

Habitat requirements of the Siberian flying squirrel in northern Finland: comparing field survey and remote sensing data

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In this study, we surveyed habitat characteristics of the Siberian flying squirrel in northern Finland. Forest structure in currently occupied sites was compared with random forest sites within the same old-growth forest area. We also studied whether the same habitat selection patterns can be detected directly from satellite images at the home-range scale. For this purpose we analysed forest characteristics that were associated with habitat use of radio-tracked individuals. Field survey showed that sites used by flying squirrels were in mixed spruce dominated forests with a relatively large amount of mature deciduous trees (particularly aspen). Similarly, the preference to mature spruce and avoidance of pine within home-ranges were also detectable from satellite images but the importance of deciduous trees was not perceived in this analysis. This study suggests that satellite imagery data provide a tool for finding potential forest sites for the Siberian flying squirrel in northern Finnish forest landscapes. However, our results also emphasise the need to develop GIS techniques further to identify very small scale forest characteristics more accurately and reliably than is possible at present.

Introduction

Habitat selection of organisms is proximately determined by necessary resources, such as food

and safe roosting sites, which they require for daily activities. Ultimately, habitat selection aims at improving the survival of individuals and enhancing their reproductive success by provid-

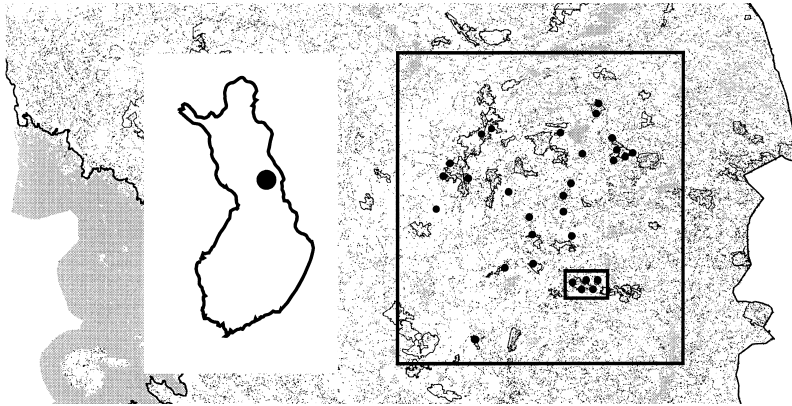


Fig. 1. The study area in Koillismaa. Field sampling sites are located within the larger frame and denoted by black dots. Small frame delineates the forest area in Metsäkylä where radio-tracking of flying squirrels was carried out. Area borders on the map refer to present nature reserves in the region.

ing food, mates and potential nesting sites. Interactions between conspecifics and other species or predation risk influence the behaviour of individuals and contribute to the habitat selection process (Cody 1985). Habitat selection can be considered as a hierarchical and scale-dependent process (Orians & Wittenberger 1991). In terms of individual fitness, habitat selection at home-range scale is likely to be more important than local or regional scale decisions because the survival of individuals and their reproductive success is obviously dependent on resources in the vicinity of the nesting site. However, identification of key habitat components and minimum requirements of the species is often difficult to perform and presumes good knowledge of the species under consideration. Thus, for management and conservation purposes it is often necessary to assume that occupied sites meet the necessary habitat requirements of individuals.

The Siberian flying squirrel (*Pteromys volans*) is a nocturnal arboreal rodent. It is distributed across the entire Eurasian boreal forest vegetation zone (Wilson & Reader 1993). In Finland, the species occurs at the westernmost edge of its global range and here its range extends from southern Finland to southern parts of Finnish Lapland. The species is relatively abundant and regularly distributed in southern Finland but becomes rather sparsely and unevenly distributed towards the north.

The species has been classified as an endangered species in Finland and it has been listed as a species of special concern in the EU (Rassi *et al.* 2000). According to the recent assessment of endangered species in Finland the principal causes of the decline of the Siberian flying squirrel are the losses of suitable habitat and changes in forest stand structure, such as tree species composition and the lack of cavity trees. In addition, Hokkanen *et al.* (1982) considered the species close to extinction in northern Finland. Intensive old-growth forest inventories in the 1990s, however, revealed that the species still exists in mature spruce-dominated forests throughout the northern parts of its range in Finland (Rassi *et al.* 1996). In southern Finland, the species can be found in a large variety of habitats including mixed spruce-dominated forests, ecotones between field and forest, lakeside forests, around settlements, and even in urban parks (Eronen 1991, Wistbacka *et al.* 1996). On the contrary, the species has been encountered almost entirely in mature forests in northern Finland, which indicates that in peripheral populations in the north either habitat requirements or availability of critical resources differ from more southern areas.

The Siberian flying squirrel is rather omnivorous but forages mainly on leaves of deciduous trees in summer and on catkins of alder (*Alnus incana*) and birch (*Betula* spp.) in winter. They often supplement their diet e.g. with buds, seeds,

and inflorescences of conifers (Mäkelä 1996a). It is important to note that abundance of different food resource types vary remarkably between the seasons of the year but the availability of food resources remains in natural conditions relatively constant from year to year. In natural forest areas individuals often use cavities (e.g. old woodpecker holes) for roosting and nesting but also frequently accept deserted Eurasian red squirrel (*Sciurus vulgaris*) dreys (Hanski 1998). In managed forests flying squirrels eagerly settle in nest boxes obviously because of the lack of natural cavities. This indicates that individuals show a clear association with cavities, even artificial ones, when they are available.

