

# Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests

Vesa Selonen and Ilpo K. Hanski

Department of Ecology and Systematics, P.O. Box 65, FIN-00014 University of Helsinki, Finland

Dispersal is a key determinant of the population dynamics of species. Thus, a better understanding of how dispersal is affected by the landscape structure and how animals make decisions about moving across different landscapes is needed. We studied the dispersal of 60 radio-collared juvenile Siberian flying squirrels (*Pteromys volans*) in southern Finland. The effect of landscape structure on selected dispersal direction, dispersal distance, and straightness of dispersal path was studied. Flying squirrels were capable of dispersing over long distances in fragmented forest landscapes. The patches used as temporary roosting sites during dispersal were of a lower quality than were those used as finally occupied patches. The patches used were larger than were patches on average in the study areas. There was a very clear directional bias in the dispersal path (i.e., it was nearly a straight line), which remained over a large scale, but wide-open areas obstructed the straightness of the path. As the distances between crossed patches increased, short-distance dispersers were found further away from their natal home range. However, there were no differences in the landscape that could explain the differences between individuals in decisions to remain philopatric or to become short- or long-distance dispersers. In addition, whereas short-distance dispersers dispersed in random directions, long-distance dispersers started to disperse in directions dominated by preferred habitat. Thus, there were behavioral differences between dispersers. Our results supported the hypotheses stating that individuals decide to disperse long or short distances before the onset of dispersal. **Key words:** dispersal path, dispersal direction, fragmentation, landscape structure, *Pteromys volans*, radio tracking, short- and long-distance. [*Behav Ecol* 15:564–571 (2004)]

In theories of spatial ecology, dispersal is a key determinant of the population dynamics of species (Hanski and Simberloff, 1997; Ims, 1995; Merriam, 1984). However, empirical work on dispersal and movement is imperfect, and for mammals such work has concentrated on small rodents such as voles (Bowers, 1997; Krohne, 1997; Stenseth and Lidicker, 1992). A better understanding of what causes an individual to become a disperser and how movements are affected by the landscape structure is needed (Dunning et al., 1992; Stenseth and Lidicker, 1992; Wiens et al., 1993). Moreover, it is largely unknown whether habitat selection is similar for breeding and dispersing individuals (Harrison, 1992).

Landscapes contain several different features that influence how animals can move (Ims, 1995; Wiens et al., 1993). Patch size and shape, the nature of the matrix habitat, and changes in landscape heterogeneity can affect path direction and colonization success (Gustafson and Gardner, 1996; Ims, 1995; Stamps et al., 1987). Connectivity of the landscape is thought to be one of the most important features affecting patch colonization (Taylor et al., 1993). One important aspect is patch edge permeability, as movement may be more obstructed through some edges than others (Haddad, 1999; Stamps et al., 1987; Wiens et al., 1997). Highly mobile animals may perceive landscape patchiness at different scales than do more sedentary animals by responding in a less-sensitive manner to patch edges (Kolasa and Rollo, 1991).

The effect of landscape structure on species' movements also depends on the mobility of the species in the habitats between patches (i.e., matrix) (Andrén, 1994). What ultimately influences colonization success is the scale of movement of an organism relative to the scale of patchiness (Fahrig and Paloheimo, 1988; With and King, 1999). Thus, the movements of an individual determine the scale at which

patchiness and spatial heterogeneity affect a species (Fahrig and Paloheimo, 1988).

A few empirical studies have shown that large-scale movements are often nearly straight paths (Bascompte and Vilà, 1997; Duvall and Schuett, 1997; Pastor et al., 1997), and in models nearly straight paths have been found to be the most successful for large-scale search (Zollner and Lima, 1999). However, the movement of an organism is usually modeled as a simple or correlated random walk based on movements in grid cells (see Turchin, 1998 and the references therein). The rules of the walk are rarely supported empirically, and it has been concluded that studies on movement and landscape structure should be based on empirical knowledge about the movement of an organism through a landscape (Tischendorf and Fahrig, 2000).

In this article, we study the natal dispersal of radiotagged Siberian flying squirrels (*Pteromys volans*) in heterogeneous forest landscapes. We investigate (1) whether young flying squirrels select their dispersal direction based on the structure of the forest landscape, (2) whether landscape structure affects movement during dispersal, and (3) the habitat structure of sites occupied after dispersal. To our knowledge, this is first animal study on natal dispersal in which the details of the dispersal path and the effects of landscape structure on the dispersal path are studied with sample sizes that enable statistical testing.

## METHODS

### Study species

The Siberian flying squirrel is a nocturnal arboreal rodent, which nests in tree cavities, twig dreys, and nest-boxes. It inhabits spruce-dominated boreal forests from Finland to eastern Siberia and Japan (Ognev, 1966). Flying squirrels depend on big aspens as a cavity source and on deciduous trees in general as a food source (Hanski, 1998; Reunanen et al., 2002) and have been declining in Finland in recent decades (Hokkanen et al. 1982).

Address correspondence to V. Selonen. E-mail: vesa.selonen@helsinki.fi.

Received 20 December 2002; revised 16 August 2003; accepted 1 September 2003.

A flying squirrel female can have one or two litters in summer (the first in April–May and the second in June) (Mäkelä, 1996; Hanski IK and Selonen V, unpublished data). The dispersal of the juveniles differs from that of most other promiscuous or polygynous mammals, being female-biased with a fraction of males remaining philopatric. Dispersal distances are large, up to 9 km with a mean of around 2.5 km for both sexes (Hanski IK and Selonen V, unpublished data). The onset of natal dispersal takes place in the same year as birth, during the late summer. During dispersal, flying squirrels often use temporary nest sites before finally settling in a new home range. Dispersal movements occur during the night, and one move is usually done in a few hours. After one move, a disperser usually stays for one or few days in a temporary nest site, after which it makes another dispersal move, again over a single night. The dispersal period ends when the disperser occupies a patch where it finally settles for the next winter. Dispersal during the following spring is rare, and breeding dispersal has not been recorded for adult flying squirrels (Jokinen, 2000; Hanski IK and Selonen V, unpublished data).

