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The flying squirrel *Pteromys volans* is an arboreal rodent and inhabitant of Palearctic boreal forests. In Finland, the flying squirrel has been classified as a declining species which needs to be monitored. I studied home ranges, habitat use and nocturnal activity of eight adult flying squirrels by radio tracking in fragmented coniferous forests in Finland during June - December, 1996. Average home-range size of the flying squirrel measured by the 100% MCP was 6.5 ha. In summer, the average size of the 95% cluster area was 2.3 ha and the 80% core area 0.5 ha. The core areas represented only 7.8% of the 100% MCP area and were composed of 2-6 separate patches in the home ranges of individual squirrels. Radio-tagged squirrels used several nests, both old woodpecker cavities and dreys for nesting and diurnal roosting. The combined density of all deciduous tree species was significantly greater in the 80% core areas than within the 100% MPC in the summer data set. In the polychotomous logistic regression model the great canopy cover, high densities of alders *Alnus incana* and *A. glutinosa* and aspen *Populus tremula* significantly explained the ranked utilisation classes (utilisation rank from highly used areas to least used areas: 80% core - 95% cluster - 100% MCP). The three most abundant deciduous trees species (birches *Betula pendula* and *B. pubescens*, aspen, alder) constituted 87% of trees used by squirrels in summer. Flying squirrels were found in aspens more often than expected according to their availability. The results show a clear preference for deciduous trees and a preference for the parts of home ranges with higher densities of alders and aspen. The flying squirrel seems to be capable of using several cover types, including young forest stands, as foraging and moving areas and are able to move across semi-open clear-cut areas.

Key words: flying squirrel, habitat use, home range, Pteromys volans, radio tracking, red-list species

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During the past century, boreal forests (taiga) have been subjected to intensive changes due to forest management practices (e.g. Hunter 1990, Kuusela 1990). Forest management has altered the structure of forests, for example, enhanced fragmentation, drastically reduced the area of old, primeval forests, favoured monocultures, changed natural dynamics, e.g. interrupted forest fires followed by natural succession (e.g. Pastor & Mladenoff 1992, Haila 1994, Syrjänen, Kalliola, Puolasmaa & Mattson 1994). In general, forest management causes both habitat loss and fragmentation and depending on the intensity, creates a mosaic of forest patches varying in size and degree of isolation (Esseen, Ehnström, Ericson & Sjöberg 1992, Gardner, Turner, Dale & O'Neill 1992, Andrén 1994). Changes in forest structure have had detrimental effects on forest dwelling species. For example, several species of birds, e.g. Siberian jay, Siberian tit and most woodpecker species, preferring primeval forests (Järvinen, Kuusela & Väisänen 1977, Helle & Järvinen 1986, Virkkala 1987, 1991, Angelstam & Mikusinski 1994) have declined, and insects specialised for living in decaying wood have become threatened or extinct (Rassi, Kaipiainen, Mannerkoski & Ståhls 1992, Siitonen & Martikainen 1994, Berg, Ehnström, Gustafsson, Hallingbäck, Jonsell & Wesli 1995).

In Finland, the forest management practices have favoured spruce *Picea abies* and pine *Pinus sylvestris* monocultures, where dead trees and deciduous trees are much less abundant than in primeval forest (Heliövaara & Väisänen 1984). In addition, selective removal of aspen, the most common cavity-forming tree, from coniferous forests has probably reduced the availability of nest sites for cavity-nesting birds and mammals.

The flying squirrel *Pteromys volans* L. is an inhabitant of coniferous boreal forest and its distribution extends from Finland to eastern Siberia and Japan (Ognev 1966). In western Europe the flying squirrel occurs only in Finland and in small numbers in the Baltic countries. It is mostly nocturnal and arboreal, roosting and nesting in tree cavities and dreys (nests on tree branch made of twigs, mosses and lichens). The food of the flying squirrel mainly consists of the leaves of deciduous trees in summer, and catkins of birch and alder supplemented with buds of both coniferous and deciduous trees in autumn and winter (Mäkelä 1996). In autumn, it stores catkins in tree or rock cavities and on branches of spruces (Sulkava & Sulkava 1993). In Finland, the flying squirrel population has declined during recent decades (Hokkanen, Törmälä & Vuorinen 1982). Therefore, in the Red Data Book, the flying squirrel has been classified as a declining species with a need for monitoring its population abundance (Rassi & Väisänen 1987, Rassi et al. 1992). In the Habitat Directive of the European Communities the flying squirrel has been classified as a priority species and it belongs to the category of species whose conservation requires the designation of special areas for conservation (Council Directive 1992).

Despite the threatened status of the flying squirrel, no quantitative data on their home ranges, movements or habitat use exist. Studies performed so far describe the habitat structure of sites occupied by flying squirrel, which mostly have been identified on the basis of faeces left under the trees during the non-breeding season (Eronen 1991). Knowledge on home-range size and movements of the animals are essential for determining the scale in which an individual animal perceives the landscape it is inhabiting, and how movements of an animal are affected by the heterogeneity of the landscape (Johnson, Wiens, Milne & Crist 1992, Wiens, Stenseth, van Horne & Ims 1993, Ims 1995). Furthermore, it is not known, what the minimum habitat requirements of the flying squirrel are, or what the tree-species composition, age and density of different tree species in the forest characteristic of an acceptable home range would be. Finally, in connection with habitat structure, it is not known which large-scale landscape structures could maintain a viable flying squirrel population. Both habitat-patch or home-range scale habitat structure and landscape-scale physiognomy and composition may affect the dynamics and persistence of animal populations (e.g. see Dunning, Danielson & Pulliam 1992).

By radio tracking individual flying squirrels I studied home range, habitat use and nightly activity at the home-range scale. This is the first time the spatial behaviour of flying squirrels outside their dens has been studied. Comparable radio-tracking studies on two smaller species of flying squirrels belonging to the genus *Glaucomys* have been done in North America (e.g. Bendel & Gates 1987, Fridell & Litvaitis 1991, Witt 1992).