The Siberian flying squirrel is not known to compete over any resource with conspecifics or with other species such as the Eurasian red squirrel. Radio-tracking studies in southern Finland have shown that the home ranges of females do not overlap with each other, whereas males use larger areas, which overlap with each other and also often with several females (Hanski 1998, Hanski *et al.* 2000b). Despite non-overlapping home ranges, no antagonistic behaviour among females has been documented so far. Males commonly occupy the same nest boxes together. The Siberian flying squirrel is preyed upon by large owls, goshawk (*Accipiter gentilis*), and pine marten (*Martes martes*) but it is not the main prey item of any of the predators (Hanski *et al.* 2000a). Therefore, the species at least in Finland is an occasional prey item in the diet of potential predators contrary to North American flying squirrels, which form a significant part of the diet of some avian predators (*see Carey et al.* 1992).

Earlier surveys have suggested that flying squirrels prefer mature mixed spruce–deciduous forests but detailed studies on habitat associations of the species in northern Finland have been missing. Such information would be very much needed because conservation of species like the Siberian flying squirrel cannot be arranged by establishing nature reserves only but efforts have to be directed to forest landscapes in general. Therefore, the development of forest management methods, which allow the continued existence of the species in intensively managed forests in northern Finland, are important.

We investigated habitat characteristics of the Siberian flying squirrel in remnant old mature forest areas in northern Finland by measuring forest structure in forest sites that were occupied or regularly visited by the species. We compared the occupied sites with randomly selected forest sites within the same forest area in order to describe the availability of habitats. We further analysed the habitat selection of the species by calculating a resource selection function (RSF) for occupied and potentially available forest sites (Boyce & McDonald 1999). In addition, we radio-tracked individuals to further see if habitat associations within individual home ranges showed the same habitat patterns as at the larger scale comparison between occupied and random forests (*see also Mönkkönen et al.* 1997, Reunanen *et al.* 2000). In this latter approach we tested if satellite imagery data can be used appropriately in ecological studies at home-range level.

Material and methods

Study area

The research was carried out in Pudasjärvi, Taivalkoski, and Kuusamo, northern Finland (65°35'N, 28°10'E). In total the study area encompasses nearly 5300 km² (Fig. 1). Phytogeographically the area belongs to northern boreal vegetation zone (Ahti *et al.* 1968). Forest land covers more than 65% of the area, peatlands (especially bogs and fens) around 25%, and water and river courses 8%. Most of the forest land (75%) is dominated by pine forests of various ages (Fig. 2). Spruce dominated forests cover one fifth of the study area and ca 5% can be classified as young deciduous-rich forests, mainly sapling and thinning stands. Old forests (> 100 years) comprise about 20% of the forest land. Most of the studied old-growth forest areas are protected as old-growth forest reserves. All radio-tracked individuals inhabited large protected areas.

Traditional management of the forest in this area involved selective logging of the most valuable saw timber. This traditional harvesting was employed until the 1950s and practically all

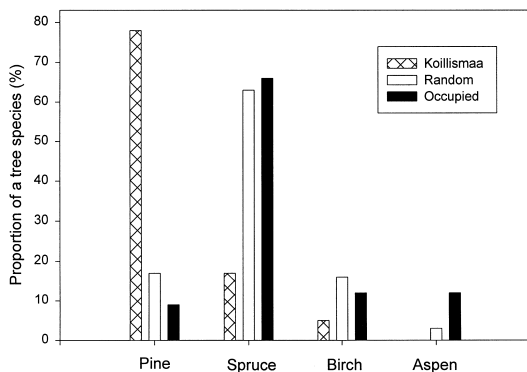


Fig. 2. Tree species composition in the study area in general and in the field sampling plots. The column for Koillismaa refers to the relative area of the total forest land dominated by pine, spruce and deciduous trees (in practice birch). Columns for random and occupied flying squirrel sites express the relative basal area of tree species in the sample plots.

forests have been logged at least once. The modern intensive forestry started in the 1950s. As a result of new methods, such as clear cuttings, pine plantations, and suppression of deciduous trees, previous natural forest landscapes were converted to landscapes where young plantation forests prevail within a few decades. Tree species composition shifted towards pine dominance (Anon. 1998). Our studies were conducted in forests intact by the modern forestry but which have been selectively logged earlier on. The topographic relief in study area ranges from 100 to 360 meters in altitude. The average altitude is more than 200 meters.

Identification of presence of the Siberian flying squirrel and the characterisation of the forest structure

Practically all forest area, which was considered natural or semi natural old-growth forests in northern Finland, were inventoried during the early 1990s for their biodiversity values. These inventories took place due to a need to augment the existing reserve network with new forest protection areas in northern Finland (Rassi *et al.* 1996). We used the information on the occur-

rence of the Siberian flying squirrel collected during old-growth forest inventories in selecting forest areas for the study of habitat use of the species. This information allowed us to disperse the study forests evenly across the entire range of the species in northern Finland in order to have a representative sample of habitat characteristics in forest sites where the Siberian flying squirrel occurs. We carried out the habitat survey in 1995, and our sample covered nearly all known occupied forest sites of that time in northern Finland.

