Spacing behaviour of the Siberian flying squirrel
- effects of landscape structure

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Academic dissertation

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This thesis is based on the following articles:

I Hanski, I. K., Stevens, P. C., Ihalempiä, P. and Selonen, V. 2000. Home-range size, movements, and nest-site use in the Siberian flying squirrel, *Pteromys volans*. — Journal of Mammalogy 81: 798-809.

II Selonen, V., Hanski, I. K. and Stevens, P. C. 2001. Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. — Ecography 24: 588-600.

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VI Selonen, V., Painter, J. and Hanski, I. K. 2002. Microsatellite variation in the declining Siberian flying squirrel. — Submitted.

These are referred to by their Roman numerals.

Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

	I	II	III	IV	V	VI
Original idea	IKH	IKH, VS	VS, IKH	VS, IKH	AD	IH, IKH, VS
Materials	IKH, PS, VS	IKH, VS	VS, IKH	VS, IKH	IKH, VS	VS, JP, IKH
Analyses	IKH	VS, IKH	VS	VS	AD	VS
Manuscript preparation	IKH, PS, VS	VS, IKH	VS	VS	AD, VS, IKH	VS

AD: André Desrochers, IH: Ilkka Hanski, IKH: Ilpo Hanski, JP: Jodie Painter, PS: Paul Stevens, VS: Vesa Selonen. In addition several field workers assisted in the field. Their contributions are acknowledged in the relevant parts of the thesis.

Supervised by	Prof. Ilpo K. Hanski University of Helsinki Finland
Reviewed by	Prof. Harto Lindén Finnish Game and Fisheries Research Institute Finland
	Dr. Luc Wauters Institute Oikos Italy
Examined by	Prof. Mikko Mönkkönen University of Oulu Finland

Introduction

Ecologists' interest toward spatial aspects increased after the introduction of the theory of island biogeography (MacArthur & Wilson 1963, 1967, MacArthur 1972). The theory aimed to explain how distance and area together regulate the balance between immigration and extinction in island populations. It was based on simple mathematical models and looked for equilibria in species numbers using the data on species occurrences. The basic assumption of equilibrium in spatially defined ecological systems was later, however, found inappropriate (see Wiens 1984, Haila 1992, 2002). As the interest towards island biogeography declined, it was replaced by metapopulation (Levins 1969) as the paradigm of spatial ecology (Merriam 1991, Harrison 1994). In addition, during the next decades after island biogeography the individual organism's response to spatial heterogeneity was emphasized much more than earlier (Hansson 1977, Wiens 1981, Lima & Zollner 1996).

This development was related in the early 1980's to the emergence of a new discipline called landscape ecology. The roots of landscape ecology are older, leading probably to the former Soviet Union, were e.g. Naumov studied endemic diseases transmitted by rodents in the steppe environment (for review, see Naumov 1972). The ideas of Naumov were probably transported to USA by Anderson, who (1970) studied permanent and temporary habitats of house mice (*Mus musculus*) (for history of landscape ecology, see Hansson 1995, Lidicker 1995). Other early works on landscape ecology include e.g. Hansson (1977), who stressed the importance of landscape heterogeneity for the stability of field vole populations. Stickel (1979) studied alternative habitats of house mice, and Wegner & Merriam (1979) stressed the importance of wood fencerows for woodland birds and rodents. On the other hand, the landscape concept can be traced to agricultural land use planning at the beginning of the 20th century (Naveh 1982, Turner 1989).

Landscape ecology focuses on the effect of spatial landscape features on ecological processes and the scaling of local process to regional patterns (Forman & Gordon 1986, Urban et al. 1987, Turner 1989, Wiens et al. 1993, Forman 1995). Spatial heterogeneity is an important aspect (Wiens 1995). Thus one major difference of landscape ecology, compared to island biogeography and to metapopulation theory, is that the matrix, i.e. habitat between preferred patches, is not seen as a featureless "distance" or hostile "sea" between patches. The real landscapes are heterogeneous (Wiens 1995).

Much of the progress in landscape ecology has been in the description and analysis of the landscape structure (Wiens 1992). However, Lidicker (1995) emphasised the holistic nature of landscape ecology and Hansson (1995, see also Tischendorf & Fahrig 2001) suggested that approaches of island biogeography and metapopulation dynamics merge into a wider concept of landscape ecology. One implication from holistic nature is that landscape ecology has to consider important biological details in a very broad scale (Ims 1995). According to Lidicker (1988, 1995) landscape can be considered as a new, higher level of biological complexity. Thus the paradigm of landscape ecology could emerge from this notion of higher level of organisation, above metapopulations and communities (Lidicker 1995). However, in the present landscape ecology questions are rarely derived from the theory (e.g. Wiens 1995, Moilanen & Hanski 2001, but see Tischendorf & Fahrig 2001), maybe partly due to the holistic nature of the discipline and difficulties in developing theory due to the complexity of the real landscapes.