My objectives were to investigate: 1) the home-range sizes and the scale of movements in the flying squirrel in the heterogeneous forest mosaic, and how flying squirrels view the landscape in their home ranges (i.e. fine or coarse grained); 2) the microhabitat use within the home range, i.e. how do tree-species composition and forest structure influence their choice of microhabitat. The general goal is to gather data on the habitat requirements of the flying squirrel which could be applied in forest management, and on how intensive management practices could be used simultaneously with maintaining the minimum habitat requirements of flying squirrels.

Methods

Study area

The study was done in Iitti, southern Finland (60°55'N, 26°30'E) in managed coniferous forests in 1996. The flying squirrels were tracked in five separate sites within an area of ca 80 km^2. The density of flying squirrels is low and occupied forest stands are scattered over the large area. Phytogeographically the area lies in the south-boreal zone (Ahti, Hämet-Ahti & Jalas 1968). The mean temperatures of the warmest month (July) and the coldest month (January) are +17°C and -9°C, respectively. The snow cover (maximum average: 50 cm) lasts from mid-November to the last half of April. The spruce-dominated forests are owned by private landowners and intensively managed. In the mature stage, spruce forests reach a height of 25-28 m. Forests in the study area are fragmented to 0.2-116 ha stands (mean 8.4 ha, median 3.4 ha) surrounded by clear-cuts, sapling stands, and young forests of various age, and to a lesser extent, by pine bogs. Large continuous forests and primeval old-growth forests are lacking. The only exception is one 20-ha old-growth forest stand close to natural condition. Forest stands are dominated by Norway spruce *Picea abies* with a mixture of Scots pine *Pinus sylvestris* and deciduous trees, mainly birches *Betula pendula* and *B. pubescens*, aspen *Populus tremula* and alders *Alnus incana* and *A. glutinosa*.

Capturing and radio tracking

Eight adult flying squirrels (four males and four females) were captured from their roosting or nesting cavities and fitted with radio-collars from Biotrack, UK. The radio-collars weighed 5.6 g representing 4.0-5.4% of the body weight of males and 3.3-3.8% of females. Capturing took place in June in five sites that were separated from each other by several kilometres. Each study site was marked in the field with coordinates in a 25-m grid to facilitate the location of observations.

Radio-collared flying squirrels were located once a night starting at half an hour after sunset, 3-5 times a week during summer (June - August) and 2-3 times a week during autumn (September - December). The tracking period coincided with the time of rearing young (at least two females had young), but not with the spring mating period. One radio-tagged animal (female no 472) was killed by an unknown predator (probably a goshawk *Accipiter gentilis*) at the end of August. Therefore, the data on autumn home ranges come from seven individuals. During tracking, I followed the signal using a portable RX-81 receiver and a 2 or 4-element Yagi antenna until I was within 15-20 m of the animal. When an approximate position of the squirrel was found, I took bearings from several directions around the site until the animal was located in a single tree, or a small group of trees if they were growing side by side. The site was marked and the exact location (fix) was measured from the nearest grid point afterwards in daylight. The range of radio signals was up to 1 km and the battery life time of the collars was 6-7 months.

In summer, flying squirrels leave their nests or diurnal roosting sites soon after sunset and return before sunrise (Hokkanen, Törmälä & Vuorinen 1977, Törmälä, Vuorinen & Hokkanen 1980, pers. obs.). Therefore, in the analyses, the fixes of subsequent nights were considered as independent observations.

In addition to nocturnal tracking, I checked the locations of radio-tagged animals in daylight at least once a week to keep track of their nesting and roosting sites and to determine if squirrels were active in daylight. The cavity or drey used by a female for rearing or potentially rearing young was defined as a nesting site, and nests used by males throughout the year and/or by females outside the young-rearing period were defined as diurnal roosting sites. When calculating home ranges only the fixes of animals outside their dens were included. When tracking, I did not seem to disturb the animals, because in almost all cases the animal stayed in the tree where it was first located, and when seen, it appeared to be undisturbed and continued foraging in the foliage.

Home-range analyses

Home ranges were analysed using the Ranges V computer package (Kenward & Hodder 1996). When the home-range sizes are presented, it is essential to give the method by which the areas were calculated. Different methods give different results (Kenward 1987, White & Garrott 1990). I present the results of three principal methods: minimum convex polygons (MCP), harmonic mean, and clustering technique (see Jennrich & Turner 1969, Dixon & Chapman 1980, Kenward & Hodder 1996). First, I used the total number of fixes to calculate the 100% minimum convex polygons to represent the area that is within the range of the animal's movements and the 95% MCPs and the 95% harmonic mean estimates which are more comparable with the results of other home-range studies on mammals (e.g. Fridell & Litvaitis 1991, Kauhala, Helle & Taskinen 1992, Witt 1992). Second, I used the clustering technique to define areas of high and low-frequency use (Kenward & Hodder 1996) and as a basis of habitat analyses performed separately with the data from summer and autumn months, respectively.

The 100% minimum convex polygon was calculated using all animal locations, thus also including outlying fixes in the margins of the area utilised by an animal. The 100% MCP overestimates the home-range size, but is useful to border an area that is potentially usable for an animal. When 5% of outlying fixes furthest from the arithmetic mean position of all fixes were excluded, the 95% MCP was formed. Finally, the harmonic mean estimate of the home range area was calculated. The 95% MCP and 95% harmonic mean are common methods of estimating an animal's home range (Fridell & Litvaitis 1991, Witt 1992).

By clustering fixes based on their nearest-neighbour distances, I calculated three distribution categories from the summer data set. First, by including 80% of the fixes, I defined core areas of home-range utilisation distribution. Second, the 95% cluster area was calculated. The 95% cluster and the 95% MCP differ from each other: the 95% MCP is a uniform area where only outliers have been left outside, whereas the 95% cluster may consist of several patches depending on the distances between fixes. Third, all fixes were included to form a 100% minimum convex polygon (see above). Definition of the 80% cluster as a core area is based on the shape of the utilisation distribution curve (Fig. 1). If fixes are clumped, i.e., animal locations are concentrated in one or several separate patches, the clustering technique produces a utilisation-distribution curve with a discontinuity point. In these data, at the point of 80% utilisation, the slope of the curve steeply rises and the standard deviation increases (see Fig. 1).