The location of occupied forest sites was identified by searching for easily identifiable faecal pellets under aspens and the largest spruces. Also leaves of aspens, birches, and alders that were consumed by the species were looked for. An area of a few hectares around the first detected droppings was searched intensively tree by tree to more precisely locate the most frequently visited sites. This method is indirect but has been observed to indicate occupied forest sites or resource patches that individuals use reliably enough (Anon. 1993). However, it does not allow us to draw any conclusions of the home-range size, number of individuals or the population density in a given area. We compared forest characteristics in occupied forest sites with randomly selected ones within the same old-growth forest area. Random sites were assigned to study areas by superimposing a grid of 200×200 meters on the forest areas where flying squirrel sites were found. One grid point per each flying squirrel site was randomly selected as a reference site. These points were allowed to be on forestland only, not, for example, on bogs or transition zones between forests and bogs.

Forest structure in flying squirrel and random sites was measured within five circular sampling plots of 10-m radius (314 m^2). The first sampling plot was placed in the forest site where the most sightings of the species were recorded (flying squirrel sites) or in the random sites. The other four sampling plots were placed at 50-meter distance in all cardinal points. In case a sampling plot was to be situated on wetland or clear-cut, a new plot was chosen in a random direction from the original point.

Forest structure within sampling plots was characterised by measuring the number of living trees species by species, volume of standing and fallen trunks. Living trees were classified into diameter classes with 5-cm intervals. Total basal area of the tree species was calculated by summing up the basal area of individual trees at DBH. Dead trees were counted and their diameter and length within sampling plot were measured. The degree of decay of downlogs was categorised into three classes (fresh, intermediately and well-decayed). The height of the dominating canopy was measured with hypsometry. Because the flying squirrel is a strictly arboreal mammal, ground vegetation was assumed not to be an important factor in determining preference to forest characteristics. From these basic measures we calculated variables that further describe forest structure (*see* Table 1).

Statistics

Statistical testing was made by comparing the structural characteristics of forest sites, which were occupied by the Siberian flying squirrel ($n = 148$), with randomly selected forest sites within the same forest area ($n = 147$). In all, forest structure was measured in 30 forest areas. The average of the five (in a few cases four) sample plots was considered as a sampling unit in statistical analysis. We used non-parametric Wilcoxon matched pairs test in the pair-wise univariate comparisons because each occupied Siberian flying squirrel site had a control site within the same forest area. In addition, we performed principal component analysis (PCA) to summarise information of the variables into principal components. Variables were either log- or square-root transformed prior to PCA to normalise their distributions. All variables in Table 1 except

Table 1. The habitat variables measured in this study with their descriptions. Asterisk (*) after the variable name indicates the variables, which were included in the logistic regression analysis. Statistical significance (p) refers to Wilcoxon matched pairs test results for flying squirrel vs. random site comparisons ($n = 30$). p -values in bold refer to statistical significant difference after sequential Bonferroni correction. Difference denotes whether the value in flying squirrel sites was larger (+) or smaller (–) than in random sites.

Variable description	Variable name in test	Difference	p
Meters above sea levels	ASL		n.s.
Canopy height in the sample plot	CANOPHEIGH*	+	$p = 0.01$
Total number of trunks	TOTNUMTR		n.s.
Total basal area	TOTBASAL	+	$p < 0.001$
Number of trees DBH < 15 cm	DIAMCLASS1*		n.s.
Number of trees DBH 15–30 cm	DIAMCLASS2*	+	$p = 0.002$
Number of trees DBH > 30 cm	DIAMCLASS3*	+	$p < 0.001$
Proportion of number of stems in the two smallest DBH classes of all trunks	LAYERS	–	$p < 0.001$
Proportion of deciduous trees of total tree numbers	DECID%	+	$p = 0.035$
Proportion of deciduous trees of total basal area	DECBASAL%*	+	$p < 0.001$
Proportion of spruces of total tree numbers	SPRUCE%		n.s.
Relative proportion of spruce of total basal area	SPRUBASAL%*	+	$p < 0.001$
Proportion of pines of total tree numbers	PINE%	–	$p < 0.001$
Relative proportion of pine of total basal area	PINEBASAL%*	–	$p = 0.009$
Proportion of aspen of total tree numbers	ASPEN%	+	$p < 0.001$
Relative proportion of aspen of total basal area	ASPENBASAL%	+	$p < 0.001$
Number of dead standing trees	STANDDEAD		n.s.
Total volume of down logs	DECAYTOT*		n.s.
Number of down logs per hectare	DLOG/HA*	+	$p = 0.021$
Volume of fresh down logs	DECCLASS1	+	$p = 0.008$
Volume of intermediately decayed down logs	DECCLASS2	+	$p = 0.012$
Volume of well decayed down logs	DECCLASS3		n.s.

those related to aspen abundance were entered into PCA; aspen variables could not be normalised even with transformations. Scores on the first two principal components between flying squirrel and random sites were compared with matched pairs *t*-test.

