

**LANDSCAPE RESPONSES OF
THE SIBERIAN FLYING
SQUIRREL (*PTEROMYS VOLANS*)
IN NORTHERN FINLAND**

The effect of scale on habitat patterns and species incidence

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University of Oulu

OULU 2001



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Abstract

Spatial structure of habitats has been found to affect the species abundance and distribution patterns in heterogeneous environments. In this thesis, I studied landscape responses of the Siberian flying squirrel in a boreal forest context in northern Finland. Studies were conducted at several spatial scales in order to identify landscape characteristics that are associated with the species occurrence at a local scale and its distribution patterns at a regional scale. Data on species presence and absence in forest areas were collected in the field. Habitat patterns in landscapes were analysed from satellite images and landscape metrics concerning landscape structure were quantified in Geographic Information Systems (GIS).

Results of this study are in agreement with the general landscape ecological theory and findings in the field. In northern Finland, the distribution of the Siberian flying squirrel primarily follows the spatial extent of spruce-dominated forests but that its actual occurrence is dependent on the scale of observation and the habitat structure. At a home range scale the abundance of deciduous trees in old spruce forest increases the probability that a forest site is occupied by the species, whereas at a local scale the amount of such spruce forests and linkages between habitat patches play an important role. At a regional scale, an increase in open areas and the dominance of pine makes the habitat unsuitable and restricts the presence of the species.

Findings of the present research forward practical forest management planning at a large scale and may help set general conservation goals for the Siberian flying squirrel. When managing the species in a complex network of habitat patches in heterogeneous landscapes, spatial dispersion of potential habitat patches as well as connecting habitat and their temporal development should be considered carefully. For this purpose, remote sensed images and GIS are valuable and useful tools. Satellite-image based landscape analysis is presently developing rapidly and hopefully this methodology will soon become a common practice in landscape ecological research and everyday forest management planning.

Keywords: landscape ecology, remote sensing, GIS

Step by step
up summer mountain –
suddenly the sea

– Kobyashi Issa

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First of all, I have to mention that this thesis is not a result of a long and lonely work in an ivory tower but rather a product of collaboration and interactions among many people. My task was to elaborate ideas, develop suggestions, implement recommendations presented by these people and, of course, formulate all this in a scientific way in order to communicate with other researchers in the field. Unfortunately, I am not able to thank everybody personally in this connection, but I must refer to the ones who had a major contribution to realisation of my thesis.

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Oulu September 2001

Pasi Reunanen

List of original papers

This thesis is based on the following publications, which are referred to in the text by their roman numerals.

I Mönkkönen M, Reunanen P, Nikula A, Inkeröinen J & Forsman J (1997) Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in boreal forests of northern Finland. *Ecography* 20: 634–642.

II Reunanen P, Mönkkönen M & Nikula A (2000) Managing boreal forest landscapes for flying squirrels. *Conservation Biology* 14: 218–226.

III Reunanen P, Nikula A & Mönkkönen M (2001) Regional scale landscape patterns and the distribution of the Siberian flying squirrel (*Pteromys volans* L.) in northern Finland. Manuscript (accepted).

IV Reunanen P, Mönkkönen M & Nikula A (2002) Habitat requirements of the Siberian flying squirrel in northern Finland: comparing field survey and remote sensing data. *Annales Zoologici Fennici* 39 (in press).

V Reunanen P, Mönkkönen M, Nikula A, Hurme E & Nivala V (2001) Predicting the occupancy of the Siberian flying squirrel in old-growth forest patches in northern Finland. Manuscript (submitted).

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Contents

Abstract	
Acknowledgements	
List of original papers	
Contents	
1 Introduction.....	13
1.1 Landscape ecology – a developing discipline	13
1.2 The domain of landscape ecology	13
1.2.1 The appropriate level of observation: the dilemma of scale	14
1.3 Theoretical and modelling approaches in landscape ecology.....	15
1.4 Boreal forest landscape: the setting of the study	17
1.4.1 Human land use history and antropogenic landscape patterns.....	18
1.5 Siberian flying squirrel as a landscape ecological object	19
1.6 Thesis objectives	20
2 Material and methods.....	21
2.1 Pellets on the ground – signature of the species presence.....	21
2.1.1 Presence/absence data in ecological research	22
2.2 Landscape pattern analysis in GIS	22
2.3 Landscape variables and statistical analysis of landscape data	23
3 Results and discussion	25
3.1 Landscape structure around old-growth forest areas in Kainuu (I)	25
3.2 Local scale habitat structure in Koillismaa (II)	26
3.3 Distribution of the Siberian flying squirrel in northern Finland (III)	27
3.4 Are large-scale landscape patterns visible at a home range scale? (IV)	28
3.5 Is the presence of the Siberian flying squirrel in a habitat patch predictable? (V)..	29
4 Conclusions.....	31
4.1 Landscape structure and the Siberian flying squirrel	31
4.1.1 Spruce dominated forest patch: a basic landscape element for the Siberian flying squirrel in northern Finland.....	31
4.1.2 Landscape connectivity at a local scale	32
4.1.3 Landscape configuration of habitat patches.....	33
4.2 Spatial scaling for the Siberian flying squirrel	34

4.3 Theoretical aspects	34
4.4 Management of the forest landscapes for the Siberian flying squirrel	35
5 Concluding remarks	37
References	
Original papers	

1 Introduction

1.1 Landscape ecology – a developing discipline

Short history of landscape ecology as an established discipline within ecological sciences dates back to the early 1980's. The origin of the landscape ecology, however, is much older having its roots in long European tradition of land use planning, and practical organisation and sound exploitation of natural resources (Naveh 1982, Golley 1994). The concept of landscape ecology was adapted by American ecologists and soon after the field began to develop towards more ecologically-orientated phrasing of questions and methodologies typical of modern ecological research. Contrary to the applied and descriptive approach in the European tradition, the American approach focused on fundamental and conceptual details in landscape pattern and function. Additionally, in America landscape ecological research was directed to natural landscapes whereas in Europe landscape ecology had routinely stressed questions regarding human dominated and strongly modified environments (Hersberger 1994).