In the summer data, I define 80% core areas, 95% cluster areas (excluding 80% core areas) and 100% MCP (excluding both 80% and 95% areas) as home-range utilisation classes. They indicate preferred areas of high-frequency use, areas of low-frequency use and areas of only marginal use, respectively. In the autumn data the number of fixes was too low (<30 fixes, see Kenward & Hodder 1996) to cluster fixes to form the same usage classes as in the summer data. Only 100% MCP and 95% cluster areas were calculated. In any case the number of fixes was too small to calculate any reliable home-range sizes in autumn and I only use autumn locations to calculate the whole home-range area and to depict the area in which animals were active during autumn. To quantify the scale of movements I calculated the distance of the nocturnal location to the nest known to be used for nesting or diurnal roosting by the focal squirrel.

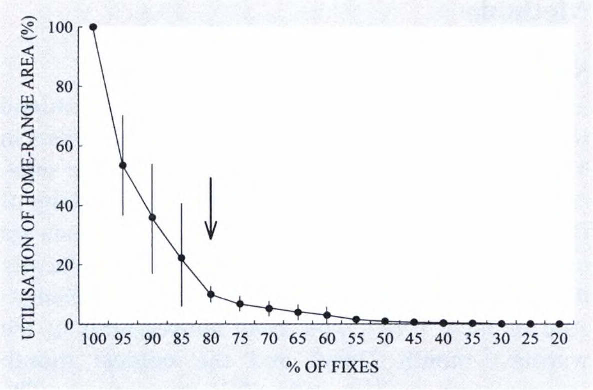

Figure 1. Utilisation distribution of the flying-squirrel home ranges (N = 8). Black dot = mean, vertical bar = ± SD, the arrow indicates the discontinuity point where the core area (80% utilisation) was selected.

Habitat analyses

On the basis of summer data, the habitat structure was measured within three utilisation classes of the home ranges: 1) within the 80% core area, 2) within the 95% cluster area excluding core areas, and 3) within the 100% minimum convex polygon excluding both 80% and 95% areas; on the basis of autumn data habitat structure was measured within the 95% cluster. Habitat description was done by measuring vegetation structure in randomly selected, 10-m radius plots (314 m^2) set up in each utilisation category. When setting up sampling plots, the coordinates of the mid point of the plot were calculated by the random number generator. Within each plot, I measured the following vegetation variables: the number of live and dead trees, the size of six tree species (pine, spruce, birch, aspen, alder and other deciduous trees) by four size categories defined according to diameter at breast height (dbh) ('small': 5-10 cm, 'medium': 10-20 cm, 'large': 20-45 cm, 'very large': >45 cm), the number of deciduous and coniferous shrubs (<5 cm dbh), tree height, canopy cover estimated from five points with 10% resolution, and the number of trees with cavities.

Depending on the individual squirrel, the areas of different utilisation classes varied in size (see Table 1 and Fig. 2), which influenced my vegetation-sampling design. In the 80% and 95% areas, I set up one vegetation-sampling plot/0.2 ha, so that when, for example, the 80% area consisted of separate patches which were smaller than 0.2 ha, each patch received at least one sampling plot. I did not set up sampling plots in open area or low sapling stands which are entirely useless for the flying squirrel, and if the area was large, I restricted the total number of plots to the maximum of 15 per utilisation class. Depending on the squirrel, the number of sampling plots was 4-8 in the 80% core, 4-10 in the 95% cluster and 4-15 in the 100% MCP area.

In the habitat data, there were only a few trees in some tree-size categories. Therefore, I combined: 1) 'large' and 'very large' trees in all tree species; 2) 'medium' and 'large' alders; and 3) all other deciduous trees to a single size class, respectively. In vegetation sampling plots I found only 33 dead trees (>20 cm dbh) among 3,719 live trees (0.9%) and only two trees with cavities. They were omitted from the analyses. As a measure of canopy cover, the mean of five cover estimates was used. From the remaining 19 habitat variables (shown in Fig. 4), I calculated mean values for each home-range utilisation class and these were used in the statistical tests.

Statistics

The habitat data were analysed: 1) univariately by comparing single habitat variables among home-range utilisation classes by non-parametric Friedman one-way ANOVA for dependent samples, and 2) by calculating the stepwise polychotomous logistic regression model (PLR). The polychotomous logistic regression allows an ordered categorical variable as a dependent variable. The categories of the dependent variable can be ranked in order, in my case the habitat-utilisation classes were ranked according to the intensity of their use (the core area was given the highest rank, i = 3, and the 100% MCP the lowest, i = 1) and were explained by independent habitat variables. I used the following habitat variables: density (trees/sampling plot) of pines, spruces, birches, aspens and alders with a dhb of more than 10 cm, tree height (m), density of deciduous and coniferous shrubs and canopy cover (arcsin-transformed percentage values). The PLR models the probability that a site belongs to the utilisation class i as a function of the vegetation measurements of the area (for a detailed description of the structure of the PLR model, see Leinonen & Rita 1995). The PLR does not make any assumptions about the multivariate distributions of the independent variables (for details of the method and its use in radiotelemetry and habitat data, see North & Reynolds 1996). The parameters of the polychotomous logistic regression model were calculated by BMDP statistical software (procedure PR; Dixon 1993).

Results

The location data of flying squirrels were analysed first, by combining all fixes from the entire tracking period and second, separately for the summer (June - August) and autumn (September - December) data sets. The number of fixes obtained per radio-tagged animal outside the nest was 28-41 in the summer and 15-20 in the autumn data sets (Table 1) and for the

Table 1. Home-range size (ha) of eight adult flying squirrels from June to December 1996, and during summer (June - August) and autumn (September - December). Number of fixes = number of night-time locations, 100% MCP = area of minimum convex polygon including all fixes, 95% MCP = area including 95% of fixes. 95% cluster = cluster area that includes 95% of fixes, 80% cluster = core area that includes 80% of fixes. Note that the autumn fixes are missing for squirrel no 472.