Distribution of resources on which an organism is dependent on can be described by resource selection functions (RSF). An RSF is a function that gives the probability of use of a particular resource unit or it can be used to scale the use of various habitats (Boyce & McDonald 1999). We generated an RSF to estimate whether clear indication of habitat selection in terms of the variables measured can be found. We do not know the total number of occupied forest sites in our study area and perhaps our data include a rather small sample of actual flying squirrel sites. Therefore, in order to estimate an RSF we used the equation

$$\hat{w}(x) = \exp[\beta_1(x_1) + \beta_2(x_2) + \dots + \beta_n(x_n)] \quad (1)$$

where $\beta_1 \dots \beta_n$ are coefficients from logistic regression analysis and $x_1 \dots x_n$ variable values (Boyce & McDonald 1999). We selected the variables for the logistic regression by examining the correlation matrix of all variables. A set of variables, which had coefficients of correlation < 0.8 were included in the analysis also keeping track on biologically important variables, i.e. in case of inter-correlated variables we selected the one which more likely is important from the flying squirrel perspective (*see* Table 1 for entered variables). Because logistic regression is fairly robust and thus insensitive to deviancies from normality we used original untransformed variables.

Home-range analysis of radio-tracking data

We trapped flying squirrels in forest sites, which were first searched for in the same fashion as we located the occupied forest sites. Traps were wooden boxes of $15 \times 20 \times 42$ cm with wire

mesh on the other end. Traps were attached on the tree trunks at ca 1.5 meters above the ground in sites which were conspicuously often visited by flying squirrels. Trapped individuals were sexed, aged and weighed. Ageing of individuals was based on weight. Individuals around 100 grams in late summer were determined as juveniles (Mäkelä 1996b). They were fitted with Biotrack TW-4 ag357 transmitters.

We captured altogether 6 individuals, 2 in 1996 and 4 in 1997 in Metsäkylä, Taivalkoski ($65^{\circ}13'N$, $28^{\circ}10'E$) (*see* Fig. 1). Individuals were tracked during their activity period at night regularly from June to September and they were usually fixed 2–3 times per night. During the light summer nights individuals could be fixed very accurately to the tree where they were foraging, whereas in autumn only to a group of trees, however, this being accurate enough for our home range and habitat use analysis. After the tracking season all the fixes were relocated in the field and they were put on the field maps (scale 1:2500). Error in accuracy of located fixes on the map was estimated to be about ten meters. Three of the six individuals lived in the same forest stand. Thus, there were four spatially separate forest areas. Our purpose was not to study the home-range size of the flying squirrel, and our data were clearly much too scanty to draw any general conclusions of the space use patterns. Nevertheless, we believe that these data are suitable for providing a within home-range scale comparison for larger scale analyses.

Home-ranges of individuals were analysed using RANGES V software (Kenward & Hodder 1996). We used minimum convex polygon (MCP) method to delineate the total home range area of the individuals. For this we used the whole set of fixes and, hence, 100% MCP refers to habitat types and tree species composition available for the individual. In order to characterise the more actively used areas within the home ranges we delineated and measured core areas by using 90% cluster analysis. The number of fixes for the core area analysis was estimated by plotting utilisation distribution of all individuals.

GIS analysis

The forest information for the analysis was derived from multi-source national forest inventory (NFI) data (Tomppo 1991, 1996). NFI exploits Landsat TM 5 satellite images, ground study plots as a reference for stand characteristics and digital masks of other land use forms in order to get geographically explicit, up-to-date information of forest resources. Originally 30×30 -m pixel size is resampled to 25×25 m during the operation. Image analysis produces estimates of growing stock for each pixel separately for pine, spruce, birch and other tree species as a combined class. The result is a rectified multi-channel image that can be imported to geographic information system (GIS) (Tomppo 1991, 1996).

After importing NFI data to GIS we superimposed our home-range data on each tree species volume layer and identified the pixels within 100% MCP and 90% cluster areas. Home range data and satellite imagery data were matched with each other using clear landmarks visible in both data such as watercourses, roads, and clear-cut edges. Both data sets (pixels on satellite image and fixes in home range data) may contain position inaccuracies of 10–20 meters (Mattiila 1993), and hence, exact matching of the data sets is impossible. The growing stock information and tree species composition for each pixel was determined simply by summing the values for each tree species. To test if 90% cluster areas differ from 100% MCP areas in terms of forest structure we conducted resampling analysis of the existing data (*see* Crowley 1992 for resampling methods) using Resampling Stats Add-in for Excel (Resampling Stats 1998). For each individual we randomly picked pixels from the data representing their 100% MCP area so that the number of pixels in samples equalled the number of pixels within 90% cluster areas. This was repeated 1000 times for each individual. Because the comparison of forest structure between occupied and random sites in the field within larger forest areas suggested that on average flying squirrels occupied forests where

total timber volume was higher and which were more clearly dominated by spruce and deciduous trees than random sites (*see* results below), our statistical hypotheses in this within-home-range analysis were one-tailed. We tested if 90% cluster areas contained larger total timber volume, higher proportion of spruces and deciduous trees and lower proportion of pines than available within 100% MCP areas. In practice we counted in how many cases out of 1000 the total timber volume, for example, in a sample was higher or equal than that observed within the 90% cluster area. This number divided by 1000 gives the risk of failure when rejecting null hypotheses.