1.2 The domain of landscape ecology

Landscape ecology is an interdisciplinary branch of science that owes much to e.g. community ecology, biogeography, and population ecology. It grew on the coattails of conservation biology, but instead of focusing on single topics, such as small population problematics or insularization and area effect *per se* (e.g. Soulé 1980, 1985), landscape ecology directs attention toward issues of spatial characteristics in various environments and the scale of ecological processes in space and time. Landscape ecological studies attempt to define the interactions between organisms and their immediate environments, i.e. how ecological systems deal with spatial heterogeneity. The structure of habitat mosaics set constraints for living organisms. For instance, the availability of suitable habitat for breeding may be limited spatially, population interactions between adjacent areas or colonisation of entirely novel areas can be hindered by structural characteristics

in the landscape. To what degree the physical structuring of a landscape (pattern) affects dynamic ecological interactions (process) in a complex landscape is the general question that landscape ecological research attempts to answer (Hansson 1977, Risser *et al.* 1984, Urban *et al.* 1987, Turner 1989, Pickett & Cadenasso 1995).

The basic concepts in landscape ecology are structure, function, and change. Structure refers to the spatial characteristics of the landscape elements and function denotes the ecological processes that take place in that space. Landscape change implies the temporal dimension of the space and, thus, the continuous dynamic development in spatial structure and function in time (Forman 1995). Landscape structure is further divided into composition, configuration, and connectivity, which determine the structural characteristics of the space in more detail (Taylor *et al.* 1993, Merriam 1995, Bennet 1998). Composition describes the proportion of qualitatively different landscape elements in space without any reference to their location. Comparatively configuration explicitly locates landscape elements in a spatial context and fixes the location and dimension of one element with respect to all other elements (Kozová 1983, Dunning *et al.* 1992). Connectivity characterises processes in a landscape that contribute to a functional demographic unit (Merriam 1984). Thus, landscape connectivity depends on the composition and configuration of landscape elements but, also, on an organism's ability to perceive and discriminate between landscape elements and cross boundaries when selecting habitat for breeding or dispersing among preferred landscape elements (Wiens *et al.* 1985, Stamps *et al.* 1987, Addicot *et al.* 1987, Hansen & di Castri 1992, Zollner 2000).

Heterogeneous landscapes constitute habitats having different qualities and ecological properties. According to these characteristics they can be structured as habitat patches (Forman 1995). Habitat patches are homogenous areas that comprise similar ecological properties and deviate in this respect from adjacent habitat patches or the surrounding habitat i.e. the landscape matrix (Forman & Godron 1981). The number and characteristics of landscape elements in space are basically determined by regional climatic conditions and underlying edaphic factors (Wiens *et al.* 1985, Zonneveld 1989). A third landscape element that is often included in landscape ecological examination is the consideration of landscape corridors. Corridors are distinct strips of particular habitat that link other habitat patches in space. However, the concept of ecological corridors can be included in landscape connectivity i.e. as a probability that an individual will traverse the space between habitat patches and colonise habitat patches in a landscape (Taylor *et al.* 1993, Bennet 1998). Population responses to heterogeneous mosaics of landscape elements result from species-specific habitat affinities (e.g. habitat selection and dispersal abilities) that can either be invariable throughout the life-history of an individual or variable when certain habitat is required only during one particular stage of a life-cycle (Wiens 1976, Haila 1990, Pearson *et al.* 1996, Andrén *et al.* 1997).

1.2.1 The appropriate level of observation: the dilemma of scale

Ecological characteristics of a habitat patch do not solely determine the ecological state and dynamics of a single patch, but processes and interactions between other habitat

patches in the surrounding environment may also influence its state. This dynamic and the influence of larger areas on local conditions imply the importance of the scale and scale-dependence in ecological phenomena. Scale is characterised by invariable patterns and processes within the extent of a particular scale. Changes and increasing variation in pattern and processes indicate the transition from one domain of a scale to another (Wiens 1989, Haila 1990, Bellehumeur & Legendre 1998). In general, for animal ecological studies, usually three domains of scale are discriminated: home range, local, and regional scales. Single individuals operate at the level of a home range, whereas dispersal and population processes occur at the local scale, and between-population interactions and patterns within a species geographic range are distinguished at regional scales of observation (Wiens *et al.* 1986, Kotliar & Wiens 1990, Fig. 1). Hence, during their life-history individuals respond to landscape characteristics that are apparent at multiple scales. Hierarchical properties of an ecological scaling strongly suggest that domains of scales are species-specific and, thus, the scale of investigation must be based on a species' ability to perceive and respond to its environment (Wiens 1989, Pearson *et al.* 1996). Spatial scaling also proposes that generalisations across scales or among species are likely to be misleading. Therefore, detailed knowledge regarding a species biology is an important prerequisite to appropriately distinguishing the correct scale of observation (Lima & Zollner 1996). In addition to spatial scaling, the temporal scale of biological events such as forest patch dynamics, generation length, population cycles and dynamics, or even evolutionary adaptation to changing environmental conditions are relevant time spans to consider (Orians & Wittenberger 1991, Fahrig 1992). Time scale of observation is often shorter than many of these processes. Since ecological processes generally occur over time frames far beyond research potential, short-term studies and temporal snapshots may fail to detect essential details or the range of variation in pattern under study (Wiens *et al.* 1986).

1.3 Theoretical and modelling approaches in landscape ecology

Landscape modelling has been much encouraged by ongoing intensive management of natural environments and accelerating loss of habitats (Franklin & Forman 1987). It is widely agreed that the current development has had several negative consequences to biological diversity and ecological processes. This has raised the question of how much original habitat should be left and how it should be embedded in an otherwise altered landscape matrix (e.g. Diamond 1975, Fahrig & Merriam 1994). The theory of island biogeography already suggested that the area of oceanic islands and their spatial arrangement had an effect on species numbers on islands (MacArthur & Wilson 1967). Subsequent research on land bridge islands showed that a progressive decrease in island size due to rising sea level after the ice age and the following breakdown of the mainland leads to a reduction in mammal and avian species numbers (Wilcox 1980). The effect of a reduction in species numbers generates a time lag during which the species pool relaxes to lower level of species diversity (Diamond 1972, Tilman *et al.* 1994). The insularization process on mainland and terrestrial ecosystems deviates from the oceanic seascapes because of a completely different matrix quality. Surrounding sea composes a hostile

matrix element for terrestrial animals but continental landscapes often constitute a heterogeneous and dynamic habitat mosaic of less hostile matrix characteristics.