		Home-range size (ha) June - December				Summer home-range size (ha) June - August				Autumn home-range size (ha) September - December		
Squirrel no	Sex	Number of fixes	100% MCP	95% MCP	95% Harmonic mean	Number of fixes	100% MCP	95% cluster	80% cluster	Number of fixes	100% MCP	95% cluster
551	♂	48	14.0	13.9	16.7	33	14.0	5.1	1.03	15	0.6	0.14
322	♂	51	16.6	15.0	14.2	31	13.8	4.3	1.32	20	10.6	4.9
362	♂	51	3.8	2.4	2.8	34	3.4	2.1	0.13	17	1.2	0.3
571	♂	46	3.5	3.0	3.8	28	3.1	2.4	0.42	18	1.0	1.0
462	♀	53	5.6	4.6	5.5	37	5.1	1.1	0.39	16	2.3	0.7
472	♀	41	4.6	4.1	5	41	4.6	1.0	0.14	-	-	-
447	♀	58	4.0	3.4	4.2	39	3.1	0.9	0.18	19	1.5	0.9
301	♀	57	3.0	2.1	3	41	3.0	1.7	0.36	16	1.0	0.7
Mean ± SD			6.9 ± 5.3	6.1 ± 5.2	6.9 ± 5.4		6.3 ± 4.8	2.3 ± 1.6	0.50 ± 0.44		2.6 ± 3.6	1.2 ± 1.6

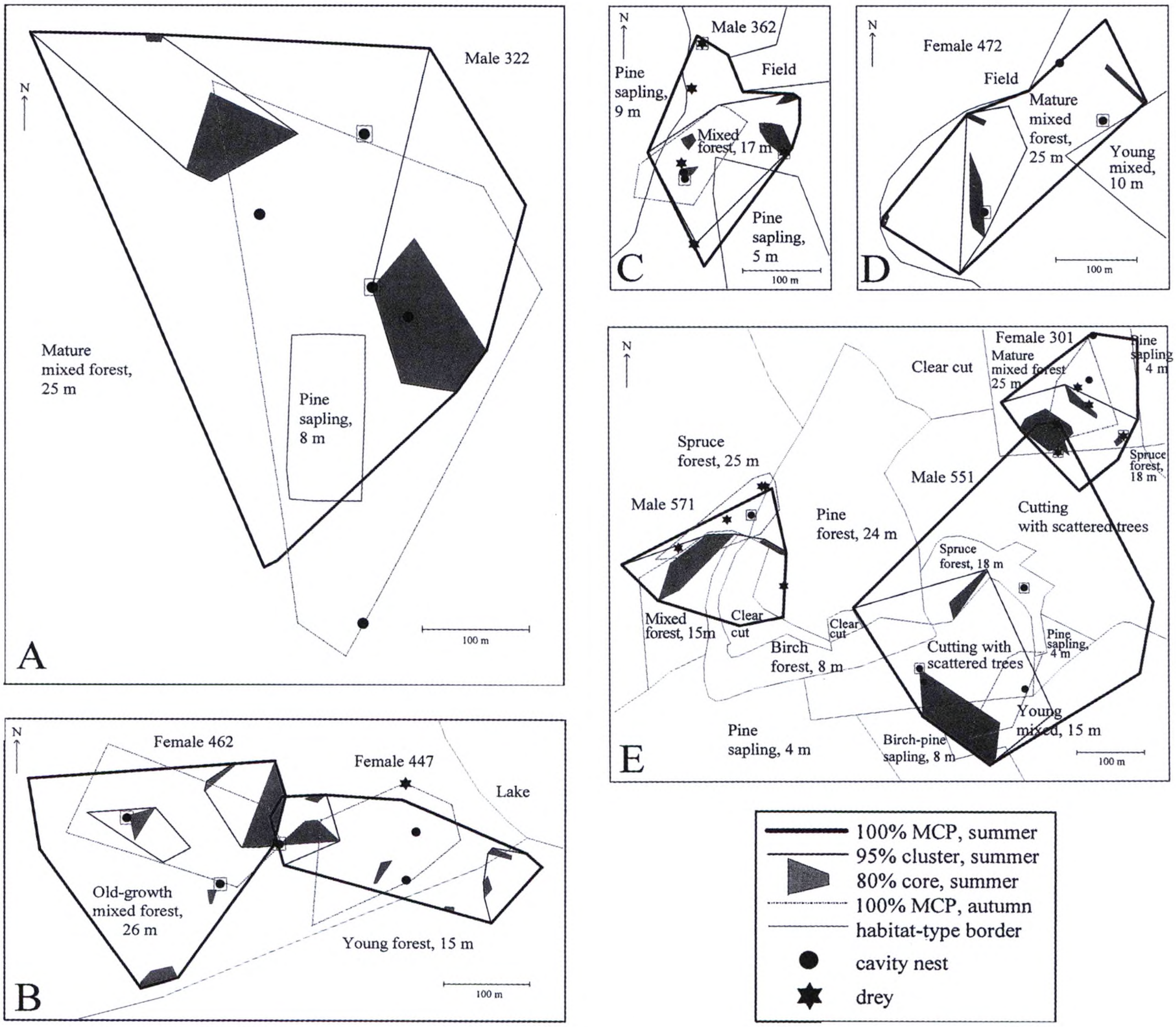

Figure 2. Home-range maps of eight flying squirrels. The sub-figures A-E depict separate tracking areas and indicate the location of home ranges in relation to forest cover type. The borders of the cover types are indicated by thin lines and the mean height (m) and type of the cover are given. Home-range boundaries were not drawn across fields. An open square around a nest symbol indicates that the nest was used >90% of time during summer.

combined data 41-58 fixes per squirrel (see Table 1). There was no significant correlation between the number of fixes and 95% MCP ($r = -0.132$, $N = 8$).

During daylight hours in summer flying squirrels were encountered outside their dens only twice out of 92 checks. At night they were in their dens 38 times out of 322 (12%) in summer and 91 times out of 212 (43%) in autumn. When squirrels were outside their nests at night, they were encountered in trees in all cases ($N = 405$ fixes) and when seen, they were foraging on leaves.

Home ranges

Home-range sizes of flying squirrels measured by the 100% minimum convex polygons ranged from 3.0 to 16.6 ha and sizes of the 95% MCP from 2.1 to 15.0 ha (see Table 1). The home ranges of the 95% harmonic mean were 2.8-16.7 ha (see Table 1). In summer the 95% cluster areas ranged from 0.9 to 5.1 ha and the 80% core areas from 0.13 to 1.32 ha (see Table 1). The core areas represented 3.0-13.5% (mean 7.8 ± 3.7%) of the 100% MCP area. The core area of a squirrel's home range was not a uniform patch, but instead, depending on the individual, was composed of 2-6 separate patches (Fig. 2). Similarly, the 95% cluster areas were not always uniform either.