Results

Forest structure in the field survey

Forest structure was described in 30 separate old-growth forest areas including both flying squirrel and random sites. All forests were spruce dominated. Owing to the dominance of the spruce bilberry type (*Vaccinium myrtillus*) moderate dry forests were the prominent forest type in study areas. Also lingonberry (*V. vitis-idaea*) type dry forests and herb-rich *Geranium sylvaticum* type forests were occasionally encountered (Ahti *et al.* 1968). Signs of selective cuttings, such as old stumps covered by mosses or the lack of large dominant canopy trees, mainly pines, could be seen practically in every sample plot.

Results of pair-wise statistical testing and significances are shown in Table 1. Pine was more common in random sites than in sites occupied by the Siberian flying squirrel (Fig. 2). Especially the number of young pines was higher in random plots than in occupied forest sites (Fig. 3). As a consequence, the proportion of pine of basal area was lower in flying squirrel than in random sites. By contrast flying squirrel sites were more spruce and deciduous tree dominated than random sites (Table 1). The proportion of deciduous trees of the total basal area and

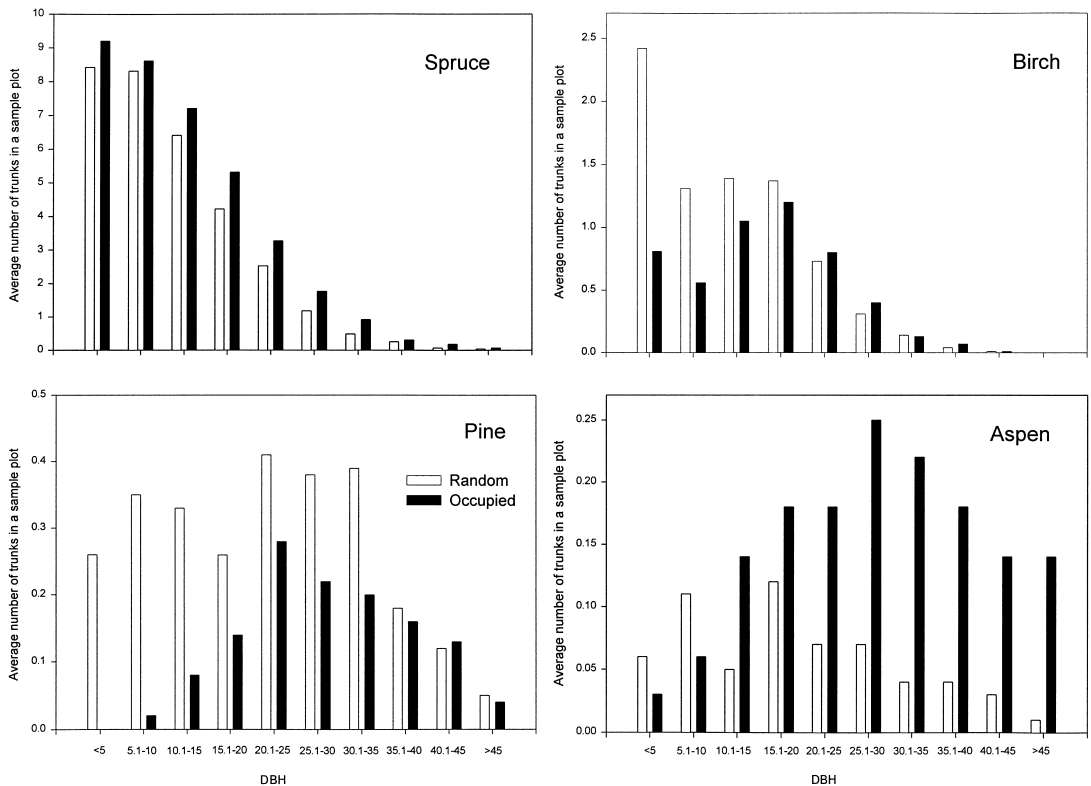


Fig. 3. The average number of trunks by species in random and occupied flying squirrel sites in the ten DBH-classes.

Table 2. Variable loadings for the first two principal components (PC1 and PC2). Loadings $> |0.5|$ are in bold face. See Table 1 for variable descriptions.

Variable	PC1	PC2
CANOPHEIGHT	0.821	-0.050
TOTNUMTR	-0.308	0.841
TOTBASAL	0.749	0.492
DIAMCLASS1	-0.412	0.751
DIAMCLASS2	0.252	0.793
DIAMCLASS3	0.737	-0.198
LAYERS	-0.530	0.154
DECID%	-0.019	0.337
DECBASAL%	0.465	0.555
SPRUCE%	0.488	-0.372
SPRUCBASAL%	0.815	0.065
PINE%	-0.479	0.012
PINEBASAL%	-0.366	0.498
STANDDEAD	0.424	0.292
DECAYTOT	0.481	0.049
DLOG/HA	0.525	0.353
% variance explained	28.5	20.2

of total tree numbers was clearly higher in occupied than randomly selected forest sites, as was the proportion of spruce of total basal area (Table 1). The total number of birches and spruces was to a large extent similar between the occupied and random plots (Fig. 2) but the size distributions of birch were clearly different (Fig. 3): there were more young trees (DBH < 15 cm) in random plots than in occupied forest sites, whereas the middle-sized trees were more common in occupied forest sites. Aspen was relatively more numerous and its proportion of basal area was higher in flying squirrel sites (Table 1 and Fig. 3). The density of fallen trees and the volume of fresh and intermediately decayed fallen trees were somewhat higher in flying squirrel sites than in random sites (Table 1).