Landscape ecological modelling approaches have provided important information on how structure in space develops and changes with the varying amount of suitable habitat. In neutral landscape models (neutral percolation models) spatial structure in model landscapes results from a random process in which all other physical and biological factors are excluded (Gardner *et al.* 1987). These simulations have demonstrated that in landscape development there are different stages that have dissimilar quantitative characteristics. After certain threshold values in the proportion of a suitable habitat landscapes lose their permeability and connections along original habitat across the space cease. The average size of habitat patches reduces rapidly, and their mean interpatch distances increase continuously (Turner & Gardner 1991). If neutral random models are made more complicated by affecting the explicit spatial location of habitat patches (e.g. fractal models) the same landscape patterns and trends prevail, but critical threshold levels change (With *et al.* 1997). For instance, the largest patch that still expands from one edge to the other and, thus, bridge the model landscape in random percolation models, breaks down when 59 % of original habitat is left, whereas in fractal models the same threshold is reached at 20–30 % level of remaining original habitat (With & Crist 1995).

Another important finding of the modelling approaches and analysis of empirical data is that although habitat loss (decrease in the amount of habitat) is normally causing the fragmentation of the landscape (subdivision of a uniform area into fragments) habitat loss effect and fragmentation effect have to be kept separate and studied as different characteristics of a functional space in terms of species existence and survival (Saunders *et al.* 1991, Andr n 1994, Fahrig 1997, Bender *et al.* 1998). It seems that much of the decline in biological diversity can be explained by habitat loss alone i.e. it is a pure area effect. However, after a certain threshold value, landscape configuration or spatial spacing of habitat patches have an additional effect and species richness and population densities tend to decrease faster than predicted by the area alone (Andr n 1994, 1996). Empirical studies suggest that the threshold for fragmentation effect in birds and mammals lies between 10–30 % of the amount of original habitat (Andr n 1994). Fahrig (1998) suggested that fragmentation effect influences the species persistence in a landscape under very narrow and limited conditions and the habitat loss effect is overwhelmingly more important than fragmentation effect. Nevertheless, the histories and qualities of real landscapes vary conspicuously from model approaches and species landscape responses cover extremely many ecological conditions that have not been included in theoretical models. Models are important for formulating new questions and to set preferences for empirical research (With 1997, With & King 1997), but more data on real landscape patterns and processes are still urgently needed to understand fragmentation problematics in a variety of taxa and under various ecological conditions (Robinson *et al.* 1992, Harrison & Bruna 1999, see also Tischendorf 2001). Recent studies on the role of the matrix habitat and its quantitative characteristics such as the gap structure indicate that the colonisation of habitat patches cannot be estimated precisely by examining habitat patch structure simply because colonisation probabilities of habitat patches in a landscape are matrix dependent (With & King 1999).

The patch-matrix concept in landscape ecology has much in common with dynamic population models (see Hanski 1999) in terms of how they divide space into units of interest and intervening area that separates them from each other. However, in landscape ecology, focal habitat is surrounded by a matrix i.e. other habitat types, whereas in population models, locations that are occupied by a population are separated by isolation. Nonetheless, both theoretical approaches define explicitly habitat patches or locations of populations in space. These approaches, however, differ in how they characterise intervening space. In landscape ecology, the matrix is quantified in more detail and the matrix quality is an important factor in a landscape pattern analysis (e.g. With & King 1999). In population models, the distance between two populations implicitly includes matrix quality and its implications for population dynamics in the system. A successful synthesis of these two approaches depends much on the importance of landscape matrix and its role in population processes. The fact that landscape responses of species vary considerably raises an interesting question: which taxa are constrained by matrix quality and which ones by pure isolation. In order to understand ecological properties of landscape context it is necessary to have a greater body of knowledge on landscape associations for a variety of species.

Despite of the recent progress and development in landscape ecological research, most of the landscape ecological studies are yet, to large extent, empirical and descriptive. Because of the short history of landscape ecology as a sovereign discipline and the complexity of spatial systems, landscape ecology still lacks a general body of theory (Zonneveld 1990, Wiens 1992). Due to the weak theoretical background rigorous hypothesis testing and experimentation have not yet been carried out in landscape ecology. However, long temporal and large spatial scales do not often enable controlled, replicated experiments (Hargrove & Pickering 1992). The body of theory of landscape ecology is developing presently (Bissonette 1997, Wiens 1995). Perhaps the fruitful combination of landscape ecology and metapopulation theory will bring new insights for formulating a theory of spatially and temporally dynamic landscapes which also incorporates hierarchical properties of ecological processes.

1.4 Boreal forest landscape: the setting of the study

In landscape ecological studies it is of great importance to consider the history and natural characteristics of a study area, but also the extent and intensity of human influence in that particular landscape. For forest-dwelling species northern boreal forest landscape is by no means a homogenous large block of forest with uniform, predictable landscape structure. On the contrary, northern taiga forest is literally a vast mosaic of several landscape elements that are in a constant dynamic state of change (Sousa 1984, Pickett & White 1985). Some elements such as water bodies and wetland areas are practically permanent parts in this mosaic, but forested land is dynamic and under repeated disturbance and recovery processes (Esseen *et al.* 1997). Common disturbances in boreal taiga range from forest fires and storm winds that operate at a large scale to small scale patch dynamics (White 1979). Subsequent forest succession in a disturbed area follows patterns that are typical of regional climatic conditions and local soil

characteristics (Bonan & Shugart 1989). These recovery processes result in a spatially heterogeneous mixture of different forest types and seral stages in a forest landscape. This dynamic framework forms a starting point to studies on all organisms that have adapted to boreal forest setting (Tiebout & Anderson 1997). The important outcome of the dynamics in boreal forest ecosystem is that at a large scale taiga forest landscape is regularly fragmented by natural non-forested areas and, secondly, forested habitats such as late seral forest patches, for instance, are spatially segregated and their location tend to change in time.