Males seemed to have slightly larger home ranges (mean of 95% MCP area 8.6 ± 6.9 ha in males and 3.6 ± 1.1 ha in females), but the difference was not statistically significant due to large individual variation and small sample size (Mann-Whitney, U = 10.0, $N_1 = 4$, $N_2 = 4$, P = 0.343). So far, the sample sizes are too small to study variation in home-range size among individuals, sexes, study sites or habitats.

During the tracking period from June to December radio-tagged animals used several nests for breeding and/or roosting (Table 2, see Fig. 2). All individuals used old woodpecker cavities in aspens and five out of eight squirrels additionally used dreys in coniferous trees. All but one of the dreys were in spruces. It is not known whether flying squirrels construct their dreys themselves or whether they only use old red squirrel *Sciurus vulgaris* dreys. One anecdotal observation indicates that they may build their own nests. Squirrel no 362 was seen beside a small drey and two days later the nest had grown bigger, apparently extended by the flying squirrel. Of the summer nests, eight were located in the 80% core area or very near it, one in the 95% cluster area and six in the 100% MCP (see Fig. 2). Only one squirrel (no 571) used dreys in winter, i.e. from October onwards.

When outside the nest, the flying squirrels were, on average, 112 m (range 0-326 m) from the nest in summer and 81 m (range 0-428 m) in autumn (see Table 2, Fig. 3). Zero distance means that the squirrel was in the foliage of the nest tree. Exceptionally, male no 322 was once found 1.5 km from his den at night, but by the next day he had returned to his den. This case was omitted from all tests. On average, flying squirrels moved significantly longer distances from their dens in summer than in autumn (Wilcoxon signed ranks test, T = 0, N = 7, P = 0.0078; see Table 2 and Fig. 3).

Table 2. Number of nests used by flying squirrels in June - December (number of nests used in summer is given in parenthesis) and mean distances (m ± SD) of nightly locations from nest during summer (June - August) and autumn (September - December).

Squirrel no	No of cavity nest	No of dreys	Mean distance (m ± SD) Summer	Mean distance (m ± SD) Autumn
551	4 (2)	1 (1)	93 ± 91	72 ± 21
322	5 (2)	0	195 ± 62	145 ± 108
362	2 (1)	5 (3)	92 ± 68	61 ± 30
571	1 (1)	5 (1)	124 ± 42	67 ± 55
462	3 (2)	0	112 ± 62	83 ± 57
472	3 (3)	0	101 ± 55	-
447	3 (1)	1 (-)	131 ± 97	74 ± 38
301	2 (1)	4 (2)	64 ± 52	45 ± 39
Mean	2.9 (1.6)	2.3 (1.0)	112 ± 77	81 ± 66

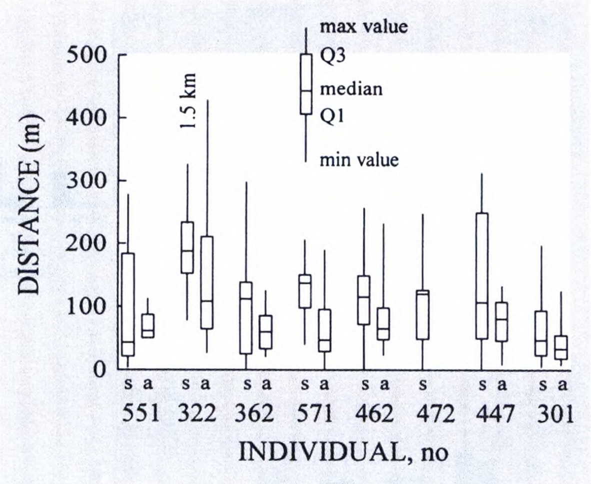

Figure 3. Distances (m) of nocturnal locations of the eight flying squirrels from their nests in summer (s) and autumn (a). The bars indicate minimum values, lower quartiles, medians, upper quartiles and maximum values.

I qualitatively examined the location of home ranges in heterogeneous forest landscapes. Five out of eight squirrels included several cover types, not only mature forests, in their home ranges (see Fig. 2). Most of the animals had their nest sites in mature forest patches but partly foraged and had part of their 80% core areas in young or semi-open stands. Male no 362 was permanently living in a 17-m high, mixed forest stand. One nest tree was located in an open area with scattered trees. Squirrels were found 23 times in trees in semi-open stands, 20 times in young forests ≤15 m high and 6 times in pine sapling stands ≤9 m high. The rest of locations (356) were in 17-28 m high forest stands.

Habitat use

In the habitat analyses, I first tested single habitat variables among utilisation classes in summer and in autumn. None of the measured tree or shrub variables nor tree height differed significantly among the home-range utilisation classes (Friedman one-way ANOVA for dependent samples, P-values of tests varied from 0.085 to 0.930; Fig. 4). I combined all deciduous tree species with a dbh of more than 10 cm