The present landscape ecological theory focuses mainly on two areas: ecological flows, e.g. movement of individuals, and scaling, e.g. effect of different scales on ecological processes (Wiens 1995, but see Lidicker 1995). Much attention is given on particular aspects of the landscape, like corridors and boundaries. However, landscape structure contains several different elements, which influence the movements of animals (Wiens et al. 1993).

Landscape connectivity has been identified as a key factor preserving populations (Taylor et al. 1993). Connectivity is a process that facilitates movement through landscapes, and it should not be confused with patterns of the landscape (Tischendorf & Fahrig 2000). How different landscape elements (like patches of preferred habitat, corridors, or matrix between patches) contribute to landscape connectivity depends on the nature of these elements, and the nature of the organism's response to them (Rosenberg et al. 1997, Beier & Noss 1998).

The reason why the theory of landscape ecology has not developed may be the lack of empirical understanding of the effect of landscape structure on the movement of organisms (Wiens 1995). Given the heterogeneous landscape structure, the way individuals move becomes important. Although during the last decade also the empirical understanding of animal movement has increased, too little effort has been put into the study of how animals respond to landscape structure (Ims 1995, Bowers 1997, Tischendorf & Fahrig 2000). Thus the lack of empirical movement data, especially on dispersal, is still a major problem (for review, see Stenseth & Lidicker 1992, Bowers 1997, Krohne 1997, Wiens 2001). Dispersal, i.e. one-way movement from a home range, is a key determinant of population dynamics of species in the present landscape ecological theory, and also in metapopulation theory (Levins 1969, Merriam 1984, Ims 1995, Hanski & Simberloff 1997, Wiens 2001). The urgent need for good movement data is not restricted to the field of landscape ecology, but also to other disciplines, like the metapopulation theory and studies of evolution of dispersal (Hanski & Simberloff 1997, Travis & French 2000).

The aims of this thesis are to understand the space use and movements of the Siberian flying squirrel (*Pteromys volans*) and the effect of landscape structure on those. This has been done by examining with radio telemetry the home-range size of adults (**I**, **II**), the characteristics of juvenile dispersal (**III**), the movements of adults within their home ranges during continuous tracking periods (**IV**), the use of matrix and corridors (**III**, **IV**), the response to edges (**V** and also **III, IV**), and by examining with microsatellite variation the genetic differentiation between different areas (**VI**). This thesis is very much empirically laded due to the developing status of the discipline of landscape ecology. The science done here is an analytical description (Haila 1988), in which data are used to describe the ecological phenomena and relate these patterns to the underlying theoretical assumptions (see also Simberloff 1982).

The Siberian flying squirrel

The Siberian flying squirrel inhabits spruce-dominated boreal forests from Finland to eastern Siberia and Japan (Ognev 1966, Wilson & Reeder 1993). It is the only flying squirrel species in the Eurasian boreal forests. In Finland, the range of the Siberian flying squirrel extends from south to the southern parts of Lapland. In northern Finland, the species is more common in eastern parts of the country than in the western parts (Reunanen 1998).

The flying squirrel is a nocturnal and arboreal rodent, which nests in tree cavities, twig dreys, and nowadays also nest boxes. Flying squirrels are dependent on cavities in large aspens and deciduous trees in general as a food source (Eronen 1991, Hanski 1998, Reunanen et al. 2002). The diet of the species consists mainly of leaves in the summer, and catkins and buds of alder (*Alnus* sp.) and birch (*Betula* sp.) in the winter, but also seeds and buds of coniferous species are used (Mäkelä 1996a) and occasionally also other food items, like bird eggs (Siivonen 1972). For winter food, flying squirrels cache catkins of alder (e.g. Sulkava & Sulkava 1993). The amount of deciduous trees within spruce forest patches influences the occurrence of flying squirrels (Reunanen et al. 2002).

The mating system of the flying squirrel is promiscuous, males having much larger home ranges than females and overlapping ranges with several females (Ihalempiä 2000, Hanski et al. 2000). Both females and males may copulate with several mates (own unpublished data). Females have one or two litters each summer. Juveniles of the first litter are born in April-May and of the second litter in June (Mäkelä 1996b, Hanski & Selonen unpublished). The dispersal of juveniles begins mainly in July-September of the year of birth (Hanski & Selonen unpublished). The natal dispersal of the flying squirrel differs from most other promiscuous or polygynous mammals being female biased. All female flying squirrels disperse away from their natal home range, whereas a fraction of males remain philopatric. However, males that do disperse reach distances similar to those dispersed by females, i.e., up to 9 kilometres with a mean of around 2.5 kilometres. Few males (but not all) that do not disperse in the first autumn may disperse during the next spring. Breeding dispersal has not been recorded for adult flying squirrels (Stevens 1998, Jokinen 2000, Hanski & Selonen unpublished).