### Study areas and data collection

The study was carried out in three areas in southern Finland in 1996–2000. Two study areas, Iitti (60°55' N, 26°30' E) and Anjalankoski (60°50' N, 26°50' E), were in managed forests owned by private landowners, and the third was in the Nuuksio National Park (60°18' N, 24°32' E). Flying squirrels in Nuuksio and Iitti nest and roost in cavities and dreys, whereas in Anjalankoski they mostly use nest-boxes.

Thirty-three juvenile male (nine in Iitti, 13 in Anjalankoski, and 11 in Nuuksio) and 27 juvenile female (seven in Iitti, 12 in Anjalankoski, and eight in Nuuksio) flying squirrels were captured from their nesting cavities or nest boxes and fitted with radio-collars (Biotrack; mass of collars was 5.3 g, which is approximately 5% of the weight of dispersing flying squirrels). Captures occurred between June and July for the first litter (53 individuals) and August and September for the second litter (seven individuals) in each year. Dispersal distances did not differ between the first and second litters, so the data were pooled (Mann Whitney *U* test,  $U = 161$ ,  $p = .58$ ). Radiotagged flying squirrels were located at night, and nest sites were located during daytime. During nocturnal tracking, each animal was recorded by walking under a single tree or a small group of trees where a flying squirrel was located. Locations were marked with flags in the forest (for more details, see Hanski, 1998), and their coordinates were obtained later with a Magellan or Alto-G12 global positioning system (GPS). During the dispersal period, flying squirrels were located approximately five times a week (both during the day and at nighttime).

By using the tracking described above, the locations of flying squirrels were recorded within their natal area, within temporary nest sites during dispersal, and within the area the squirrel finally occupied. In addition, to get information on actual movement routes, we followed flying squirrels continuously. We managed to follow five dispersing individuals and three individuals during an exploratory trip. Continuous following started after sunset and lasted 1–4 h, depending on whether the individual started to disperse. When an individual started to disperse, it was followed on foot until it stopped. The dispersal movement usually started soon after sunset (data not shown). Because the flying squirrels moved fast, the tracker was usually far behind. All the places where the animal was located were marked. To avoid unnecessary disturbance during continuous tracking, we attempted to maintain a distance of at least 30 m to the focal animal. In general, the tracking did not seem to disturb the flying squirrels (see Selonen, 2002).

### Dispersal data

Movements made during one night between the natal home range, each temporary nest place, and a new home range were classified as a dispersal move (see Turchin, 1998). The distance of each move was calculated as the distance between successive nest sites. Different moves formed the dispersal path for each individual. For every dispersal path, we used MapInfo software and the Ranges V computer package (Kenward and Hodder, 1996) to calculate the length of moves, angles between moves (according to the method of Zar, 1999), and the net distance as a sum of moves. The total dispersal distance was calculated as a straight line between the natal nest and the final occupied nest.

The movements of the eight individuals followed continuously during one night (see Data Collection) were divided into steps. These were formed from the points where individuals were located while they were moving. The move path was formed from steps in a similar way as the dispersal path was formed from dispersal moves.

We used the fractal index of Katz and George (1985) to characterize the dispersal and move paths. This is recommended for use with short radio-telemetry data sets (Bascompte and Vilà, 1997). With this method the fractal index ( $D$ ) of a path is calculated as follows:

$$D = \log(n) / [\log(n) + \log(d/L)],$$

where  $n$  is the number of steps or moves,  $L$  is the sum of the lengths of the steps or moves (i.e., the total distance), and  $d$  is the maximum straight line distance between two points. As the index  $D$  approaches one, the path approaches a straight line; the path and is a straight line when  $D = 1$ . For a random walk,  $D$  approaches two. The main advantage of this method is that  $D$  is easy to calculate and can be used with small data sets while still permitting statistical comparisons (Bascompte and Vilà, 1997). Move and dispersal paths were not assumed to be on the same scale and were treated separately (see Turchin, 1998). However, within move and dispersal data, paths were assumed to be on the same scale, as  $D$  was not correlated with the number of steps or moves or with the length of path (Spearman rank correlations, all  $p > .3$ ).  $D$  was calculated for paths with two or more steps or moves.