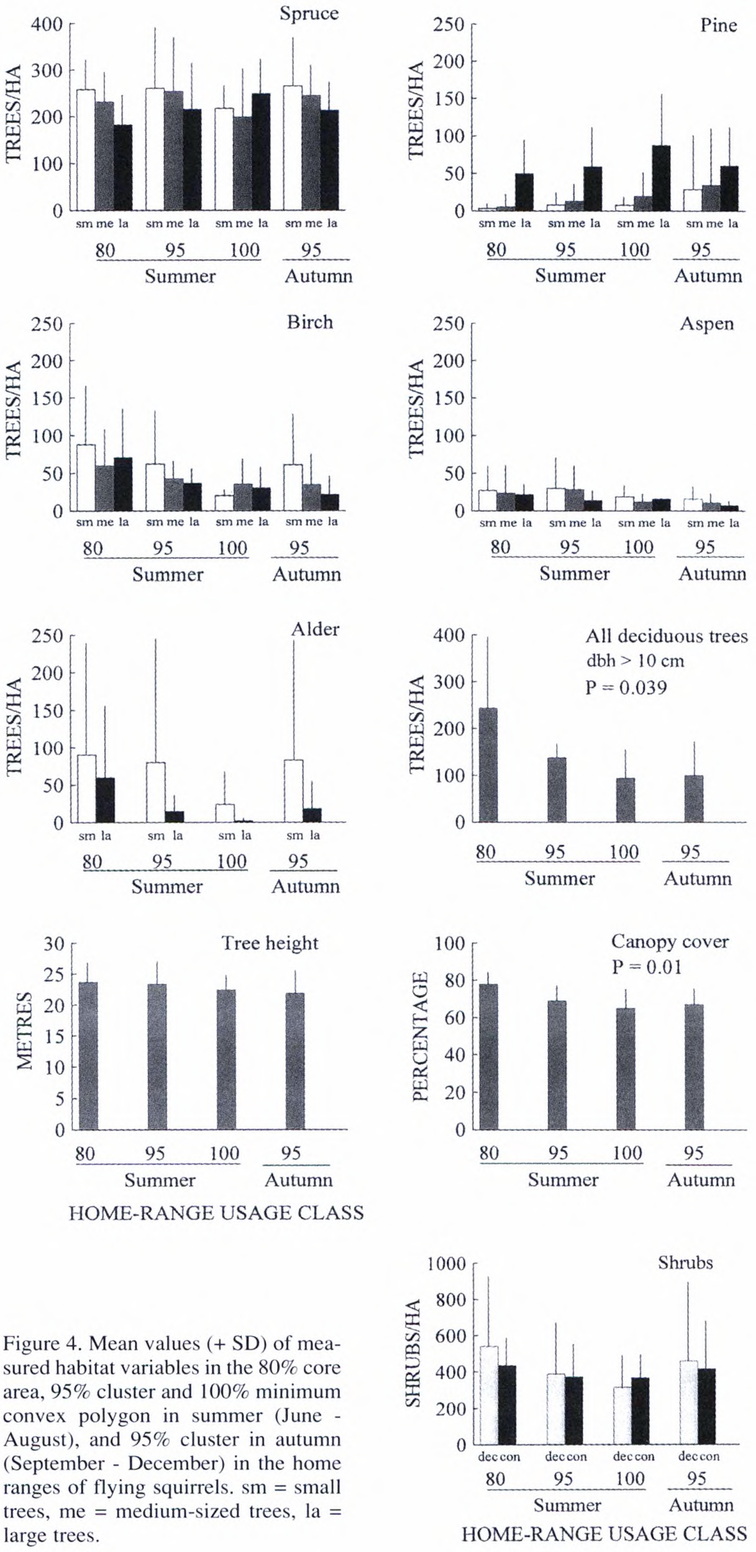

Figure 4. Mean values (+ SD) of measured habitat variables in the 80% core area, 95% cluster and 100% minimum convex polygon in summer (June - August), and 95% cluster in autumn (September - December) in the home ranges of flying squirrels. sm = small trees, me = medium-sized trees, la = large trees.

to form a single variable. In the summer data set, the amount of all deciduous trees differed significantly among usage classes (Friedman, χ^2 = 8.31, df = 2, P = 0.016): in 80% core areas there were more deciduous trees/ha than in 100% MCPs (nonparametric, *a posteriori* pairwise comparison between groups, P < 0.05, see Fig. 4). When adding the autumn sample to the test the result was significant (χ^2 = 8.014, df = 3, P = 0.046), but there were no significant differences in *a posteriori* comparisons. The second variable that differed among classes was the tree-canopy cover (χ^2 = 9.75, df = 3, P = 0.008; see Fig. 4). In pairwise comparisons, the 80% core area differed significantly from the 95% cluster, the 100% MCP, and the autumn area. The denser canopy cover in the core area can be explained by a significant correlation (r = 0.549, df = 22, P < 0.01) between cover and total number of deciduous trees in summer.

In the polychotomous logistic regression model the canopy cover and the density of alders and aspen significantly explained the habitat-utilisation rank (i = 3-1; 3 = 80% core area, 2 = 95% cluster, 1 = 100% MCP; Table 3). The regression coefficients were negative indicating that the values of canopy cover and densities of alders and aspen were lower along the rank in the utilisation classes (see Table 3), i.e. densities were highest in the 80% core areas, second highest in the 95% clusters and lowest in the 100% MCP areas. In the model, the cumulative probability that a randomly selected site falls in the utilisation class i is denoted by $\gamma_i(x)$. The cumulative probabilities were transformed into the logistic scale and modelled using linear regression:

Table 3. Parameter estimates of the stepwise polychotomous logistic regression model and likelihood-ratio χ^2-tests. Negative values of regression coefficients indicate the tendency of decreasing values of explaining variables from highly used areas to least used areas (core - 95% cluster - 100% MCP) of the utilisation classes.

		Likelihood-ratio test		
Parameter	Coefficient	df	χ^2	P
α_1	11.97			
α_2	9.547			
β_1 Canopy cover	-11.230	1	7.756	0.0054
β_2 Alder	-1.676	1	6.702	0.0096
β_3 Aspen	-1.049	1	4.089	0.0432

$$\log\left(\frac{\gamma_i(x)}{1-\gamma_i(x)}\right) = \alpha_1 + \alpha_2 - \beta_1(\text{canopy cover}) - \beta_2(\text{alder}) - \beta_3(\text{aspen})$$

where i = 3, 2, 1, α_1 and α_2 are constants and β_1, β_2 and β_3 coefficients of significant habitat variables.

I compared the distribution of trees with a dbh of more than 10 cm used by flying squirrels with the abundance distribution of the same species available within the 80% core areas of home ranges. First, I compared the three most abundant deciduous tree species (birch, aspen, alder). These species constituted 87% of the trees used by squirrels in summer and 46% in autumn. In the summer, the tree-species distribution used differed significantly from the distribution of available trees ($\chi^2 = 9.28$, df = 2, P = 0.0096; Fig. 5A). Flying squirrels were found in aspens more often than was expected according to their availability in the 80% core areas. In addition, squirrels were found 20 times (12%) in spruces but only once in a pine. In the autumn data set, the corresponding test was done by comparing the distribution of deciduous trees used with the trees available within the area of 95% clusters (Fig. 5B). The difference was significant ($\chi^2 = 15.93$, df = 2, P = 0.012), but this time aspens were used less and birches more often than expected. In autumn, however, squirrels were more often found in spruces and pines, 29 (31%) and 21 (22%) times, respectively. When pine was included in the test, the result remained significant ($\chi^2 = 12.84$, df = 3, P = 0.016; see Fig. 5B). Spruce was not included in the tests because of its superior dominance in all home ranges.