1.4.1 Human land use history and antropogenic landscape patterns

In northern Finland, man has interacted with his immediate environment ever since the first settlers invaded the large tracts of forest. In the course of history, human influence in terms of the exploitation of forests has become more extensive and intensive (Kimmins 1997). Before modern times human induced changes in boreal forest ecosystem were subtle and local. Compared with natural disturbances, they tended to have a minor effect on overall landscape structure. At a forest stand level, household harvesting or slash-and-burn-cultivation altered profoundly only forest stand structure but, on the other hand, at the same time these activities were a source of e.g. deciduous-rich forest sites (Aarnio 2001). When forest harvesting in Finland was organised in the middle of the 1800's and forests became an important raw material reserve for the growing saw and paper industry, systematic forest management began at a larger scale (e.g. Cajander 1910). In the 20th century, forest practises were pursued throughout the forestland in Finland and harvesting operations were extended to the Finnish Lapland. However, although forestry now operated at a large scale and the whole forest landscape was subject to human influence, "old-fashioned" forest harvesting did not bring about dramatic changes in landscape structure. The age structure of stands was mostly affected by selective cutting of large diameter timber, but composition of forest types and their configuration or large scale connectivity in forest landscapes altered only relatively little. Since the 1950's, in parallel with the modernisation of forest harvesting methods, intensity and efficiency of forest practises became a new paradigm (Leikola 1983). New methods such as clear-cutting, regeneration of stands by pine plantations, suppression of broad-leaved trees, and soil preparation shaped the forest landscape in a new fashion. Gradually, but inevitably modern forestry altered landscape structure and converted it into economic forest landscape (Franklin & Forman 1987, Hunter 1990). A consequence of this trend was that landscape composition on public land turned towards pine dominance and homogenous even-aged forest stand structure (Anon. 1998). Landscape configuration resulted from rational forest planning and natural landscape connectivity was often decimated by large clear-cuts and dense sapling stands that fragmented previously continuous forest blocks (Mykrä *et al.* 2000). The present day landscape structure is largely a product of relatively short-term intensive forest planning and management and it is likely that this will have an impact on ecological processes in forest landscapes still in the future (Rolstad 1991).

1.5 Siberian flying squirrel as a landscape ecological object

The Siberian flying squirrel (*Pteromys volans*) is distributed through the Eurasian boreal taiga zone from Hokkaido, Japan, to the Baltic countries and Finland (Ognev 1940, Wilson & Reader 1993, Dobson 1994). In Finland, the species range extends from southern country to southern parts of the Finnish Lapland. In the south the range seems to be rather continuous, whereas in northern Finland the species is more common in western Kainuu and Koillismaa than along the eastern border of the country. There are no recent documented observations of the species from northern Ostrobothnia (Reunanen 1998). No permanent populations appear to have been established on the Swedish side of the Tornioriver, although some historical observations from Finnish Lapland exist (Hokkanen *et al.* 1982).

The Siberian flying squirrel is a nocturnal arboreal species. The species prefers mature mixed spruce forests and tends to favour forest sites that are conspicuously rich in deciduous trees, especially aspen (*Populus tremula*), and distinctively large spruces (*Picea abies*; Hanski 1998). The species is omnivorous, but its diet principally constitutes of leaves in summer and catkins and buds of alder (*Alnus* sp.) and birch (*Betula* sp.) in winter. Supplementary food items, such as seeds and buds of conifers, are consumed frequently (Mäkelä 1996, own observations). Hence, food availability does not seem to be a limiting factor restricting its space use in forest landscapes. The Siberian flying squirrel is predated mainly by large owls and the goshawks (*Accipiter gentilis*), and to some extent by martens (*Martes martes*). However, due to relatively low population densities of the species, it appears to be of minor importance to predators and only occurs occasionally as a prey item in their diet (see e.g. Huhtala *et al.* 1976), unlike North American flying squirrels that are an important prey for some avian predators (Carey *et al.* 1992). The occupied forest sites apparently provide the species sufficient food reserves and cavities for safe breeding and roosting. Also, red squirrel dreys are frequently used for roosting (Hanski *et al.* 2000, own observations). In addition to forest habitats, the Siberian flying squirrel also occurs in cultural environments in southern Finland (see Sulkava *et al.* 1994, Wistbacka *et al.* 1996).

Home range sizes differ remarkably between the sexes. Mean home range size for males is close to 60 hectares and this area contains several separate habitat patches that are visited regularly. Females are more site tenacious and concentrate their activities principally on one habitat patch. The average home range size for females is 8.3 hectares. Home ranges for females do not overlap and they inhabit their own habitat patches; in comparison, males frequently include more than one female in their range and, therefore, move regularly among sometimes rather distant habitat patches (Hanski 1998, Hanski *et al.* 2000, own observations). Juveniles disperse in late summer and establish their own home ranges within a mean distance of two kilometres. However, some individuals, more often females, disperse distances of up to eight kilometres (Selonen & Hanski 2000). During the dispersal they can cross open areas up to 100–150 meters (own observations). The Siberian flying squirrel has been listed as an endangered species in Finland (Rassi *et al.* 2000). Public and game inquiries in the late 1970's indicated that the decline of the species has apparently been continuous since the 1950's (Hokkanen *et al.* 1982). This negative population trend was recently documented also in smaller, more intensively

studied areas in southern Finland (Anon. 2001). The decline of the species was attributed to habitat loss and general degradation of remaining habitat patch quality. Also, fragmentation of forest areas was seen as a process that creates unfavourable landscape patterns for the local long-term persistence of the species (Hokkanen *et al.* 1982, Rassi *et al.* 2000).

1.6 Thesis objectives

The aim of this study was to examine landscape responses of the Siberian flying squirrel in northern Finland where the species occurs at the north-westernmost limit of its global range. In order to characterise landscape patterns quantitatively three functionally different habitat types were in focus: first, mature spruce dominated habitat patches preferred by the species, second, areas that act as connecting habitat for the species, and, third, unsuitable habitats, such as sapling stands and treeless open areas. Spatial structure of these landscape elements was investigated empirically in Kainuu and Koillismaa regions to detect which landscape patterns are associated with the occurrence of the species and to find relative priorities of landscape characteristics (I, II, III). Moreover, in these studies, the spatial resolution ranged from home range (IV) to local (I, II) and regional scales (III) (Fig. 1). In order to gain more accurate information on how the spatial structure of these functionally different landscape elements correlates with the occurrence of the species at a local scale, presence/absence data sets from well-defined study areas in Koillismaa were analysed (V). These studies also yield information on the relevancy of remote sensed images and the applicability of GIS techniques in specific ecological and conservation issues. The practical outcome of this research suggests some general guidelines for forests management planning and single-species conservation efforts.