PCA extracted five principal components with eigenvalue larger than 1. The first two axes explained altogether 48.7% of the variation in

the data. PC1 correlated positively with the canopy height, the number of large trees, total basal area, proportion of spruce of basal area and the density of down-logs, and negatively with the proportion of small trees (Table 2). Therefore, sites scoring high on this axis contained more large trees, more dead wood, more spruce and less small trees than lower scoring sites. The second principal component was positively related to the total number of trunks (particularly small and intermediate sized trees) and the proportion of deciduous trees of basal area. The second axis can be interpreted to scale the sites from fairly open conifer dominated sites on the negative end to a high proportion of deciduous trees on the positive end of the axis (Table 2).

The location of flying squirrel and random sites on PC1 and PC2 differed significantly from each other (PC1: $t = 6.96$, $p < 0.001$; PC2: $t = 2.21$, $p = 0.036$; $n = 30$ in both cases). Figure 4 shows that flying squirrel sites were situated closer to the positive end of the axes than random sites suggesting that flying squirrels preferred older, spruce and deciduous dominated forests with closed canopy. These results match well with the univariate comparisons (Table 1). There was, however, some overlap in the location of flying squirrel and random sites on both principal components.

We carried out logistic regression by assigning a value 0 for random sites and 1 for occupied forest sites and using the variables indicated in Table 1 as continuous independent variables. In forward stepwise logistic regression the model that best fitted with the data included total basal area of the deciduous trees and spruces (Table 3). These two variables alone correctly classified 75% of the cases. The coefficients from logistic

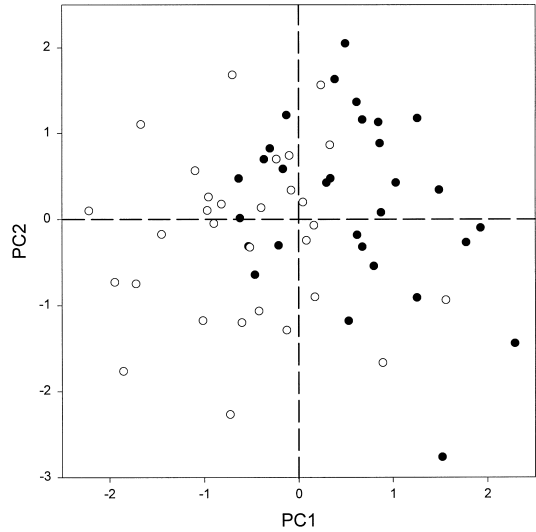


Fig. 4. The location of random (open dots) and occupied flying squirrel (black dots) sites on PC1 and PC2.

regression were used to calculate the RSF. The function was standardised to average values of RSF for random sites and thereafter scaled by taking logarithm of those values. The results indicate clear selection for forest sites where the basal area of deciduous trees and spruces is high ($n = 60$, $t = -6.572$, $p < 0.001$) (Fig. 5).

Habitat preference patterns within individual home ranges

We analysed habitat structure in home ranges of two adult males, one adult female, and three juvenile males. In our data, one adult male (Number 083) differed from all other individuals in terms of home-range size due to a short tracking period because that individual was pre-

Table 3. The final logistic regression models after a forward step-wise analysis for occupied and random sampling sites. Step# gives the order in which the variables entered the model. Deviance indicates the improvement of the model when the variable has entered the model and p denotes the significance of the improvement. Direction of effect shows whether the variable has a positive or a negative effect on the probability of forest site being occupied. See Table 1 for variable descriptions.

Step#	Variable in the model	Deviance	df	p	Variance explained (%)	Direction of the effect
1	DECBASAL%	63.086	1	0.0000	68.33	+
2	SPRBASAL%	50.751	2	0.0004	75.00	+

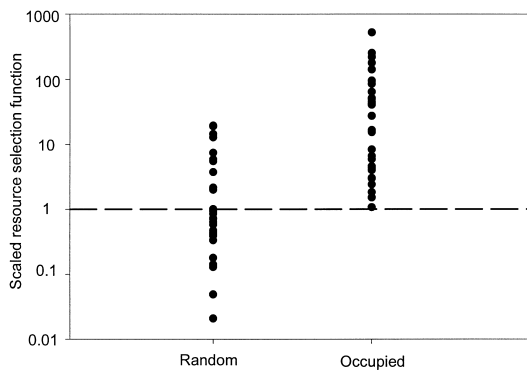


Fig. 5. Values of the resource selection function based on forest characteristics from the logistic regression analysis for random and occupied flying squirrel sites. The values are scaled so that 1 is the average value of predictor variables (basal area of spruces and deciduous trees) in the random sites.

dated by a goshawk (Table 4). Two of the juveniles seemed to have established their home ranges or stayed in their natal site, whereas one juvenile (#093) dispersed in the end of September. However, the observations from October–November were excluded from the analysis because there were not enough fixes outside nests from this new site in order to calculate the size of home range.