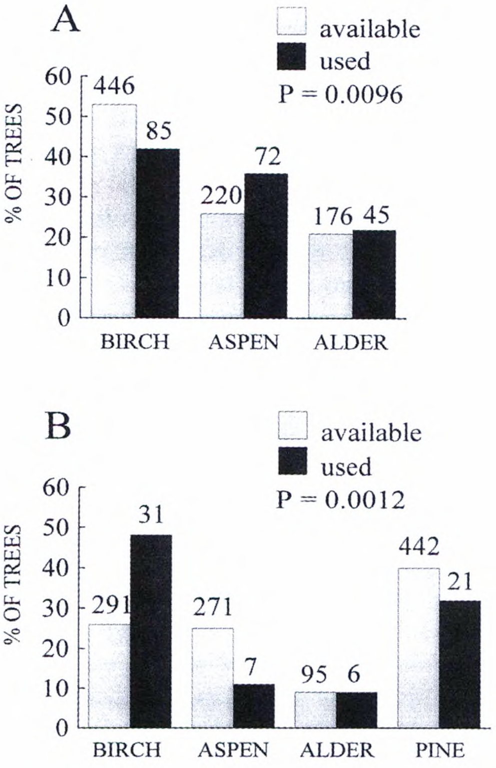

Figure 5. Three most abundant deciduous trees (birch, aspen, alder) used by flying squirrels and the availability of deciduous trees >10 cm dbh, in the 80% core areas in summer, A. The same trees and pine in the 95% cluster areas in autumn, B. Numbers indicate the actual number of trees.

Discussion

Home ranges and movements

Home-range sizes of flying squirrels measured by the 100% minimum convex polygons ranged from 2.2 to 14.7 ha. However, squirrels concentrated their activities on small patches (80% core areas) which represented on average only 7.8% of the 100% MCP area. Home ranges of the Eurasian flying squirrel were fairly equal in size or larger than the home ranges of the North American sister species. Fridell & Litvaitis (1991) reported the 95% MCP home ranges of the southern flying squirrel *Glaucomys volans* to be on average 9.9 ha in males and 3.4 ha in females. Corresponding areas calculated by the harmonic mean method were 16.0 and 7.2 ha. In the northern flying squirrel *G. sabrinus* the minimum convex polygons were on average 3.7 ha (range 3.4-4.2 ha) (Witt 1992). Furthermore, the home ranges of the Eurasian flying squirrel were much smaller than those of the Eurasian red squirrel *Sciurus vulgaris*. Andrén & Delin (1994) reported mean areas of 121.6 ha in males and 23.0 ha in females in Swedish coniferous forests. However, home-range sizes of mammals may vary remarkably even within the same species in different geographical areas, landscapes and habitat types (in Eurasian red squirrel; see Andrén & Delin 1994, Wauters, Casale & Dhondt 1994, Delin 1996) or depending on the time of season or amount of food resources (e.g. Fridell & Litvaitis 1991, Lovari, Valier & Ricci Lucci 1994, Sheperd & Swihart 1995, Powell, Zimmerman & Seaman 1997).

Before my study nothing was known about the distances that flying squirrels move at night from their nests or diurnal roosting sites. It is evident that they are able to move fairly long distances. However, the landscape structure, for example forest fragmentation, may restrict their movements. At present it is not known if they are able to cross large open areas or low sapling stands from one forest patch to another, but at least they can use semi-open areas if there are scattered trees. Flying squirrels can glide more than 60 m (pers. obs.) and do not seem to avoid semi-open areas. They were seen foraging in, and moving across, cut areas with scattered trees. Males nos 551 and 571 regularly foraged in single trees that were left standing in the cut area (see Fig. 2E) and female no 447, who was nesting in an old-growth, mixed forest, regularly moved to forage in a young, thinned stand nearby (see Fig. 2B). Similarly, male no 362 foraged in pine plantations in the autumn (see Fig. 2C). The shorter distances moved in autumn may reflect reduced activity during autumn and winter, and use of food stores. Several mammal species have been reported to maintain smaller home ranges in autumn and winter than during summer (e.g. Slade & Swihart 1983, Sheperd & Swihart 1995) or to reduce their activities when ambient temperatures are low (e.g. Doebel & McGinnes 1974).

At present it is not known how flying squirrels perceive the landscape in the scale of a local population. Data on movements between isolated forest patches or on juvenile dispersal are lacking. However, at the home-range scale, the flying squirrel seems to view the landscape as fine-grained. Levins (1968) defined an environment to be fine-grained if an animal encounters several habitat types in its lifetime and is able to wander among habitat patches in a heterogeneous environment. Although preferring forests (but not only mature forests), the flying squirrels used and included several other cover types in their home ranges. Furthermore, several cover-type patches were found within the scale of the observed nightly movements (300-400 m) of the flying squirrels from the nest. The mean home-range size (6.3 ha) coincides well with the mean patch size of forests >17 m high (8.4 ha) and young forests (7.7 ha) in the area (I. Hanski, unpubl. data). The definition of the grain size I used differs from that of Addicott, Aho, Antolin, Padilla, Richardson & Soluk (1987), who stated that if an animal in a heterogeneous environment utilises different patch types randomly, i.e. utilises different habitat types in proportion to their availability, the response of an animal is fine grained. Note that recently there have been discussions on the different definitions and the use of grain size in ecology (Norton & Lord 1990, Wiens 1990).

Home-range and habitat use

Studies on other species of flying squirrels have revealed activity nuclei within home ranges (Baba, Doi & Ono 1982, Bendel & Gates 1987, Fridell & Litvaitis 1991, Witt 1992). However, the definition of the core area differs among studies. Each 25-m square in the study area containing more than 10% of fixes was defined as a core area in the giant flying squirrel *Petaurista leucogenys* (Baba et al. 1982), the area containing 35% of fixes by Bendel & Gates (1987) and on average 36.9% in Fridell & Litvaitis (1991) for the southern flying squirrel, and 50% in the fox squirrel *Sciurus niger* (Sheperd & Swihart 1995). In my study the flying squirrels concentrated a great majority of their activity (80%) in small parts of their home ranges.