2 Material and methods

2.1 Pellets on the ground – signature of the species presence

The occupancy pattern of the Siberian flying squirrel in larger forest areas or its presence/absence in single habitat patches was determined by searching for visible signs of the species in the field. This species is nocturnal and rather difficult to observe, thus, faecal pellets at the base of prominent spruces and foraged leaves under large canopy deciduous trees provide a means to track its presence in the wild (Skarén 1978). Field signs are fairly reliable in confirming the presence of the species, but its absence is more difficult to ascertain. Radio-tracking of the individuals has suggested that forest sites that are clearly marked with droppings normally belong to central parts of the home range and are also permanently occupied (own observations). This applies particularly to female home ranges. Males that regularly visit several habitat patches may remain undetected, especially if the habitat patch is not occupied by a female. Therefore, some good quality forest sites that are in fact occupied may be extremely difficult to identify in the field as occupied by looking for the pellets only. Foraged leaves found on the ground indicate the actual presence of the species. However, some habitat patches of seemingly lower quality may have been in temporary use or traversed by dispersing juveniles, but one can easily find pellets there and label that particular patch as occupied.

Another source of error comes from forest management practices. After logging some stands formerly suitable for the Siberian flying squirrel become deserted and individuals colonise remaining nearby remnants of forest that are of lower quality (Taulman *et al.* 1998). Temporal inaccuracies depend on the forest site properties because the decay rate of droppings vary from one to three years and, thus, entail a considerable time lag in patch occupancy (Putman 1984). Therefore, a recent occupancy of a habitat may still be discovered after a few years, which is likely to have an influence on very short-term studies by overestimating the number of inhabited habitat patches. However, most of the occupied habitat patches were clearly occupied (judged by the number of recent droppings) at the time of observation. The occupancy status of only a few habitat patches was based on very small number or single pellets. The proportion of those habitat patches was around 10 %.

2.1.1 Presence/absence data in ecological research

The advantage of presence/absence data is that it is easy to collect and enables to extend the scale of the study because habitat sampling is not so time consuming. The data are quantitatively neutral and characterise essentially the qualitative occupancy status of the habitat patch. Thus, all habitat patches despite of their size or other ecological attributes are of the same value and ranked equally. Any population density estimate classifies patches and gives quantitative information on habitat patches (Raivio 1992). Presence/absence data sets are often temporal snapshots and contain no information on variation in time or turnover times in occupancy pattern. Therefore, long-term studies help distinguish habitat patches that are permanently occupied from the ones that are most of the time vacant, but by chance can be occupied at the time of observation.

Incidence data have often been used in predictive models to account for species habitat preferences or occurrence patterns (see e.g. Rita & Ranta 1993, Boyce & McDonald 1999). Results of predictive models should always be validated with an independent data set and the fit of the model must be carefully considered. The examination of the source of prediction errors and the origin of false positive and/or false negative predictions must be analysed to assess the accuracy and generality of the model (Fielding & Bell 1997, Araújo & Williams 2000). Although predictive models are conventionally intended to allow broader generalisations within the limits of their domain they tend to be specific and apply only to a well-defined group of species (Cherill *et al.* 1995, Miller *et al.* 2000). However, species' landscape responses may further vary even among congeners (Lindenmayer *et al.* 1999). At a large continental scale, estimates of primary productivity or rough habitat type classification can be used to predict very general species richness patterns (Danell *et al.* 1996). This further suggests that it is crucial to measure independent habitat and landscape variables at correct scales. Variables measured at the regional scale can confuse the interpretation of local scale processes and most likely result in a lack of true landscape responses of the species (McDonalds *et al.* 1996, Cardillo *et al.* 1999).

2.2 Landscape pattern analysis in GIS

The rise of landscape ecology coincides roughly with the development of commercially available remote sensing techniques (accurate aerial photographs and digitised satellite images) and advanced geographic information systems (GIS). These new methods provide certain evident advances allowing the examination of larger scale landscape patterns and provide tools capable of handling and processing large multiscale data sets. They further facilitate the computation of landscape metrics and the analysis of often complex landscape structure (Pukkala 1985, Star & Estes 1990, Haines-Young 1993). Large-scale changes in a landscape structure in time can also be analysed by comparing images from different time periods (Johnson 1990). Modern satellite images are reasonable high in resolution allowing the detection of landscape responses of species at rather small scales, that is, if habitat characteristics are discernible from the images and classification of satellite images is correct, relevant, and precise.

This study exploits Landsat TM 5 satellite images. Land use and forest resource data were derived from Finnish national forest inventories (NFI; Tomppo 1991, 1993, Tomppo *et al.* 1998). The interpretation of satellite images is based on comparisons of nearest neighbouring ground study plots to adjust the reliable classification of images (Tomppo & Katila 1993). The resolution, i.e. pixel size, of the system is 25 x 25 meters. Digital maps were utilised to distinguish non-forested landscape classes (fields, wetlands, settlement etc.) from forested ones. In this system, up-to-date forest stand age and timber volume estimates for all main tree species can be produced. This classified satellite image can further be reclassified in GIS to analyse landscape patterns.

GIS procedures are prone to two types of error: positional and attribute accuracy of the satellite data (Mattila 1993). Positional accuracy refers to the spatial shape, size, and exact location of an element. In this data this error has been estimated to be 0.5–1.0 pixels, which is unlikely to have any significant effect on larger scale landscape responses of organisms. However, in small-scale studies, the relevancy of this error must be considered carefully and its effect on results clearly understood. Attribute accuracy deals with the system's ability to discriminate different habitat types. Definition of focal habitat is basically subjective and is premised on the understanding of the species ecology. In heterogeneous landscapes the boundaries of habitat patches are often subtle and diffuse, that is why they are sometimes difficult to identify from habitat mosaics (Gustafson & Gardner 1996, Knight & Morris 1996). Therefore, inaccuracies in landscape classification and habitat patch identification may confound landscape effects or even bias results. For instance, coniferous trees (pine and spruce) are more accurately separated when either species clearly dominates the canopy, but estimates for mixed stands are less precise. Deciduous trees are to large extent discriminated from conifers, but different broad-leaved tree species cannot be discriminated (Tomppo & Katila 1993). Transition zones between habitat types or pixels that are located at the edge of water bodies are a constant source of error and become frequently misclassified (Kalliola & Syrjänen 1991, Tomppo *et al.* 1998). Nonetheless, forest management has increased the contrast between landscape elements and created sharp landscape boundaries, which facilitates the discrimination of habitat patches and reduces the risk of misclassifications. Generally, the smaller the scale of observation the larger error limits one has to accept. In present studies, classification error has to be examined at two levels. At larger scale studies (I, II, III) classification inaccuracies cannot be controlled completely. However, this error is systematic and misclassified habitat patches are in principal small in size. At smaller scale studies (IV, V), this source of error can be controlled by excluding human caused changes in a landscape structure and by checking habitat patches from aerial photographs and in the field.