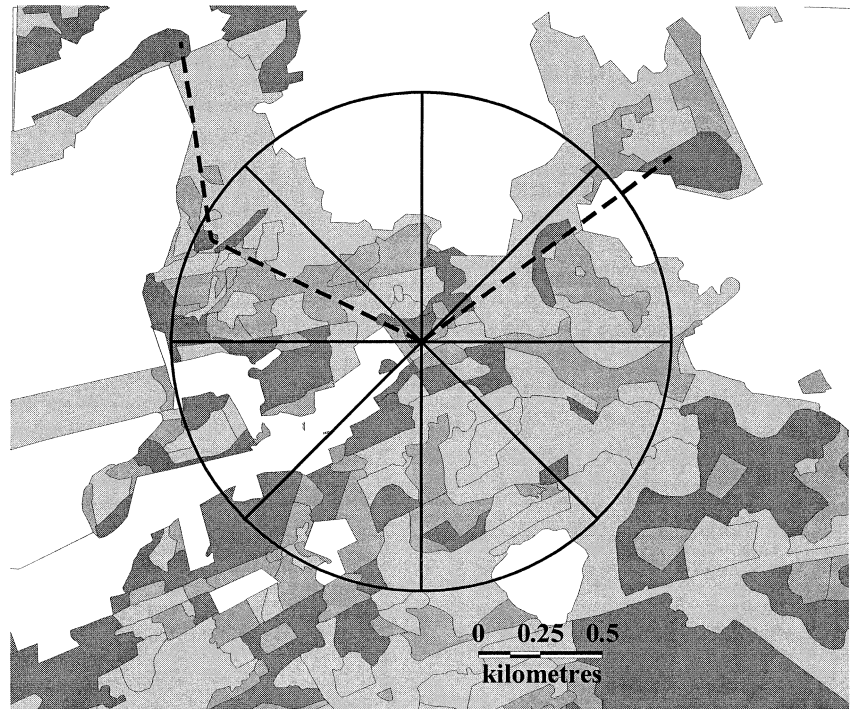
Juveniles were divided into philopatric individuals (distance moved less than 400 m from birth nest,  $n = 11$ ), short-distance dispersers (400–2500 m,  $n = 33$ ), and long-distance dispersers (more than 2500 m,  $n = 16$ ). These distances were based, respectively, on the distance at which a juvenile was outside the mother's home range (mean female home range size is 8.3 ha, thus 400 m is more than two times the radius of a circle enclosing the female home range) (Hanski et al., 2000) and the mean distance of all dispersers. Philopatric individuals were omitted from the dispersal analyses. Dispersal distances did not significantly differ between sexes (Hanski IK and Selonen V, unpublished), and sexes were evenly present in short- and long-distance dispersal categories, (two-by-two table,  $p = .55$ ). Thus, sexes were combined for the results presented.

### Landscape structure

Landscape maps from the study areas were digitized from aerial photographs by using the MapInfo software package. The sizes of the digitized areas were 71 km<sup>2</sup> in Iitti, 28 km<sup>2</sup> in Anjalankoski, and 30 km<sup>2</sup> in Nuuksio. Based on habitat use by adult flying squirrels (Selonen et al., 2001), we classified landscape elements as preferred habitat (spruce-dominated forests, and also a few small deciduous-dominated forest patches were included) and three matrix types: good movement habitat (e.g., pine forests and young forest), poor

**Figure 1**

Landscape map from the Anjalankoski study area with dispersal paths of two short-distance dispersing flying squirrels (dashed lines) and the buffer of 1-km radius divided into eight sectors around the natal nest site. Dark grey indicates preferred habitat; light grey, good movement habitat; lightest grey, poor movement habitat; and white, open areas.



movement habitat (e.g., sapling stands and pine bogs), and open areas (fields and other open areas, e.g., open bogs and lakes). Trees were 1.5–8 m high in the sapling stands and less than 15 m high in young forests.

The proportion of preferred habitat was 41.0% in Nuuksio, 20.1% in Iitti, and 20.3% in Anjalankoski. The proportion of open areas was 10.7% in Nuuksio, 22.0% in Iitti, and 26.2% in Anjalankoski (for information on other landscape elements, see Selonen et al., 2001). Although there was variation in landscape structure, the dispersal distances or straightness of the path (fractal index) did not differ between the study areas (data not shown). Therefore, the data from the different study areas were combined.

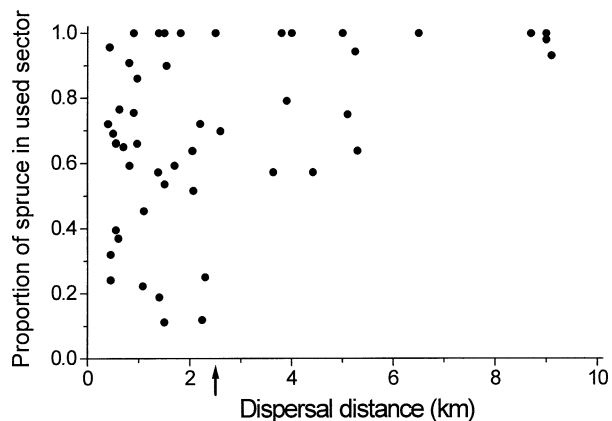
The landscapes surrounding each natal home-range area were measured by placing a buffer of 1-km radius around the natal nest site (Figure 1). The area of preferred habitat within this buffer zone described the local abundance of preferred habitat around the nest site. A radius of 1 km was selected to describe the area near the home range, which is probably larger than the area that flying squirrels can perceive. In the study of Zollner (2000), the perceptual range of individuals of three North American forest squirrel species was a few hundred meters (chipmunk, 120 m; gray squirrel, 300 m; and fox squirrel, 400 m). The perceptual range of the flying squirrel is probably at least the same and may be more, because flying squirrels spent most of their time high up in trees and not in the ground layer as the individuals in Zollner's (2000) study did. Many juveniles (mainly short-distance dispersers; data not shown) made exploratory trips before dispersal, usually of distances of less than 1 km from the birth site. Thus, many of the flying squirrels probably had some information about the landscape around their birth site before dispersal. However, within temporary home ranges, exploratory trips were usually short, rarely exceeding a few hundred meters (data not shown).

To study the direction selected for dispersal, we divided the buffer zone into eight sectors, and calculated the percentage of preferred habitat in each sector: the sector with the highest

area of preferred habitat was given a value of one, with the remaining sectors having values between 0 and 1, based on the proportion of preferred habitat calculated from the sector with the highest area of preferred habitat in the buffer zone. This abundance-corrected proportion describes how much of the preferred habitat was present in one sector compared with other sectors in that buffer. However, testing whether flying squirrels preferred some sectors to others was complicated by the fact that sectors within one buffer were not independent of each other. To test whether flying squirrels used sectors nonrandomly, the sectors were ranked according to the proportion of preferred habitat within each sector (from one, highest, to eight, lowest). The sectors were placed in the same position in all sites.