Forest structure derived from NFI data differed between the four areas where individuals were radio-tracked (Table 5). Home-range sizes varied considerably between individuals under survey but 90% cluster areas were in all cases less than one third of the 100% MCP (*see* Table 4). In all cases, however, the average timber volume was well above $100 \text{ m}^3 \text{ ha}^{-1}$; $100 \text{ m}^3 \text{ ha}^{-1}$ corresponds to 100–120 years in age in this region (Tomppo *et al.* 1998). In all cases spruce

and deciduous trees together comprised about 50% or more of total timber volume within 100% MCP home ranges.

Actively used areas within home ranges seemed to rather systematically differ from overall home ranges. First, in five out of six cases total timber volume was higher in 90% cluster than in 100% MCP areas and in three cases this difference was statistically significant (Table 5). Second, 90% cluster areas tended to be more spruce dominated than home ranges in general; again, three differences were statistically significant. Spruce and deciduous trees together made up 55% to 85% of timber volume within 90% cluster areas. Third, all six individuals (two individuals significantly) used more actively areas where pine domination was lower than within their home range in general.

Discussion

The results of our field survey suggest that the Siberian flying squirrel favours forest sites where the density and size of spruces is larger than on average in mature spruce forests as indicated by the larger basal area of spruces in flying squirrel than in random sites. Another obvious requirement for an occupied forest site was the presence of deciduous trees and especially aspens. There was, however, some overlap between the location of flying squirrel and random sites in multivariate space (Fig. 4). This obviously results from the fact that random sites located within the very same forest areas as flying squirrel sites and, therefore, at least some of them were potential but at that moment vacant flying squirrel sites or even currently occupied. On the other hand,

Table 4. Statistics of the home range analysis. 100% MCP presents the total area of the individual home range. 90% clusters indicate areas within the entire home range where 90% of all fixes were concentrated.

Individual	Age and sex	Tracking period	Number of fixes	100% MCP (ha)	90% Cluster (ha)
#083	Adult male	7.VI.–30.VI.1997	26	1.01	0.12
#055	Adult male	26.VII.–23.IX.1997	41	82.45	20.85
#062	Adult female	1.VII.–26.IX.1997	42	14.45	1.81
#504	Juvenile male	17.VIII.–25.IX.1997	27	3.76	0.19
#093	Juvenile male	13.VIII.–27.IX.1996	27	3.55	0.92
#073	Juvenile male	13.VIII.–26.IX.1996	28	2.29	0.14

nearly half of the occupied sites clearly fell outside the range of variation among random sites suggesting clear habitat selection by flying squirrels in terms of measured variables. The same pattern was clearly shown by the RSF-analysis (Fig. 5). Some outliers among flying squirrel sites are possibly due to recent forest harvesting, which have forced individuals to move to less preferred sites (*see* Taulman *et al.* 1998).

Interestingly, results from the home-range analysis in GIS were to a large extent in line with the results from our field survey. Radio-tracked individuals tended to prefer forest sites where total timber volume and spruce dominance were higher, and pine dominance lower than available within their home-ranges on average. At the home-range scale, however, we did not find a clear preference for deciduous trees. This discrepancy between the two studies apparently stems from inaccuracies and resolution of our GIS data (Kalliola & Syrjänen 1991, *see*

also Orrock *et al.* 2000) but the sample size in the study may have been too small to detect any differences. Both geometric and spectral resolution of NFI data may not be accurate enough to detect small scale variation in the amount of deciduous trees. At very small spatial scales (in samples of a very few pixels) and small areas like at home-range level of the species satellite image classification, which is based on forest inventory data, is generally fairly inaccurate as to detailed forest structure characteristics (Tokola & Heikkilä 1997). Depending on tree species composition, estimates of growing stock at this level can have a relative error of several tens of percent, but it decreases to some 10%–20% for the areas > 30 ha (Tokola & Heikkilä 1997). Especially, the identification of tree species that grow sparsely among and mixed with dominant tree species has been shown to be inaccurate. Aspen, for example, is commonly patchily distributed because of its clonal growth mode and,

Table 5. A comparison between pixels within 100% MCP home ranges (available) and 90% clusters (actively used) in terms of total timber volume and percentage of spruce, deciduous trees and pine. *n* refers to number of pixels encompassed by 90% cluster areas (upper row) and 100% MCP home ranges (available). *p* gives the risk of type I error based on randomisation tests. Note that our statistical hypotheses — and therefore also significance levels — were one-tailed. Individuals #073, #083 and #093 lived in the same forest and their home ranges overlapped considerably.