2.3 Landscape variables and statistical analysis of landscape data

Landscape structure is characterised by variables that describe a single habitat patch and the spatial distribution of this habitat type in space or landscape structure in general. The measurement of landscape metrics was carried out in GIS by employing FRAGSTATS software (McGarical & Marks 1995). Several variables that quantify the landscape

structure were calculated. Variables were continuous, but they are often strongly intercorrelated and do not always distribute normally. The number of variables that are easily available and their statistical properties, hence, require attention in statistical analysis. The selection of appropriate variables is of foremost importance during early stages of a study. It is not necessary to accept all the variables of seeming relevancy, but only the minimum set of variables should be considered to make the analysis of large data sets simple. The variables have to be straightforward to interpret and firmly linked with the ecology of the focal species or the process of interest. Most criticism directed to the commonly used landscape metrics concern correlations between variables and the range of their utility (Schumaker 1996, Hargis *et al.* 1998). Deviations from normality are mainly due to frequent zero values in data and the fact that, for example, habitat patch sizes in human modified landscapes are skewed to smaller size classes. Strongly correlated explanatory variables are undesirable, but, if they clearly express distinct and separate landscape characteristics, it is justified to include these variables in the statistical analysis. Correlations and the lack of normality call for non-parametric statistics (Sokal & Rohlf 1995). Multivariate statistical methods are appropriate for the analysis of multivariate landscape data sets. Multivariate statistics enable the compression and simplification of often complex data and helps to detect structural patterns in the data (Jongman *et al.* 1987, James & McCulloch 1990). For data sets where the dependent variable is binary, i.e. presence/absence data, logistic regression methods provide a convenient statistical modelling tool for multivariate landscape data.

3 Results and discussion

3.1 Landscape structure around old-growth forest areas in Kainuu (I)

In Kainuu, landscape characteristics of occupied and unoccupied old-growth forest areas were compared to investigate which landscape patterns account for the presence/absence of the species in relative large and continuous forest areas. Twenty old-growth areas in Kainuu were systematically selected and checked to examine the occupancy of the Siberian flying squirrel. Because the number of observed occupied forest sites per study forest areas ranged from total absence to several observations they were classified into two categories: first, forest areas that host a population and, second, the ones that lack the species or where population densities are likely to be very low. Landscape analysis included seven landscape classes and the landscape structure was studied at seven spatial scales (Fig. 1).

The main result of this study was that old-growth forest areas that were unoccupied by the Siberian flying squirrel were surrounded more often by open areas. This habitat type was proportionally more dominant and patches of open area were larger in size and their nearest neighbour distances were shorter than in occupied forest areas. The quality of the matrix is likely to decrease the probability of occupancy so that even large areas of suitable habitat remain uncolonised if open habitats (lakes, wetlands, clear cuts, or fields) constitute a significant portion. The other interesting result of the study was that the small-scale variation at the level of home range within forest areas promotes the species occurrence. This may be caused by small openings in the forest canopy and the regeneration of deciduous trees in the vicinity of these canopy gaps. The dominance of mixed pine-spruce forest at the home range scale in unoccupied forest areas indicates the role of some qualitative aspects of the forest area. It suggests that the shift from spruce dominated to more pine dominated forest habitats may be unfavourable to the Siberian flying squirrel. Therefore, the abundance of pine-dominated forests is likely to influence the habitat selection process of the species at the forest site scale and colonisation rates at larger scales. The observed absence of the species from eastern parts of Kainuu further suggests that there may be a regional-scale gradient in habitat quality, which affects the species distribution. The size of old-growth fragments does not seem to play a role in

occupancy patterns, which is quite expected, for all forest areas were large (often $\gg 1$ km²) and could easily include several individual home ranges or even host a local population.

Far reaching conclusions on the basis of this data set cannot be drawn because of the broad landscape classification. At larger scales of observation, variation in the landscape types tends to increase. However, for the habitat classification at larger scales many landscape classes must be combined and, therefore, some of them lose their identity in the analysis. For example, in this study landscape matrix included several ecologically discrete landscape elements e.g. sapling stands whose role was masked by the classification. Also the amount of pine in the pine-spruce landscape class can vary between 20 and 80 %. At the large scale ($r > 5$ km), the proportion of matrix habitat becomes overwhelming and the variation between examined landscapes disappears i.e. landscapes become similar in terms of a landscape structure. However, at smaller scales ($r < 5$ km) landscape classification performs sufficiently well and points out important landscape responses of the Siberian flying squirrel at these particular scales.

3.2 Local scale habitat structure in Koillismaa (II)

In order to examine local scale patterns in habitat patch occupancy of the Siberian flying squirrel in Koillismaa the distribution of the species and the location of occupied forest sites were mapped in the field. Landscape structure around occupied forest sites was examined to characterise patterns in landscape composition and connectivity that are associated with the presence of the species. Landscape structure around occupied forest sites at scales of one and three kilometres were compared to randomly drawn locations on forestland to yield a reference landscape structure (Fig. 1). The landscape was classified into ten landscape categories but they were handled as three functionally different landscape classes: breeding, dispersal habitat and unsuitable open areas.

Forest landscapes where the Siberian flying squirrel was present contained more breeding habitat and were better connected to other habitat patches by suitable habitat for movement than other landscapes. Landscape structure around random locations consisted of smaller habitat patches and higher patch densities, which indicate a more fragmented landscape structure (Turner & Gardner 1991). This suggests that landscape graininess turns from coarse in occupied landscapes to finer grain size in random landscapes (see Rolstad & Wegge 1989). For persistence of the Siberian flying squirrel coarse graininess at a local scale is likely to be beneficial if not necessary. At the scale of one kilometre, the proportion of dispersal habitat in occupied landscapes covers over 50 % of the area but decreases to 40 % when the scale is widened to three kilometres.