Because we had data from siblings and from several years, some of the juveniles originated from the same area, and therefore, the data derived from them were spatially correlated. Hence, to avoid nonindependence of data, we deleted all nonindependent individuals in each dispersal category from the buffer and sector analyses above (two philopatric, eight short-distance dispersers). Omitting these individuals did not change the results (data not shown). However, nonindependent individuals dispersed in different directions and colonized different patches. Thus, all individuals were used in the analyses of dispersal paths.

To describe the landscape of areas through which dispersal occurred, we drew a line following the dispersal path by using MapInfo. The distances moved in different landscape elements that the path intersected were calculated and transformed to percentage values, by dividing the distance moved in each landscape element with the total length of the path. This made paths with different lengths comparable with each other. We counted the number of patches (defined here as preferred habitat patches including a few young and deciduous forest patches that were used as temporary nest sites) that were probably crossed by a disperser. This was done by fixing the dispersal path to go through patches that were not in contact with dispersal path but were likely to have been crossed during



**Figure 2**  
Proportion of preferred habitat, as a proportion from the sector with highest area of preferred habitat in buffer, in sector used for dispersal in relation to dispersal distance of flying squirrels. The arrow indicates the point of separation between short- and long-distance dispersers.

dispersal. This fixing of the dispersal path was done based on our experience about dispersal movement (see results). In practice, depending on the landscape and move length, patches a distance up to 200 m from the path were considered as crossed. The distance between patches and the percentage of preferred habitat and open areas along the dispersal path were regressed against the dispersal distance. The percentage of open areas did not correlate with the percentage of preferred habitat ( $n = 41$ ,  $r = -.08$ ,  $p = .6$ ) or with the distance between patches ( $n = 41$ ,  $r = -.04$ ,  $p = .8$ ), but the percentage of preferred habitat correlated negatively with the distance between patches ( $n = 41$ ,  $r = -.67$ ,  $p < .001$ ). We did not separate the effects of these two correlated variables and instead analyzed these data with multiple linear regressions.

### Temporary and final patches

For 20 temporary and 22 occupied patches, we measured the size of the patch, average tree height, tree cover, and tree-species composition (using a relascope). The measures were taken near the nest site of the flying squirrel. All the measures of temporary and occupied patches were compared, and the size of these patches was compared to the size of preferred habitat patches not used in the study areas.

## RESULTS

### Natal landscape and dispersal direction

The area of preferred habitat within the 1-km buffer around natal nests did not differ between philopatric individuals, short-distance dispersers, or long-distance dispersers (philopatric:  $76.6 \pm 41.5$  ha,  $n = 9$ ; short-distance dispersers:  $78.7 \pm 35.4$  ha,  $n = 25$ ; long-distance dispersers:  $84.9 \pm 30.8$  ha,  $n = 16$ ; ANOVA,  $F_{2,49} = 0.39$ ,  $p = .68$ ).

When both short- and long-distance dispersers were included, the sector of a buffer used for dispersal, ordered according to the proportion of preferred habitat, did not differ from the random use of sectors (Kolmogorov-Smirnov test,  $d_{max} = 0.21$ ,  $n = 41$ ,  $p = .32$ ). However, for long-distance dispersers, the difference from random use was significant ( $d_{max} = 0.56$ ,  $n = 16$ ,  $p = .01$ ), as long-distance dispersers selected sectors dominated by preferred habitat, whereas

**Table 1**  
Characteristics of the dispersal paths of short- and long-distance dispersing flying squirrels

	Short-distance dispersers ( $n = 33$ )	Long-distance dispersers ( $n = 16$ )
Dispersal distance	$1140 \pm 590$ m	$5490 \pm 2290$ m
Crossed patches	$1.7 \pm 1.3$	$7.2 \pm 3.3$ , $n = 13^a$
Distance between patches	$236 \pm 173$ m, $n = 28^b$	$269 \pm 139$ m, $n = 13^a$
Preferred habitat along path	$45 \pm 24\%$	$36 \pm 11\%$ , $n = 13^a$
Open areas along path	$13 \pm 16\%$	$13 \pm 8\%$ , $n = 13^a$
Move length	$886 \pm 446$ m	$2094 \pm 600$ m
Number of moves	$1.18 \pm 0.39$	$2.76 \pm 1.09$

<sup>a</sup> Three individuals moved out from the landscape map.

<sup>b</sup> Five individuals did not change patches.

short-distance dispersers did not ( $d_{max} = 0.57$ ,  $n_1 = 25$ ,  $n_2 = 16$ ,  $p = .003$ ) (Figure 2).

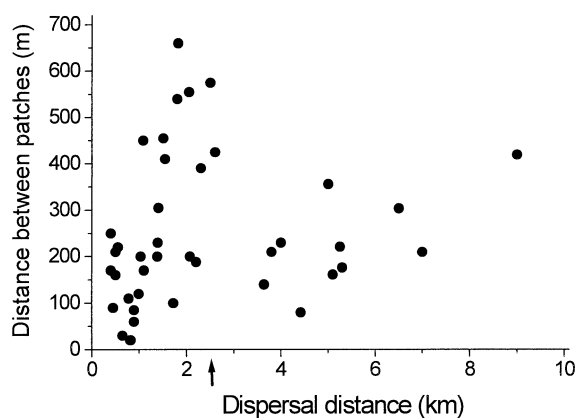
The area of preferred habitat in the sector selected for dispersal correlated with the total area of preferred habitat within the whole buffer (including both the short- and the long-distance dispersers:  $n = 41$ ,  $r_s = .36$ ,  $p = .03$ ). However, the abundance-corrected proportion of preferred habitat (ordered according to the proportion of preferred habitat) in the selected direction did not correlate with the total area of preferred habitat within the buffer ( $n = 41$ ,  $r_s = -.18$ ,  $p = .25$ ). Thus, the relative abundance of preferred habitat in the dispersal direction was independent of the overall local abundance of preferred habitat.