The flying squirrel is preyed upon by large owls (eagle owl, *Bubo bubo*, Ural owl, *Strix uralensis*, tawny owl, *S. aluco*), goshawk (*Accipiter gentilis*), and probably by pine marten (*Martes martes*), but usually occurs only occasionally as a prey item in their diet (for a review, see Hanski et al. 2000). However, we have observed high mortality on a flying squirrel population by the Ural owl (*Strix uralensis*) in one of our study areas (unpublished data), but to the larger extent the effect of predation on flying squirrel population dynamics is unknown.

The fragmentation of forest landscapes in Finland by humans is due to the cutting of mature spruce forests, and thus the decline of flying squirrel numbers in Finland is thought to be due to forestry (Hokkanen et al. 1982, Rassi et al. 2000). According to Hokkanen et al. (1982) the flying squirrel population has severely declined in Finland from 1950 – 1982. In Hokkanen et al.'s abundance index, based on game inquiry data, there was a linear decline from 0.8 in 1950 to 0.4 in 1980. The decline appears to have continued since then. It has been suggested that during the last decade the population has decreased by about 30 % (Hanski et al. 2001). In the Finnish red data book, the flying squirrel has been classified as a vulnerable species (Rassi et al. 2000). The habitat directive of the European Union classified the flying squirrel as a priority species, which requires special areas for conservation (Anonymous 1992).

Methods – radio telemetry, GIS and microsatellites

There are three main methods used in the thesis: radio telemetry, GIS, and microsatellites. Radio telemetry has proven to be the best space-use descriptor of animals (Andreassen et al. 1993), and with GIS space use of the species can be linked to landscape level (e.g. Turner

1990). The use of microsatellites has increased dramatically in past two decades, and it has become a standard tool for studies of conservation and behavioural ecology, and population genetics (Luikart & England 1999).

The radio-telemetry studies were done in three areas in southern Finland, i.e., Iitti, Anjalankoski, and in the Nuuksio National Park. The hair samples for microsatellite analyses were collected from eight sampling sites. Five sampling sites were in southern Finland (AnjalankoskiW and E, Iitti, Kuusankoski and Nuuksio) and three others (Alavus, Mustasaari, and Luoto) in Western Finland (see Fig. 1 in **VI**). Of those, the Iitti study area was one large forest patch that was surrounded by fields and a lake, but connected to other forest areas by a 40-m wide forest strip. Iitti and Kuusankoski of the microsatellite study (**VI**) were together the area called Iitti for radio-telemetry studies (**I-V**). The Luoto study area was a peninsula on the coast of the Gulf of Bothnia, connected to the mainland by a less than 1-km wide land area (see Fig. 1 in **VI**).

Radio telemetry (I-V)

Radio telemetry begun to be used at the same time as the formulation of paradigm of the space and inter-population movement (e.g. island biogeography and metapopulation theories). Since the pioneering study by Cochran & Lord (1963), radio telemetry has been a popular method for obtaining data on space use in mammals (Andreassen et al. 1993). The success of radio telemetry has been based on several advantages of the method as compared to alternative methods, for example capture-mark-recapture.

The receiving range of radio equipments is usually long. The signal of the transmitters used in flying squirrels usually ranged from 0.5 to 2 km, even up to 3 km, depending on the landscape between transmitter and receiver. The time that transmitters are working without the need for battery change can also be quite long. The flying squirrel transmitters lasted mostly 6-7 months before battery failure. The spatial resolution is generally good in radio-telemetry studies, although certain measurement error is usually associated (e.g. Springer 1979). In this study, the measurement error should be minimal as the flying squirrels were generally located in the accuracy of a single or few trees, both in day and night time (Hanski 1998, **I**, **II**, **IV**), except for directly followed individuals (**III**, **IV**).

However, there are also disadvantages from the use of radio telemetry. A general, unverified, assumption usually is that radio tracking imposes very little disturbance for study objects (e.g. Ostfeld 1986, Andreassen et al. 1993). However, there is evidence that significant effects on the study animals can occur, and the effects of tracking have not been rigorously evaluated (Murray & Fuller 2001). It is also common that researchers tend to overlook or ignore the effects of marking in their study (Murray & Fuller 2001). The evaluation of the effects of tagging of flying squirrels is lacking. However, litter size did not seem to differ in tagged and non-tagged females (unpublished data).

It is hard to evaluate how a presence of the tracker would have influenced flying squirrel movement. Flying squirrels usually continued foraging although the tracker was only some tens of meters away from it, and they did not usually seem to respond to the tracker. If the tracker was very close (5 - 10 m) to the tracked flying squirrel, and the flying squirrel was in small trees or low down in large trees, the animal climbed higher or waited still until the tracker moved further away. However, disturbance events were usually rare because flying squirrels spent most of their time on top of large trees. Based on my own experience, flying squirrels appeared to ignore the tracker while in large trees.