In this study occupied landscapes were compared with random and thus the general landscape pattern. The use of random locations as a null landscape structure may not entail important landscape characteristics that contribute to the absence of the species. Hence, landscape patterns that are linked with the occurrence of the species are only of indicative importance for the presence of the species. The actual comparison does not provide information on which characteristics are harmful or even detrimental for the spatial distribution of the species and, thus, gives no clue to account for the absence of the

species. For practical forest management information on landscape characteristics that promote species presence is as important to understand as the ones that are unsustainable and disadvantageous for the species.

3.3 Distribution of the Siberian flying squirrel in northern Finland (III)

Till the mid 1990's the distribution of the Siberian flying squirrel in northern Finland was basically unknown and it was generally based on single observations of the species over this vast area. Hokkanen *et al.* (1982) even predicted that the northern populations of the species will go extinct in the near future. Nevertheless, biodiversity inventories in old-growth fragments in the early 1990's (Rassi *et al.* 1996) and systematic mapping of the species in Kainuu and Koillismaa (I, II) showed that the Siberian flying squirrel still occurs in natural forest areas in northern Finland. However, the present range appeared to be irregular and suggests that the species is rather common only in the western parts of Kainuu and Koillismaa. In Pohjanmaa the species seems to be absent and rather rare in eastern Kainuu. In this survey, landscape structure at regional scale was described to account for the observed distribution of the Siberian flying squirrel in northern Finland. Large-scale habitat patterns of seven landscape classes and their spatial arrangement were investigated and landscape patterns were compared between three regions (Fig. 1). Additionally, natural fragmentation was separated from human caused subdivision of forest landscapes. This was estimated by comparing the present overall landscape structure to habitat structure in protected nature reserves.

Results of this study suggest that the presence of spruce dominated forests at a large scale contribute to the presence of the species whereas an increasing proportion of peatlands i.e. unsuitable habitat correlates with the species absence. The gradient from more luxuriant forest types in the western parts of Kainuu to poor soil types and pine dominated forests in the east, as already suggested in (I), seem to account for irregular patterns in occupancy and, probably also, lower population densities. It was assumed in the study that existing nature reserves present more original habitat structure than the present managed forest landscapes. Comparisons of landscape patterns among nature reserves and regional landscapes show clear differences in habitat composition and stand age class distribution. Because the actual occurrence of the Siberian flying squirrel in all sampled nature reserves and landscape squares is not known, any threshold proportion of spruce forests cannot be determined from the present study design.

The division of the north Finnish forest landscape into three subregions was basically subjective because exact boundaries of the range of the Siberian flying squirrel in northern Finland could not be outlined. The boundary between Pohjanmaa and Koillismaa is rather sharp due to geological factors and follows the highest shoreline after the ice age (Anon. 1992). The limit that demarcates Koillismaa from Kainuu is diffuse and extremely difficult to identify. However, regional scale landscape patterns seem to influence the distribution of the Siberian flying squirrel. Surveys of biodiversity values in Russian Karelian natural forests did not document a single sighting of the species (Pyykkö 1996). Long term inventories on mammal fauna in Kostamuksha nature reserve

just opposite to Kainuu in Russian Karelia report only occasional findings (Pozdnyakov 1997). Habitat type mapping in Russian Karelia shows that large forest areas on the Russian side of the border are pine dominated and spruce forests cover approximately from 10 to 30 % of the area (Gromtsev 1996, Pyykkö 1996). This result also suggests likelihood that the Siberian flying squirrel colonised northern Finland from the south and not from the east. The result also gives a hint why the species is still missing from the fauna of Sweden.

3.4 Are large-scale landscape patterns visible at a home range scale?

(IV)

Habitat selection of an organism depends on necessary resources for foraging and breeding and it ultimately takes place at a relatively small scale. Therefore, habitat composition analysis within a home range of an individual is fundamental information for understanding landscape responses of a species. In a field survey, forest structure in forest sites that were actively used by the Siberian flying squirrel was characterised and compared to randomly chosen forest sites in old-growth forest area. In addition, habitat composition in home ranges of radio-collared individuals was analysed from satellite images (Fig. 1). Results from these two approaches were compared to determine which habitat characteristics were in common and more interestingly discernible from satellite images in GIS.

Data from field surveys showed that occupied sites are distinctively situated in forest sites where timber volume of spruces is higher than on average in the stand, and that deciduous trees comprised a marked proportion of these forest sites. Large aspens seem to be well represented. Satellite imagery data agree to a large extent with field observations. Intensively used locations in home range tended to have higher timber volume estimates, especially that of spruce, than on average for home ranges. There was a tendency to avoid pine dominated forest sites suggesting a marginal role of pine for breeding and foraging when other better quality habitats were available. However, although deciduous trees were an important component in forest structure in the field study they were not pronounced in GIS analysis.

It has been previously documented that deciduous trees are important habitat constituents of forest sites occupied by the Siberian flying squirrels (e.g. Hanski 1998). Therefore, the proportion of deciduous trees and their spatial dispersion in forest habitat patches is an evident measure of the quality of that habitat patch. Empirical findings showed that broad-leaved trees were firmly linked with the occurrence of the species in northern Finland. Failure to detect deciduous trees in mixed forest in GIS analysis is mainly due to inaccurate discrimination of broad-leaved trees from satellite images but also due to the resolution i.e. pixel size (Tokola & Heikkilä 1997). However, the number of sampled individuals and pixels in the resampling analysis were relative low and probably insufficient to draw substantial conclusions.

3.5 Is the presence of the Siberian flying squirrel in a habitat patch predictable? (V)

In order to have more detailed information on species' landscape responses other than general correlative spatial patterns at local or regional scales, research should be conducted at the habitat patch level. These studies have to include data on habitat patch characteristics and its spatial context as well as the status of the species, i.e. its presence/absence or population density, in that particular habitat patch. Therefore, habitat patch occupancy of the Siberian flying squirrel was investigated at the scale of discrete habitat patches to build a predictive landscape model for occupancy patterns at a local scale (Fig. 1). Suitable forest habitat patches were sampled in four study areas to determine the presence/absence pattern of the Siberian flying squirrel in habitat patches. Landscape data on habitat patch quality, structure of the surrounding landscape, and landscape connectivity were gathered to correlate observed presence/absence pattern with landscape characteristics.

Logistic regression modelling suggested that habitat patch quality (size and proportion of deciduous trees) seems to be the most important single factor that affects the probability of occupancy in a habitat patch. However, structural connectivity in a landscape increased the probability of species occurrence; even lower quality well connected habitat patches were occupied. The amount of habitat patches in the surrounding landscape seems to have a minor effect on occupancy. Predictions of the landscape model were tested with an independent data set. The landscape model, however, predicted the occurrence of the species in habitat patches in the test data set worse than in the training data set. In addition, the model predicted the absence of the species better than its presence.