### Dispersal distance

Dispersal distances and characteristics of paths are shown in Table 1. When all individuals were included in the multiple linear regression, the dispersal distance was not affected by the percentage of preferred habitat or open areas along the dispersal path or by the distance between patches through which dispersal occurred ( $r^2 = .15$ , VIF: 1.0–1.7,  $F_{3,37} = 2.2$ ,  $p = .11$ ) (Figure 3). However, the response differed between short- and long-distance dispersers (in the regression of distance between patches and dispersal distance, the slopes differed between the dispersal groups,  $t = 12$ ,  $df = 37$ ,  $p < .0001$ ) (see Zar, 1999: 360). Thus, we analyzed short- and long-distance dispersers separately. For short-distance dispersers, the distance between patches had a positive effect on the dispersal distance ( $t = 2.16$ ,  $p = .03$ , overall model  $r^2 = .28$ , VIF: 1.0–2.0,  $F_{3,24} = 3.11$ ,  $p = .05$ ) (Figure 3). For long-distance dispersers, the distance between patches had no effect (distance between patches:  $t = -1.16$ ,  $p = .28$ ,  $r^2 = .63$ , VIF: 1.1–1.2,  $F_{3,9} = 3.23$ ,  $p = .08$ ). These results indicate that dispersing flying squirrels obviously had to move a longer distance as the distance between crossed patches increased, but this was not a general trend for our study animals and could not explain the difference in dispersal distance between short- and long-distance dispersers.

### Path shape

The average turning angles for dispersal and move paths were fairly large, but because flying squirrels tended to keep moving



**Figure 3**  
Dispersal distances of flying squirrels in relation to the average distance between preferred habitat patches crossed. Distances between patches were measured from the edges of the patches. The arrow indicates the point of separation between short- and long-distance dispersers.

in one direction, the observed fractal index ( $D$ ) for both paths indicated a nearly straight line movement (Table 2).

For dispersal paths, the average move length of short-distance dispersers was less than the average move length of long-distance dispersers ( $U = 23$ ,  $p < .0001$ ) (Table 1). Forty-five percent of moves (from 87 moves) were made during one night, but for the rest of the cases the individuals were not located every day (mostly 1-day gaps in telemetry coverage, which is less than dispersers usually spend within temporary home-ranges). Thus, for some cases it was possible that what was recorded as one move was actually two or more moves. However, there were probably only a few cases in which the classification of the move was incorrect, because move lengths for cases known to be one-night moves were not significantly shorter than for moves not known to be one-night moves (respectively, mean =  $1330 \pm 910$  m and  $1574 \pm 984$  m,  $U = 779$ ,  $n_1 = 39$ ,  $n_2 = 48$ ,  $p = .18$ ). The longest move observed (4960 m) was made during one night.

The number of observed moves per individual ranged from one to five (Table 1). The total dispersal distance correlated with the number of moves ( $r_s = 0.803$ ,  $n = 49$ ,  $p < .0001$ ). For long-distance dispersers, the average move length decreased with ordinal number of move ( $r_s = -.42$ ,  $n = 44$ ,  $p = .005$ ), so that the first moves were longer than moves made later during dispersal (Figure 4).

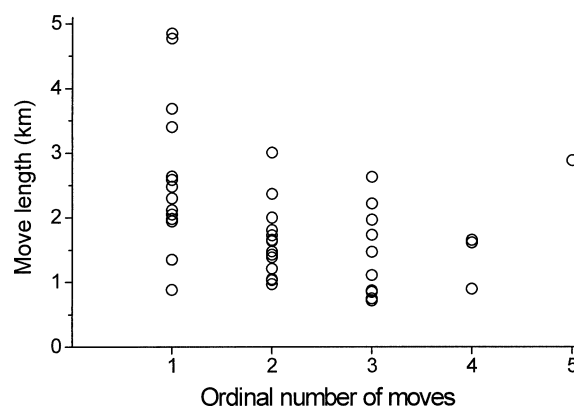
For the move paths of the eight directly followed individuals, the average step length between locations was  $182 \pm 91$  m and the mean total move length was  $673 \pm 287$  m (number of steps  $3.9 \pm 1.4$ ).

We divided dispersal paths into two groups based on the landscape structure: (1) those in which moves were in contact with gaps consisting of wide open areas (wider than 130 m) or wide

**Table 2**  
Fractal index  $D$  and angles between moves or steps of flying squirrel dispersal and move paths

	Moves ( $n = 22$ )	Steps ( $n = 8$ )	Test measure	$p$
$D$	$1.08 \pm 0.07$	$1.14 \pm 0.18$		
Angle (degrees)	28.8	37.7	$F_{1,34} = 0.07^a$	$> .5$

<sup>a</sup> Watson-Williams test (see Zar 1999: 625).



**Figure 4**  
Dispersal move length in relation to ordinal number of moves (from first move taken from natal area to last one leading to finally colonized patch) for long-distance dispersing flying squirrels.

pine bogs (wider than 300 m), and (2) those not containing gaps along the moves. Both the average value of  $D$  and the turning angle were smaller for cases without gaps than for those with gaps (Table 3, step or move length did not differ between paths with and without gaps). The path direction was changed seven times owing to fields, seven times owing to lakes or rivers, and four times owing to large pine bogs. In three cases, a wide field was probably circumvented, but we did not observe change in direction of the dispersal path. The width of noncrossed gaps ranged from 120–1100 m ( $n = 17$ , median = 240 m). The narrowest noncrossed gap was the 120–140-m-wide river in the Iitti study area that blocked the way for two dispersers.