In addition, the movement routes of adult males seemed to be uninfluenced by the presence of the tracker. During my fieldwork, I noticed that the inter-patch movement patterns did not seem to change in the cases when a flying squirrel was tracked from the distance of some tens of meters or triangulated from the distance of a few hundred meters. Thus it seems likely that radio tracking did not have any major effects on the individuals that would influence the results.

GIS (II-V)

The use of geographical information system (GIS) has emerged to be a useful tool when studying landscape-level questions (e.g. Turner 1990). The landscape maps facilitate the computation of landscape metrics and complex landscape structures (Star & Estes 1990).

We linked the information gained by radio telemetry to landscape level by using landscape maps that were digitised from aerial photographs. The number of landscape elements used differed between studies:

II: Ten types of landscape elements were defined: spruce forest, deciduous forest, young forest, sapling stand, clear cut with trees, clear cut, pine forest, pine bog, field, and other open (e.g. lakes and gravel pits).

III, **IV**: Based on the results of habitat use by the flying squirrel (**II**), four types of landscape elements were defined: 1) *Preferred habitat* (spruce- or deciduous-dominated forests), and three matrix types; 2) *Good movement habitat* (pine forest, young spruce, young deciduous forest and clear cuts with trees); 3) *Poor movement habitat* (sapling stands, young pine forest, pine bogs and clear cuts); 4) *Open areas* (fields and other open areas, e.g. open bogs and lakes).

V: For the study of edge effects the landscape was divided to three elements: 1) P*referred habitat*; 2) *Movement habitat (good movement habitat + poor movement habitat)*; 3) *Open areas*.

The differences between mature/young forest and young forest/sapling were identified by the density of trees in the aerial photographs and by checks made in field. In sapling areas trees were 1.5-8 meters high and in young forests less than 15 meters high. In clear cuts with trees there were several trees interspersed over the cut area. Clear cuts often had a few single trees, but considerably less than clear cuts with trees (seed-tree cutting). Fields and other open areas were the only landscape elements entirely without trees.

Landscape structure was analysed with different methods in different studies depending on the purpose of the study:

II: We studied (i) habitat preferences of the flying squirrel, and (ii) the effect of landscape structure on the use of different habitat types, number of used patches, and size of home range. For (i), we used compositional analysis (Aebischer et al. 1993). For (ii), we measured the size of used spruce patches, distance between different spruce patches, and area of different landscape elements within buffers around home range.

III: We investigated (i) whether young flying squirrels selected the dispersal direction based on the structure of forest landscape, (ii) whether the landscape structure affected movements during dispersal, and (iii) what was the habitat structure in the site occupied after dispersal. For (i), we measured landscape elements within a 1-km buffer around juvenile nest sites. Buffer was divided in eight sectors. For (ii), we draw a line following the dispersal path. The distances moved in different landscape elements that the path intersected were calculated. In addition, the number of spruce patches crossed and the distances between spruce patches along dispersal path were counted. The effect of landscape structure to the straightness of the dispersal path of flying squirrels was studied by dividing paths to those containing wide-open gaps and those not containing open gaps. For (iii), the size and tree composition of patches used for temporary nest sites and for the patch finally occupied was compared to patches not used in the study areas.

IV: We compared (i) movement paths in spruce forest patches and in movement habitat matrix, and (ii) calculated a leaving probability for spruce patches that were used by flying squirrels and compared that to different landscape measures. For (ii), we used landscape measures patch size, proportion of deciduous trees within patches, distance between patches, connection type of patches to other patches (spruce forest corridors vs. matrix of poor- or good movement habitat), and proportion of different edge habitats.

V: We analysed the nocturnal locations of radio-tagged flying squirrels and their nesting and roosting sites in relation to edges between preferred habitat and two types of matrix habitat (movement habitat and open areas). The mean distance of observed locations of each individual to edges was compared to expected distance to edges. The expected distance was calculated from points laid out systematically at 10-meter intervals.

Microsatellites (VI)

Microsatellites are short tandemly repeating sequence units (for example CA or GA repeats) that are found randomly through the genome. They are expected to be selectively neutral and are highly polymorphic, thus being powerful tools to be used for example in population biology (Jarne & Lagoda 1996). Microsatellites have been detected in eucaryote genomes for over 20 years. However, not until late 1980's, since the development of the polymerase chain reaction (PCR, Mullis & Faloona 1987), the usefulness of microsatellites for ecological studies was realized (Jarne & Lagoda 1996). Due to new powerful computer programs (Rousset & Raymond 1997, Luikart & England 1999) it has been suggested that microsatellites may have revolutionary effects on the development of conservation biology and population genetics (Luikart & England 1999). However, many important aspects, as the mutation model of microsatellites, has not reached full consensus (Jarne & Lagoda 1996, Balloux & Lugon-Moulin 2002), and the final conclusion of the impact of microsatellites on the different fields of ecology and genetics will be seen in the future.

We used seven microsatellite loci to study genetic variation in the flying squirrel in Finland. The details of microsatellite primer development and PCR procedure are presented in Painter et al. (manuscript).