An animal can concentrate its activities to particular patches for various reasons: 1) high-activity or preferred areas may have abundant food resources (e.g. Baba et al. 1982, Andrén 1990, Powell 1994, Powell et al. 1997); 2) those areas may have more nest sites or shelter for example from predators (e.g. Bendel & Gates 1987, Andrén 1990, Powell et al. 1997). It is highly unlikely that the preference for the core areas found in my study should have any relation to mating behaviour because the study was carried out almost entirely outside the mating period of the flying squirrel (Ognev 1966, Mäkelä 1996).

The core areas did not have more nest sites, i.e. cavities, than the rest of the home range; only a few nests were located in the middle of the core area, more were located on the edges of the core area, and half of the nests were located outside the core area. Altogether the density of cavity trees is very low in managed forests in southern Finland, which may restrict the nest-site choice of flying squirrels.

If the probability of encountering predators is lower in the core areas, for example due to better cover, I would have expected the vegetation volume to be higher in the core areas than in the other parts of the home range. This could be a result of the higher density of medium-sized and large spruces (e.g. Andrén 1990) and/or increased tree height. However, this was not the case. The density of spruces or tree height did not differ between the utilisation classes. The only supporting evidence was a denser canopy cover in the core area than in the 100% MCP area, and that the canopy cover was a significant explaining variable in the PLR model. However, this may be equally well explained by the significant correlation between the cover and the total number of deciduous trees in summer. The correlation between cover and spruces ('medium' and 'large' spruces combined) was not significant ($r = 0.207$, $df = 22$, $P > 0.05$). Another aspect against the cover-preference hypothesis is the observed smaller canopy cover (measured after leaf fall) in the autumn areas.

Within the core areas used in summer the combined density of deciduous trees (birches, aspen, alders) was higher than in the 100% MCP area, but there were no significant differences in single tree or other habitat variables among the home-range utilisation classes. However, in the polychotomous logistic regression model the canopy cover and the densities of alders and aspens were significant in explaining the ranked utilisation classes. In summer, the flying squirrels foraged almost exclusively in deciduous trees with a preference for aspen, but in autumn they also used coniferous trees. Hence, the most plausible explanation is that the flying squirrels concentrated their activities in the areas where summer food, especially the densities of alder and aspen, was abundant. However, in addition to providing food, deciduous foliage may offer cover for a foraging squirrel in summer, and therefore, in these data, the cover hypothesis cannot be totally ruled out.

The division of the tracking data into summer and autumn data sets was artificial but the cutpoint at the end of August coincided well with the time when deciduous trees started to lose their chlorophyll and turn yellow simultaneously losing their nutritional value. My habitat-use results show differences in tree-species use between summer and autumn and may indicate a change from summer-time leaf diet to autumn catkin and bud diet (Mäkelä 1996). In autumn, the use of aspen (preferred food in summer) was less frequent, whereas the use of birch and pine was more frequent than expected.

The fact that flying squirrels concentrated their activities in small core areas does not mean that other parts of the home range are useless. Half of the summer nests and most of the autumn nests were located outside the core areas. However, this may reflect the nest-site choice of woodpeckers rather than that of the flying squirrel, and in fact, in managed forests cavity trees are so few that flying squirrels are forced to use virtually all cavities irrespective of their location. One explanation for the observed separate foraging patches might be that squirrels prefer to forage far from a nest to conceal its location from predators, but no data to support this explanation are yet available.

During the tracking period all flying squirrels changed their nesting sites. Although empirical evidence is lacking, the site changes may reduce the number of ectoparasites or make prey searching by predators more difficult. Apparently, diurnal roosting in cavities is energetically advantageous compared to roosting in dreys and this may be the reason why most squirrels were roosting in cavities from October onwards. Both ectoparasite, predator and energetic explanations may hold true, because flying squirrels had several nests which they used regularly in both cold (Baba et al. 1982) and warm seasons of the year (Bendel & Gates 1987). Giant flying squirrels used dreys only in summer, not in the cold winter (Baba et al. 1982).

Forest management implications

The results show a clear preference by flying squirrels for deciduous trees, especially the use of aspen in summer and alder and aspen explaining significantly the rank of utilisation classes. In autumn, the flying squirrels also used coniferous trees. Therefore, a prominent mixture of deciduous trees in the coniferous taiga is an essential feature of the flying-squirrel habitat. During recent decades, forest management practices have favoured spruce or pine monocultures (Järvinen et al. 1977, Heliövaara & Väisänen 1984), which alone do not fulfil the habitat requirements of the flying squirrel. The second important feature is the presence of cavities. Although most of the radio-tagged squirrels used dreys as nesting and/or roosting sites, all squirrels regularly used cavities in aspens. The tree cavity may be a safer nest site for young than a drey. The results show that the flying squirrels almost exclusively used cavities in winter. This may indicate that the cavity provides better protection against adverse weather conditions than a drey. In Finland the selective cutting of aspens in forests as a tree species of low economic value and as a host of a fungal disease of the Scots pine has probably had detrimental effects on the flying squirrel.

As an arboreal mammal, the flying squirrel apparently suffers when areas are clear cut. The size requirements of the home range may prevent the flying squirrel from occupying small, isolated forest stands. At present, in my study area the forests are heavily managed and the mean size of a forest stand is very close to the mean home-range size of the flying squirrel (8.4 ha vs 6.3 ha, respectively).

However, although mostly utilising mature stands, the flying squirrel seems to be capable of using several cover types, including young forest stands, as foraging and moving areas and is able to move across semi-open cutting areas if trees are left standing at some 10-metre intervals. However, at present it is not known if flying squirrels are able to cross stands of low saplings or colonise isolated forest patches. Mature forest stands large enough to fulfil the size requirements of the home range together with a fine-grained mosaic of cover types of different age and tree-species composition may maintain the home-range requirements of a single flying squirrel. However, the dynamics of local subpopulations, the interactions of individuals between them and natal dispersal of flying squirrels need to be studied further.

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