Move paths for individuals that were followed directly were in a heterogeneous landscape, and all moves were influenced by the landscape structure. Thus, we were unable to study movements without gaps in move paths. The direction of the move path was clearly changed owing to fields six times and three times owing to clear cuts and sapling stands. Without a clear direction change, matrix habitats were crossed on a total of 11 occasions (by eight individuals). Five of these crossings were through fields (30–150 m wide, for the widest crossing the individual probably used trees growing in the middle of the field), three crossings were through pine/young forests, and three crossings were through saplings/clear cut. On average, the distance moved in preferred habitat was  $74.1 \pm 25.7\%$  of total distance moved. The use of preferred habitat may be overestimated, because the tracking of individuals was started in the natal spruce patch.

In addition to move paths, four of our study juveniles are known to have crossed fields more than 100 m wide that were

**Table 3**  
Difference in fractal index  $D$  and angles between moves for flying squirrel dispersal paths with and without wide gaps owing to open areas (see text)

	Without gaps	With gaps	Test measure	$p$
$D$	$1.03 \pm 0.02$ , $n = 6$	$1.10 \pm 0.07$ , $n = 16$	$U = 15^a$	.02
Angle (degrees)	12.6, $n = 12$	45.4, $n = 16$	$F_{1,26} = 22.2^b$	$< .0001$

<sup>a</sup> Mann-Whitney  $U$  test.

<sup>b</sup> Watson-Williams test.

impossible to circumvent. Three individuals crossed 110-, 120-, and 130-m-wide fields, and one individual crossed a 300-m-wide field, probably using bushes on the banks of ditches.

The proportion of good or poor movement habitat and open areas along dispersal paths (Table 1) may be overestimated, because some of these areas may have been circumvented. However most individuals (25 individuals out of 33 in Iitti and Anjalankoski) also crossed areas of movement habitats that could not be circumvented (crossings in good movement habitats:  $n = 26$ , mean =  $437 \pm 212$  m, max = 990 m; crossings in poor movement habitats:  $n = 23$ , mean =  $381 \pm 199$  m, max = 820 m, only areas wider than 150 m included).

### Size and quality of temporary and final patches

Temporary and finally occupied patches were larger than all other patches in the study areas (size of temporary patches:  $11.1 \pm 16.0$  ha,  $n = 20$ ; final patches:  $11.1 \pm 11.2$  ha,  $n = 22$ ; unused patches:  $4.8 \pm 7.0$  ha,  $n = 178$ ; Kruskal-Wallis  $F = 10.25$ ,  $df = 3$ ,  $p = .0001$ , Tukey  $p < .05$ ). The difference was similar when small patches (less than 1 ha) were omitted from the analysis.

In the final patches, the proportion of aspen was higher than in patches used as temporary home ranges (final =  $10.7 \pm 13.4\%$ , temporary =  $6.4 \pm 16.3\%$ ,  $U = 138.5$ ,  $n_1 = 22$ ,  $n_2 = 20$ ,  $p = .03$ ). The total proportion of deciduous trees did not differ between final and temporary patches (final =  $24.2 \pm 20.3\%$ , temporary =  $28.9 \pm 29.1\%$ ,  $U = 186.5$ ,  $n_1 = 22$ ,  $n_2 = 18$ ,  $p = .96$ , two temporary patches were birch forest and were omitted), but the height of trees was lower in temporary patches than in final patches (final =  $27.5 \pm 4.5$  m, temporary =  $23.7 \pm 4.6$  m,  $U = 114$ ,  $n_1 = 22$ ,  $n_2 = 19$ ,  $p = .01$ , one temporary patch was young forest and was omitted). All 49 final patches were mature spruce-dominated forest, although four individuals also had nests in other habitats close to the edge of spruce forest (two in a young spruce forest, one in a young deciduous forest, and one in a pine bog). Of the 38 temporary patches, nine were in young spruce forest, three in young deciduous forest, and the rest in mature spruce forest. In the temporary patches of deciduous forest, a few spruces were always present, and these were used for roosting.

## DISCUSSION

### Dispersal behavior

Our results show that young flying squirrels could disperse over large distances in fragmented forest landscapes. They preferred spruce forest as a dispersal habitat but were able to cross wide areas of other habitats with trees and open gaps, relying on trees within the habitat if gaps were larger than could be crossed in one glide. Landscape structure influenced dispersal movements of individuals in four ways: (1) as the distances between crossed patches increased, short-distance dispersers were found further away from their natal home range; (2) wide open areas obstructed the straightness of the dispersal path; (3) near the natal site, long-distance dispersers started to disperse in the direction dominated by preferred habitat; and (4) the habitat quality of patches, that is, the size and age of patches and the proportion of aspen within patches, influenced settlement patterns.

Philopatry was not related to landscape structure near the natal site, and there were no differences in landscape structure along the dispersal path (Figure 3) or within the natal home range between short- and long-distance dispersers. Thus, the observed difference in the selection of dispersal direction between short- and long-distance dispersers seems

to indicate behavioral differences between dispersing individuals that are not related to differences in the landscape structure within the dispersal path or natal home range. These results support the idea that individual dispersal behavior is determined before the onset of dispersal.

Possible proximate factors affecting dispersal behavior and dispersal distance before the onset of dispersal could include social structure, landscape structure within natal home range (Kenward et al., 2001; Loew, 1999; Lurz et al., 1997; Wauters and Dhondt, 1993; Wauters et al., 1994), and genetic factors (Johnson and Gaines, 1990; Murrel et al., 2002). Other studies have also shown that the decision of an individual to disperse over short or long distances had been made either before the onset or at the beginning of dispersal. Fraser et al. (2001) linked long distances moved in Trinidad killifish (*Rivulus hartii*) to boldness of individuals observed in a tank experiment. Kenward et al. (2001) found that large dispersal distances in buzzards (*Buteo buteo*) were associated with small brood size and landscape structure near the nest site, although genetic factors might also be involved. For flying squirrels we have no indication that brood size or weight of dispersers influence dispersal distances (data not shown). That genetic factors could play a role in flying squirrel dispersal might be supported by the fact that the timing of dispersal is strongly fixed to occur within a short period, lasting less than 1 month per litter during the first autumn after birth (data not shown).