Results and discussion

In this section, I summarize the main results of the original papers of the thesis.

Home ranges and movements of adults

The Siberian flying squirrel has very good movement abilities (**I**, **II**, **III**, **IV**) as compared with other similar sized mammals (Swihart et al. 1988). Average home-range size, measured by 100 % minimum convex polygons, was 59.9 ha for males and 8.3 ha for females (**I**). For both sexes this was much more than could be predicted according to body mass model by Swihart et al. (1988). Most likely, the explanation for great mobility was a combined result of the low densities of flying squirrels and good movement abilities due to gliding.

There was an indication that gliding ability increased mobility, and thus home-range size, by the fact that also for other flying squirrel species the body mass model by Swihart et al. (1988) predicted much lower home-range sizes (**I**) that was observed (*Glaucomys volans,* Fridell & Litvaitis 1991; *G. sabrinus*, Witt 1992, the density of these species is much higher than in *Pteromys*, see **I**). That low density influenced large home-range size in Siberian flying squirrel was indicated: First, by the even larger home-range size in *Pteromys* than in other flying squirrels with higher densities, and second, by the larger inter-sexual difference in the home range size in *Pteromys* than is observed in other species of small and medium-sized mammals (**I**). Males have to move over larger areas to reach females when female density is low. The low densities of *Pteromy*s were probably due to the landscape structure, as spruce forest patches with large aspen for cavity resource and deciduous trees for food resource were scarce in the landscape (**II, IV**).

There was also indication that the lack of cavity trees influences flying squirrels space use: First, because of the smaller male home-range size in the study area with a large number of nest boxes (and thus increased density of females), and second, because of the use of smaller spruce forest patches in the area with nest boxes than in natural conditions, where finding cavities may be easier in large patches (**II**). That nest cavities might be an important resource for the flying squirrel may also indicated by the fact that natal dispersal is female biased (Stevens 1998, Jokinen 2000, Hanski & Selonen unpublished, **III**). The dispersal in polygynous mammals is usually male biased, and the deviations from this pattern are thought to indicate resource competition between females (e.g. Greenwood 1980, Wolff 1994). The most likely resource that would be the object of competition among females is the nest cavity. However, especially in winter, the amount of food may be limited.

As female space use is thought to be determined by the amount and distribution of food resources and/or defence of young (Lambin et al. 1992, Wolff 1993), male space use of polygynous/promiscuous mammals is largely determined by the spatiotemporal distribution of receptive mates (Ims 1987). The space use of male flying squirrels seemed to be related to the location and number of female home ranges. In the study area where female density was high, the home ranges of males were small (**II**).

Dispersal of juveniles

Natal dispersal distances were long in juvenile flying squirrels (Hanski & Selonen manuscript, **III**) as compared to other similar sized mammals (Stenseth & Lidicker 1992, Wauters et al. 1994).

In the natal dispersal of flying squirrels, there was a very clear directional bias. The straightness of the path remained over a large scale, whenever it was not obstructed by wide open areas (**III**). The path was divided into moves made during separate nights. When a disperser continued to disperse after spending a day or two within a temporary home range, it continued to the direction it previously had. A few other empirical studies have also found that large-scale movements are often nearly straight paths (Bascompte & Vilà 1997, Duvall & Schuett 1997, Pastor et al. 1997). In theoretical models, nearly straight paths have been found to be most successful for large-scale search (Zollner & Lima 1999). However, Turchin (1998, p. 267) doubted whether any animal disperses in an even approximately straight line. Thus our result of a straight, non-random path is important for the mathematical basis of simulation studies. The movement of animals is usually modelled as a simple or correlated random walk based on movements in grid cells (see Turchin 1998 and refs. therein). However, in the basic correlated random walk even very high degrees of correlation do not remain straight for long distances (Johnson et al. 1992, Zollner & Lima 1999).

Good movement abilities of the flying squirrel in the matrix habitat enabled the straightness of paths (**III**, **IV**). Flying squirrels were also able to use habitats other than spruce forest for temporary roosting patches during dispersal, in the cases when spruce forest was not present. It has been found that dispersing Iberian lynx individuals also seemed to use habitats of lower quality than resident individuals (Palomares et al. 2000).

There were no such differences in the landscape in the natal area or within the landscape dispersed, which could have explained the individual differences in the decisions to remain philopatric, or to become a short-distance or a long-distance disperser (**III**). In addition, whereas short-distance dispersers started to disperse to random directions, long-distance dispersers selected spruce-dominated directions, indicating that there are behavioural differences between dispersers. Based on that, our results seemed to support the hypotheses stating that the individual decision to disperse far or short has been done before the onset of dispersal (see **III**).

Most likely flying squirrels are able to perceive the landscape for few hundreds of meters, as observed in other squirrel species (Zollner 2000), and thus are able select the dispersal direction based on the landscape structure. Many of the juveniles also made exploratory trips before dispersal, usually less than 1 km, but up to 2 km, from the birth site, and thus probably had some information about the landscape around their birth site before dispersal (Hanski & Selonen unpublished).

