–651

Selonen V, Hanski IK (2006) Habitat exploration and use in dispersing juvenile flying squirrels. J Anim Ecol 75:1440–1449

Selonen V, Hanski IK (2010) Decision making in dispersing Siberian flying squirrels. Behav Ecol 21:219–225

Selonen V, Hanski IK, Desrochers A (2010) Measuring habitat availability for dispersing animals. Landscape Ecol 25:331–335

Sing T, Sander O, Beerenwinkel N, Lengauer T (2005) ROCR: visualizing classifier performance in R. Bioinformatics 21:3940–3941

Smith WP, Person DK (2007) Estimated persistence of northern flying squirrel populations in temperate rainforest fragments of southeast Alaska. Biol Conser 137:626–636

Smith AC, Koper N, Francis CM, Fahrig L (2009) Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. Landscape Ecol 24:1271–1285

Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68:571–572

R Development Core Team (2005) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from www.r-project.org. Accessed 30 January 2010

Tewksbury JJ, Levey DJ, Haddad NM, Sargent S, Orrock JL, Weldon A, Danielson BJ, Brinkerhoff J, Damschen EI, Townsend P (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. Proc Natl Acad Sci USA 99:12923–12926

Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecol Appl 9:586–593

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197

Urban DL, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. Ecology 82:393–401

Vernes K (2001) Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forest of eastern Canada. J Mammal 82:1026–1033

Vernes K (2004) Breeding biology and seasonal capture success of northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudson*icus) in southern New Brunswick. Northeastern Nat 11:123–136

Vierikko K, Pellikka J, Hanski IK, Myllyviita T, Niemelä J, Vehkamäki S, Lindén H (2010) Indicators of sustainable forestry: the association between wildlife species and forest structure in Finland. Ecol Indic 10:361–369

Villa LJ, Carey AB, Wilson TM, Glos KE (1999) Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. USDA Forest Service General Technical Report PNW-GTR-444

Villard M-A, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv Biol 13:774–783

Wiegand T, Revilla E, Moloney KA (2005) Effects of habitat loss and fragmentation on population dynamics. Conserv Biol 19:108–121

Wiens JA (1976) Population responses to patchy environments. Annu Rev Ecol Syst 7:81–120

With KA, Crist TO (1995) Critical thresholds in species' responses to landscape structure. Ecology 76:2446–2459