Social structure within the new home range (Waser, 1985) and habitat within the dispersal path or within the new home range (see Ims, 1995) can all act as proximate factors affecting dispersal behavior and dispersal distance after the onset of dispersal. Social interactions probably had some effect on selection of the final patch, but we do not have any data to test this. Of the other factors, landscape structure within the dispersal path did not explain the dispersal distance by all the study individuals (Figure 3). However, habitat quality within the new home range seemed to be an important factor explaining the occupancy of the final patch, because the amount of aspen was higher than in the temporary patches.

The patches used by the flying squirrels during dispersal were also larger on average than other patches found in the study areas. In Selonen et al. (2001) we suggested that the use of larger patches by adult flying squirrels was probably owing to a higher probability of finding a nest cavity in a larger patch. The higher probability of finding a good-quality settlement area in a large patch probably partly explains the occupancy patterns found in the current study (see also Mönkkönen et al., 1997; Reunanen et al., 2000).

### Dispersal path

There was a very clear directional bias in the dispersal paths of the flying squirrels, and this remained over a large scale. The paths were divided into moves made over separate nights. When a disperser continued to disperse after spending a day or two within a temporary home range, it continued in the direction it had previously taken. However, large totally open areas and large pine bogs forced them to change their direction. For individuals that were followed directly, angles between steps moved were quite large, because the landscape was very heterogeneous, but the fractal index indicated that the overall path remained quite straight. The fact that the path can be variable on a small scale in a heterogeneous landscape, but still remain directional, can create difficulties in modeling studies using correlated random walks (Turchin, 1998). In the correlated random walk, even very high degrees of correlation do not yield a straight path over long distances (Zollner and Lima, 1999). In addition, factors such as the nonrandom

selection of dispersal direction by long-distance dispersers strongly influence settlement patterns and could, in some cases, direct long-distance dispersal to only one direction.

A species' ability to cross gaps is reflected in its sensitivity to boundaries (Bélisle et al., 2001; Haddad, 1999; Lidicker, 1999; Stamps et al., 1987). Clearly, flying squirrels were not very sensitive to boundaries, other than between forest and wide open areas (see also Selonen and Hanski, 2003). Wide treeless areas functioned as a hard edge, because flying squirrels avoid running on the ground. The small number of crossings of treeless fields wider than 100 m probably represented examples of the rare exceptions to this. Other edges were more or less soft and permeable to dispersers. Openings, which could be reached with one glide (30–70 m), were crossed as well as gaps a few hundred meters wide containing a few trees or bushes. Even very wide areas of good and poor movement habitat were crossed. This was well demonstrated by one young female, who started to disperse through 800 m of pine bog. Thus, although the dispersal of flying squirrels was influenced by the landscape structure in several ways, most animals moved through very heterogeneous areas without direction changes.

Several characteristics of flying squirrel dispersal may be more general for dispersing animals. Dispersal moves were shorter at the end of the dispersal than in the beginning. Dispersing juvenile spotted owls (*Strix occidentalis*) behave similarly (Turchin, 1998: 274). Flying squirrels were able to use habitats other than preferred habitat for temporary roosting patches during dispersal. Similarly, it has been found that dispersing juvenile Iberian lynx individuals seem to use habitats of lower quality than do resident individuals (Palomares et al., 2000). In addition, the observed behavioral polymorphism in dispersing flying squirrels is found also for other species (Fraser et al., 2001; Kenward et al., 2001). These results demonstrate that a random walk is not a suitable model for animal movement (see Tischendorf and Fahrig, 2000). We think our successful combination of data on landscape structure and radio telemetry (see also Kenward et al., 2001) emphasizes the need for such data to be collected for other species before general conclusions can be made that can be used for modeling dispersal patterns and success.

We thank Mikko Hannonen, Petri Ihalempiä, Maarit Jokinen, Eva Kallio, Henna Piha, Heikki Savolainen, Paul Stevens, and Hanna Uusimaa for helping in the field. Hannu Rita gave statistical help. Jon Brommer, André Desrochers, Bob O'Hara, and Luc Wauters gave valuable comments on earlier drafts of the manuscript. The study was financially supported by Ministry of Environment, Ministry of Education (LUOVA graduate school to VS), the Ella and Georg Ehrnrooth Foundation, the Maj and Tor Nessling Foundation, and the Oskar Öflund Foundation (to I.K.H.).