Factors explaining differences in dispersal behaviour and dispersal distance can be divided to those having an influence before the onset of dispersal (social structure and landscape structure within a natal home range, Waser 1985, Loew 1999, Kenward et al. 2001; genetic factors, Johnson & Gaines 1990, Krebs 1992, Murrel et al. 2002), and to those having an influence after the onset of dispersal (social structure within new home range, Waser 1985;

landscape structure within a dispersal path or within new home range, e.g. Ims 1995). Our results seemed to support factors within a natal landscape other than landscape structure (**III**).

The effect of landscape structure on flying squirrel movements

Landscape structure influenced movement patterns both in adults within their home range and juveniles during dispersal (**II, III, IV**).

Adults

Within their home range, adult males moved between several different spruce patches, but females usually stayed within one patch (**II**). The spacing behaviour of males was affected by the structure of the landscape in a way that individuals were found more often in the matrix, home ranges were larger, and individuals used more spruce patches in the more highly fragmented landscape. Female's space use was not affected by the landscape structure, except that, when the area of matrix with trees increased, individuals were found more often in the matrix. The influence of patch size on animal behaviour indicates that all the resources needed cannot be found from one small patch (Dunning et al. 1992). For female flying squirrels, this recourse was mainly food and nest site, but for males also females as they expanded their home range to include several females (**II**). However, it is clear that both male and female flying squirrels were able to compensate for the lack of resources in one patch by using matrix or other patches.

For males, our results indicated the expansion response to fragmentation (Ims et al. 1993). In the expansion response, the habitat patch size is smaller than the minimum space requirements and individuals expand their home ranges to include several patches. For females in our study, the hypothesis by Ims et al. (1993) was not relevant (**II**). However, two females living in small, 1-ha patches moved frequently to an other patch, indicating that in certain situations the expansion response may be the case also for females (unpublished data).

In the fission response, the overlap between individual home ranges should decrease when habitat patch size approaches the minimum space requirements of an individual. In the fusion response, the home-range size should decrease and the overlap between individuals increases (Ims et al. 1993). Several studies among vertebrates have found support for the expansion response (Wegge & Rolstad 1986, Carey et al. 1992, Geffen et al. 1992, Tjernberg et al. 1993, Wauters et al. 1994, Redpath 1995, Andreassen et al. 1998) and the fusion response (Andreassen et al. 1996, 1998, Wolff et al. 1997).

We could not separate the effect of patch size from the effect of connecting landscape elements to the home-range size and patch use of males (**II**), although it seemed that the former had the main effect. However, the probability of continuously followed individuals leaving the patch was influenced by the size of the patch, but not by the type of connection the patch had to other patches (**IV**). Thus it seemed that lack of connection was not restricting the movements of adult flying squirrels.

While moving between patches, male flying squirrels stopped less frequently and moved in a straighter line in matrix habitats than in spruce forest (**IV**). Most likely, it is inefficient to use a movement strategy other than moving straight towards the subject, when individuals have experience in an environment and are capable of remembering locations of resources or preferred patches (Ims 1995, Zollner & Lima 1999). This was the case for male flying squirrels, who seem to know the area of their home range and usually moved between patches to visit the home range areas of different females.

Flying squirrels did not avoid edges. On the contrary, they seemed to slightly prefer some types of edges (**V**). Wide treeless areas functioned as a hard edge (see Stamps et al. 1987), but other edges were more or less soft and permeable for both adults and dispersing juveniles (**III**, **IV, V**). Association of flying squirrels with edges was dependent on type of edge, spatial scale, and activity (nesting or roosting vs. other activity) **(V)**.

Most mammals investigated to date have occurred predominantly near habitat edges (Hansson 1994, Kremsater & Bunnell 1999). In flying squirrels, response to edges was mostly likely a combination of three factors: First, predation risk is often considered an important driving force causing edge effects. Second, edges would act as movement barriers channelling flying squirrels, thus individuals would spend a disproportionate amount of time in edges (Haddad 1999, Desrochers & Fortin 2000). Third, edges seemed to reflect food abundance. When in spruce forest, flying squirrels responded more strongly to field edges than to recent clear-cut edges, probably as a result of the presence of more deciduous trees in field edges, unlike in clear-cut edges.

Juveniles

The response of flying squirrels to landscape structure seemed to depend on the age of the flying squirrel. Dispersing juveniles crossed much wider open and treed matrix areas (**III**) than adults (**IV**). This suggests that juveniles had a higher motivation to move in fragmented landscapes than adults. However, totally open gaps that exceeded the gliding ability of the flying squirrel (> 100 m), like large fields and wide rivers, were usually not permeable.