	<i>n</i>	Total timber volume m ³ ha ⁻¹	% Spruce	% Deciduous trees	% Pine
055 adult male	152	131.3	49.8	19.6	30.6
Available	1074	104.9	39.3	16.7	44.0
<i>p</i>		< 0.001	< 0.001	< 0.001	< 0.001
062 adult female	41	161.2	42.1	12.9	45.1
Available	251	150.6	36.5	12.2	51.3
<i>p</i>		0.094	0.048	0.287	0.061
504 juvenile male	16	135.3	55.5	21.7	22.8
Available	108	129.5	45.8	22.8	31.5
<i>p</i>		0.318	0.024	0.643	0.033
073 juvenile male	4	182.5	64.0	21.9	14.1
Available	55	155.9	57.2	24.0	18.8
<i>p</i>		0.043	0.160	0.537	0.214
093 juvenile male	18	139.1	55.4	26.0	18.6
Available	55	148.0	56.3	22.9	20.8
<i>p</i>		0.820	0.607	0.139	0.369
083 adult male	9	159.1	61.4	20.1	18.5
Available	31	126.3	53.2	21.3	25.5
<i>p</i>		0.013	0.138	0.615	0.236

thus, may go unnoticed in NFI analysis (Tomppo *et al.* 1998). In relation to the Siberian flying squirrel this suggests that NFI data may not be accurate enough to detect important small-scale variation in the amount of deciduous trees viz. aspen within spruce-dominated forests.

Based on our results, it is not possible to determine whether or not the age of the forest is important for the Siberian flying squirrel in its habitat selection (c.f. Chapin *et al.* 1997) because all study areas were located in remaining spruce-dominated old-growth forests (*see also* Johnson 1980). Our results, however, clearly indicated the importance of spruce (in both analyses) and deciduous trees (in the field study only) (*see also* Hanski 1998). Our study was based on correlative data, and therefore, ultimate reasons for these habitat preferences remain speculative. The species is rather omnivorous and food availability is not likely to be a limiting factor affecting the habitat use of the species. Safe nesting sites in cavities and woodpecker holes are evidently playing an important role in habitat selection by the Siberian flying squirrel (Hanski *et al.* 2000b). Deciduous-rich forest sites provide not only optimal foraging areas but also cavity trees for nesting and roosting. Preference for spruce might stem from the cover it provides against predators. On the other hand productive, deciduous-rich forests in the northern boreal vegetation zone are often spruce dominated in Finland.

Habitat preferences of the Siberian flying squirrel in southern Finland seem to be more variable than in northern Finland. In northern Finland flying squirrels have almost exclusively been found in old-growth forests whereas in southern Finland they occupy managed forests as well as semi rural and semi urban habitats (Eronen 1991, Wistbacka *et al.* 1996). Nevertheless, also in southern Finland the species have been shown to favour spruce-dominated forest patches (Selonen *et al.* 2001) and preference for deciduous-rich patches is also obvious although they regularly use other habitat types for movements and foraging (Hanski 1998). These deviant habitat-use patterns are likely to arise from differences in forest and land use history between regions, and thus consequently, landscape context. In northern Finland the remaining old-

growth forest areas comprise about 20% of forest land, and forest structure within these forests has not been altered during the past 70 years. At landscape scale, remaining old-growth forest areas are embedded in the matrix of younger regeneration stands. In the southern Finland forest, land is a more mosaic-like patchwork of many landscape elements such as fields, lakes, and settlements. From the flying squirrel point of view northern Finnish forest landscapes are less variable in terms of habitat suitability than in the south. In contrast to southern Finnish forests, which have often been managed at the stand level as well, our results represent habitat use patterns under relatively original circumstances. The relative generalist habitat-use pattern of the species in the south may simply be because of a wider availability of suitable habitat types.

Results of the present study indicate that the Siberian flying squirrel tend to be selective in its habitat use (*see* Hanski 1998). At home-range scale mature mixed forest sites play an important role in determining the presence of the species in boreal old-growth forests in northern Finland. The characterisation of key elements in forest structure is important for the conservation efforts of this declining species. This information forms the background for supporting viable populations in northern parts of the species present range in Finland and also helps to create a sound basis for the stand level forest management. For example, our results clearly point out the importance of deciduous trees (*see also* Hanski 1998). Deciduous forest sites are a transient stage in boreal forest succession (Pickett & White 1985, Esseen *et al.* 1997). The age of deciduous trees in closed canopy forest is estimated to be on average 150 but less than 250 years (Spies & Franklin 1996). The recent forest management practices have favoured conifers whereas deciduous trees, particularly aspen, have been actively suppressed in public land (Elo 1983, Savilampi 1994). Forest management should therefore treat the remaining deciduous-rich sites as key biotopes and ensure the continued recovery of such sites.

At larger spatial scales satellite imagery data have been shown to reliably identify potentially inhabitable forest patches for the Siberian flying

squirrel, particularly when accompanied with landscape metrics that quantify landscape composition and configuration (Reunanen *et al.* 2000). Although our home-range data are far too small and preliminary to serve as a quantitative test to identify flying squirrel habitats from satellite image, the results of the within home-range analysis are encouraging. Our results suggest that the GIS analysis is accurate enough for extracting general patterns in habitat use of the Siberian flying squirrel even within home ranges. These results indicate that remote sensing data can be applied in planning forest management practices not only at local and landscape scales but, also, at very home-range level. However, GIS techniques needs to be developed further in order to identify key forest characteristics, such as deciduous tree species, more accurately at lower spatial scales than at present.

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