## 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.
- Bascompte J, Vilà C, 1997. Fractals and search paths in mammals. *Lands Ecol* 12:213–221.
- Bélisle M, Desrochers A, Fortin M-J, 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82: 1893–1904.
- Bowers MA, 1997. Mammalian landscape ecology. *J Mammal* 78: 997–998.
- Dunning JB, Danielson BJ, Pulliam RH, 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175.
- Duvall D, Schuett GW, 1997. Straight-line movement and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. *Anim Behav* 54:329–334.
- Fahrig L, Paloheimo JE, 1988. Determinants of local population size in patchy habitats. *Theor Popul Biol* 34:194–213.
- Fraser DF, Gilliam JF, Daley MJ, Le An N, Garrick TS, 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am Nat* 158:124–135.
- Gustafson EJ, Gardner RH, 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77:94–107.
- Haddad NM, 1999. Corridor use predicted from behaviors at habitat boundaries. *Am Nat* 153:215–227.
- Hanski IK, 1998. Home ranges and habitat use in the declining flying squirrel, *Pteromys volans*, in managed forests. *Wildl Biol* 4:33–46.
- Hanski I, Simberloff D, 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: *Metapopulation biology: ecology, genetics and evolution* (Hanski I, Gilpin M, eds). London: Academic Press; 5–26.
- Hanski IK, Stevens PC, Ihalempiä P, Selonen V, 2000. Home-range size, movements, and nest-site use in the Siberian flying squirrel, *Pteromys volans*. *J Mammal* 81:798–809.
- Harrison RL, 1992. Toward a theory of inter-refuge corridor design. *Cons Biol* 6:293–295.
- Hokkanen H, Törmälä T, Vuorinen H, 1982. Decline of the flying squirrel *Pteromys volans* L. populations in Finland. *Biol Cons* 23:273–284.
- Ims RA, 1995. Movement patterns relate to spatial structures. In: *Mosaic landscapes and ecological processes* (Hansson L, Fahrig L, Merriam G, eds). London: Chapman & Hall; 85–109.
- Johnson ML, Gaines MS, 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Ann Rev Ecol Syst* 21:449–480.
- Jokinen M, 2000. Sukupuolierot liito-oravan (*Pteromys volans*) synnyinpaikkauskollisuudessa ja dispersaalissa (master's thesis). Helsinki: University of Helsinki.
- Katz MJ, George E, 1985. Fractals and the analysis of the growth paths. *Bull Math Biol* 47:273–286.
- Kenward RE, Hodder KH, 1996. Ranges V: an analysis system for biological location data. Wareham: Institute of Terrestrial Ecology.
- Kenward RE, Walls SS, Hodder KH, 2001. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. *J Anim Ecol* 70:1–13.
- Kolasa J, Rollo CD, 1991. Introduction: the heterogeneity of heterogeneity: a glossary. In: *Ecological heterogeneity* (Kolasa J, Pickett ST, eds). New York: Springer; 1–23.
- Krohne DT, 1997. Dynamics of metapopulations of small mammals. *J Mammal* 78:1014–1026.
- Lidicker WZ Jr, 1999. Responses of mammals to habitat edges: an overview. *Lands Ecol* 14:333–343.
- Loew S, 1999. Sex-biased dispersal in eastern chipmunks, *Tamias striatus*. *Evol Ecol* 13:557–577.
- Lurz PWW, Garson PJ, Wauters LA, 1997. Effects of temporal and spatial variation in habitat quality on red squirrel dispersal behaviour. *Anim Behav* 54:427–435.
- Mäkelä A, 1996. Liito-oravan (*Pteromys volans* L.) lisääntymisbiologiasta. In: *WWF Finland reports no 8*. Helsinki: WWF Finland; 45–49.
- Merriam G, 1984. Connectivity: a fundamental ecological characteristic of landscape ecology. In: *Proceedings of the 1st international seminar on methodology in landscape ecological research and planning* (Brandt J, Agger P, eds). Denmark: Roskilde University; 5–15.
- Mönkkönen M, Reunanen P, Nikula A, Inkeröinen J, Forsman J, 1997. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. *Ecography* 20:634–642.
- Murrel DJ, Travis JMJ, Dytham C, 2002. The evolution of dispersal distance in spatially-structured populations. *Oikos* 97:229–236.
- Ognev SI, 1966. Mammals of the U.S.S.R. and adjacent countries. VOL. IV. Jerusalem: Israel Program for Scientific Translations.
- Palomares P, Delibes P, Ferreras P, Fedriani JM, Calzada J, Revilla E, 2000. Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. *Cons Biol* 14:809–818.
- Pastor J, Moen R, Cohen Y, 1997. Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. *J Mammal* 78:1040–1052.
- Reunanen P, Mönkkönen M, Nikula A, 2000. Managing boreal forest landscapes for flying squirrels. *Cons Biol* 14:218–226.

- Reunanen P, Mönkkönen M, Nikula A, 2002. Habitat requirements of the Siberian flying squirrel in northern Finland: comparing field survey and remote sensing data. *Ann Zool Fenn* 39:7–20.
- Selonen V, 2002. Spacing behaviour of the Siberian flying squirrel: effects of landscape structure (PhD thesis). Helsinki: University of Helsinki.
- Selonen V, Hanski IK, 2003. Movements of the flying squirrel *Pteromys volans* in corridors and in matrix habitat. *Ecography* 26:641–651.
- Selonen V, Hanski IK, Stevens PC, 2001. Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. *Ecography* 24:588–600.
- Stamps JA, Buechner M, Krishnan VV, 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Am Nat* 129:533–552.
- Stenseth NC, Lidicker WZ, 1992. Animal dispersal: small mammals as a model. London: Chapman & Hall.
- Taylor PD, Fahrig L, Henein K, Merriam G, 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571–573.
- Tischendorf L, Fahrig L, 2000. On the usage and measurement of landscape connectivity. *Oikos* 90:7–19.
- Turchin P, 1998. Quantitative analysis of movement: measuring and modelling population redistribution in animals and plants. Sunderland, Massachusetts: Sinauer Associates.
- Waser PM, 1985. Does competition drive dispersal? *Ecology* 66:1170–1175.
- Wauters L, Casale P, Dhondt AA, 1994. Space use and dispersal of red squirrel in fragmented habitats. *Oikos* 69:140–146.
- Wauters L, Dhondt AA, 1993. Immigration pattern and success in red squirrels. *Behav Ecol Sociobiol* 33:159–167.
- Wiens JA, Schooley RL, Weeks RD Jr, 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78:257–264.
- Wiens JA, Stenseth NC, Van Horne B, Ims RA, 1993. Ecological mechanism and landscape ecology. *Oikos* 66:369–380.
- With KA, King AW, 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Lands Ecol* 14:73–82.
- Zar JH, 1999. Biostatistical analysis. Upper Saddle River, New Jersey: Prentice Hall.
- Zollner PA, 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Lands Ecol* 15:523–533.
- Zollner PA, Lima SL, 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030.