Landscape structure influenced the dispersal movements of individuals in four ways (**III**): First, if the distances between crossed spruce patches increased, dispersers were found further away from their natal home range. Second, wide open areas obstructed the straightness of the path. Third, near natal site, long-distance dispersers started to disperse to spruce-dominated direction. Fourth, the habitat quality of patches seemed to influence colonization patterns.

Many of the dispersing flying squirrels settled in patches where the habitat quality was probably low (i.e. there were no cavities, own observation). It is doubtful whether long-term occupancy of these patches was possible. The quality of the patch seemed to be an important factor explaining the occupancy of the final patch, as the amount of aspen was higher in the final than in the temporary patches used during dispersal (**III**). Patches used during dispersal were also larger than average patches in the study areas (**III**). The use of large patches by adult flying squirrels may be due to a higher probability of finding a nest cavity in a larger patch. In addition, the higher probability to find a good-quality settlement area in a large patch probably explained the occupancy patterns found in dispersing juveniles (**III**). In northern Finland, the area of preferred habitats has also been larger in occupied areas than in unoccupied areas. There were also more large open areas around unoccupied spruce forest sites than in occupied sites in northern Finland (Mönkkönen et al. 1997, Reunanen et al. 2000).

Clearly, our results are consistent with the view that patch size, nature of the matrix habitat, and changes in landscape heterogeneity can affect path direction and colonization success of species (Stamps et al. 1987, Gutzwiller & Anderson 1992, Ims 1995, Gustafson & Gardner 1996). However, the landscape in our study areas seemed to be functionally continuous for the flying squirrel. Both adults and juveniles were capable of moving between spruce patches through less preferred habitats. In studies in more fragmented areas, isolation and patch size have affected the occurrence of squirrel species (Verboom & Apeldoorn 1990, Apeldoorn et al. 1994, Celada et al. 1994, Wauters et al. 1994, Rosenblatt et al. 1999, Nubb & Swihart 2000).

Microsatellite variation in Finnish flying squirrels

Heterozygosity levels were similar in the flying squirrel (expected heterozygosity 0.53-0.75) to those found in other Sciurid species (Stevens et al. 1997, Goossens et al. 2001, Schulte-Hostedde et al. 2001). The genetic structure of the flying squirrel populations was affected by isolation due to increasing distances between sites and large-scale barriers for gene flow. There was no indication for isolation, in small spatial scale, for Iitti study site, that was one spruce forest patch surrounded by fields (see Fig. 1 in **VI**). This supports the results by radio telemetry that flying squirrels are able to move over large distances using also other habitats than spruce forest (**II**, **III**). However, the limits for flying squirrel gene flow were found in the form of Kymi River and isolation of Luoto study site in the peninsula, which both influenced genetic patterns in flying squirrels (**VI**).

Based on census data, flying squirrel numbers have declined during the last decades in Finland. However, microsatellite data did not find evidence for this in most study sites. This may be the true situation, as there was no indication that small number of loci and samples would have decreased the power of the tests (**VI**). In addition, for the cases that recent decline was indicated, Anjalankoski is the nest box study area, where the flying squirrel numbers actually may have increased in past five years, and Luoto, situated in the isolated peninsula that is not very representative of the situation in the mainland. The observed signal for population decline in Anjalankoski can be questioned, because there may have been immigration from adjacent areas in past yeas (see **VI**). Pope (2000) showed that a false bottleneck signal, as defined by Cornuet & Luikart (1996), might occur if there is strong deviation from the basic assumption of absence of migration.

Thus it seems that the recent decline of the flying squirrel has not been so severe that it could have been detected by the used methods. The major cutting of forests in southern Finland has occurred in the decades after 1950's, but there does not seem to have been any bottleneck like decrease in the flying squirrel population in Finland (**VI**). However, the differentiation between sites was fairly large, which may be associated with the decreased gene flow due to a small number of good-quality patches for flying squirrels. These areas may be isolated from each other if the spruce forests between function as a sink habitat that reduce the amount of gene flow between suitable patches.

Heterozygote excess was significant and was larger for males than for females indicating female-biased dispersal (**VI**). Reason for this is most likely a higher relatedness between males than females and reduced inbreeding due to dispersal of females (see Crow & Denniston 1988, Sugg et al. 1996).

Management implications

Considering the ability of flying squirrels to move in matrix habitat and the landscape structure of southern Finland, it is unlikely that planning of forestry focusing, for example, on ecological corridors for flying squirrels in southern Finland has much use. In addition, flying squirrels do not need large patches of spruce forest including large areas of interior, as they did not avoid using edges. Of the area of Finland 68% are forest, 10% lakes and 6% fields (Finnish Forest Research Institute 2000). Flying squirrels should be, in most cases, able to move over large areas due to their good movement abilities in managed forest landscapes. Due to a low amount of good-quality spruce patches in Finnish managed forest landscape, dispersers often end up in patches that contain low amounts of deciduous trees and no cavities (**III, VI**).

Our results seem to indicate that habitat loss may be more important than effects of fragmentation for population dynamics of the flying squirrel in southern Finland. Similarly, for several bird species in boreal forest landscapes it seems that habitat loss may be more important than the effects of fragmentation (Schmiegelow & Mönkkönen 2002, see also Haila et al. 1994, Fahrig 2002). It may be that the effects of fragmentation are not such an issue for many species living in boreal forests in the same extent than for forest species in more agriculturally driven landscapes, because of the transient nature of the matrix (Fahrig 2001, Schmiegelow & Mönkkönen 2002).

In northern Finland, the amount of spruce forests and linkages between spruce forest patches influence the occurrence of the species at the landscape scale (Mönkkönen et al. 1997, Reunanen et al. 2000). However, the response of flying squirrels to landscape structure may differ in southern and northern Finland. In northern Finland the species is living at the northern limit of its range and occupies mainly good-quality patches of old-growth forest (Reunanen 1998). In northern Finland, the size of landscape elements is also larger and thus the landscape is more coarse-gained than in southern Finland (Mönkkönen et al. 1997, Hanski et al. 2000, Reunanen et al. 2002).

Although we have some scepticism on the usefulness of corridor planning in the conservation of the southern Finnish flying squirrel population (**IV**), we can provide some connectivity guidelines that may influence the persistence of local populations. Management of landscapes occupied by flying squirrels should ensure that occupied patches would not be isolated by gaps of completely open areas that exceed the gliding ability of flying squirrels (< 100 m). Open gaps of 30-50 m are easily crossed, but wider areas may influence the willingness of flying squirrels to cross the gap. In general, flying squirrels are able to disperse in the forested landscapes of southern Finland. However, if two known flying squirrel sub-populations are separated by a completely open area clearly wider than 100 m that cannot be circumvented, a corridor of trees is needed to enable the movement.

Because long-distance dispersing flying squirrels tend to select dispersal directions with maximum area of spruce forest (**III**), the direction of dispersal can also be directed to certain patches by ensuring that the landscape towards that direction is spruce-dominated forest. However, this kind of planning is probably not very practical for the conservation of flying squirrel in general, but could be used in some special cases. The amount of food (deciduous trees) and availability of nesting sites (big aspens with cavities), make forest landscape patchy for the flying squirrel. Therefore, it is not surprising that the flying squirrel is able to move over large and heterogeneous areas.

Presently, we are not able to define the required area of suitable spruce forest for the flying squirrel or the threshold where the effects of fragmentation would start, together with habitat loss, to influence flying squirrel populations. However, for example in the Iitti study area, the proportion of spruce patches that contain mature aspen and other deciduous trees is 19 % of the total spruce forest area and 3 % of the total land area (unpublished data). We do not know whether this is sufficient for the long-term persistence of the flying squirrel population in Iitti. At present, there are flying squirrels in the area, but the major cutting of forests in southern Finland has occurred in the decades after 1950's. During 1950-1990 there was a big shift in the age class of spruce forest, so that a large amount of 50-70 year old forests were replaced by 10-30 year old forests (Finnish Forest Research Institute 2000). Therefore, it is possible that the population in Iitti has not yet fully responded to the changes in the environment.

Conclusions

In this thesis I have studied how the Siberian flying squirrel uses the space during its life cycle and how the landscape structure and individual behaviour can affect movement and space use of the flying squirrel. Based on the observed associations between movements and landscape structure, the results were related to underlying theories of landscape ecology and dispersal.

Movements and dispersal of the flying squirrel were affected in several ways by the landscape structure and individual behaviour. However, in the landscape of our study areas, the movement of flying squirrels did not actually seem to be much restricted due to the good movement abilities of the flying squirrel. Still, the gene flow over large areas seemed to be low.

The ability of individuals to move in space is the general characteristics of all organisms (e.g. Ims 1995). This ability is naturally highly variable among species. In addition, the movement responses to landscape structures do not only vary among species, but also by the life cycle of the species (Lidicker & Stenseth 1992, **IV**). The response may also vary within species in different regions with different landscape structures. Thus it is not surprising that general conclusions for the effects of habitat loss and fragmentation seem to be impossible to draw, for example for management purposes (Haila 2002), because both habitat preferences and dispersal abilities greatly vary among species. However, clear knowledge on species' space use and responses to landscape structure gives a better understanding on species population dynamics, and thus at least species-specific conclusions for management purposes can be achieved.

Conclusions on the population dynamics of the flying squirrel remain as a challenge for the future. For example, the threshold for the habitat loss and fragmentation, below which the flying squirrel cannot survive, remains unsolved. However, the synthetic approach (see e.g. Turchin 1999, Ford & Ishii 2001) on the population dynamics of flying squirrel, linking our data with modelling, is possible. In addition, to data presented in this thesis on the spacing behaviour, we have data on flying squirrel survival and fecundity (unpublished). By using modelling approach, with individual based spatially explicit models, combining our data and landscape structure, it should be possible to form predictions on flying squirrel responses to landscape structure in the population level.

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