Results of this study suggest that generalisations even in the same region can be risky and require careful consideration. The failure in predicting the presence of the species better rises some questions of underlying ecological processes i.e. turnover dynamics and/or recent changes in the landscape structure such as forest harvesting that affect the pattern in patch occupancy. The use of principal component analysis further conceals the effect of single variables and prevents the estimation of their independent contribution to the probability of patch occupancy. In large-scale studies where a habitat patch is used as a sampling unit, the importance of correct classification of habitat patches is a precondition to detailed habitat structure analysis and plausible landscape responses of the species in interest.

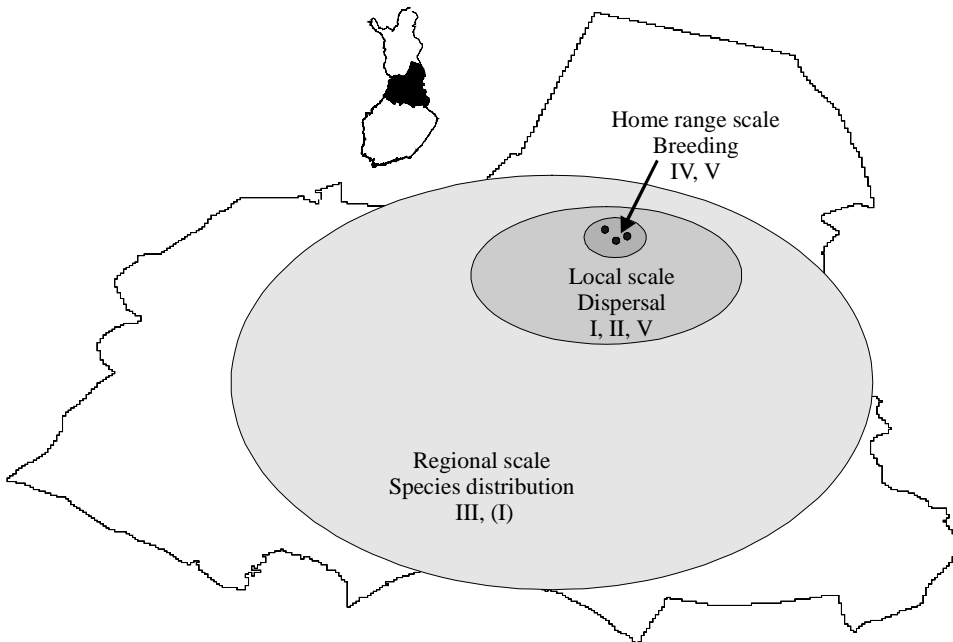


Fig. 1. Hierarchy of scales for the Siberian flying squirrel. Different hierarchical levels indicate ecological patterns from individuals at a home range level to local dynamic population and groups of populations at a large regional scale. Roman numerals refer to research papers in the thesis.

4 Conclusions

4.1 Landscape structure and the Siberian flying squirrel

4.1.1 Spruce dominated forest patch: a basic landscape element for the Siberian flying squirrel in northern Finland

Boreal taiga landscapes are diverse and heterogeneous in habitat types and their spatial and temporal patterns. Despite this general heterogeneity, forest habitat patches in landscapes are dominated by a few tree species. In northwestern Europe, boreal forests are mainly dominated by spruce and pine while broad-leaved trees occur principally on more nutrient rich soil types. Deciduous trees are also abundant during early stages of forest succession and in southern parts of boreal forest vegetation zone. The Siberian flying squirrel inhabits spruce and spruce-dominated forest habitats in Finnish boreal taiga and, therefore, the grain of the landscape for the species is delineated by individual spruce-dominated forest patches (*sensu* Wiens 1989, II, IV, V). Although the species seems to have accepted rural and semi-urban habitats in southern Finland, the extent of its distribution in northern Finland is determined by the amount of spruce forest and its spatial dispersion (Wiens 1989, I, III). At the habitat patch scale, the Siberian flying squirrel responds to the internal structure of a spruce forest patch (IV, V). The occurrence of the species in habitat patches has been shown to be associated with deciduous trees (Eronen 1996, Hanski 1998). Deciduous trees provide food and cavities for safe nesting and roosting, resources considered necessary for the species (Hanski *et al.* 2000). Deciduous forest sites are patchily located in natural forests and they are relatively small in size in the north of Finland. The size of a spruce forest patch and the amount of deciduous habitat inside the spruce forest determine the quality of the habitat patch, and affect the probability that the habitat patch is occupied in northern Finland (V) (Table 1).

But are spruce-dominated forest habitat patches the smallest landscape units to which the species is responding? Radiotracking studies have shown that adult individuals move among habitat patches and males especially visit even remote habitat patches frequently

(Hanski *et al.* 2000, own observations). This suggests that a single habitat patch as such might not be a sufficient landscape unit for individuals in landscapes where habitat patches are in general small in size, but instead a group of habitat patches forms an ecologically functional unit for persistence. Individuals may complement and/or supplement (*sensu* Dunning *et al.* 1992) necessary resources (nutrition, nests, mates etc.) that are spatially and temporally dispersed among habitat patches.

4.1.2 Landscape connectivity at a local scale

In order to estimate landscape connectivity, landscape structural characteristics that promote the movement of a focal species in a landscape matrix need to be identified. Also information on functional characteristics such as immigration and emigration rates from habitat patches and survival probabilities of individuals in a matrix during movements should be available (Tischendorf & Fahrig 2000a, b). Because these data are seldom obtainable, landscape connectivity in empirical studies refers in practice to structural characteristics in landscapes. The lack of demographic data on the Siberian flying squirrel does not allow to fully incorporate the functional aspect of connectivity into landscape connectivity measures.

At a local scale, landscapes that contain occupied habitat patches are structured in a coarse grain manner and they are less fragmented i.e. there are fewer but larger habitat patches for movement than in northern Finnish forest landscapes on average (c.f. Rolstad & Wegge 1987). Coarse graininess enhances landscape connectivity by providing larger uniform landscape units for movement. Habitat edges and the increase in contrast between habitat patches are likely to lower the probability of crossing the boundary (Wiens *et al.* 1985, Åberg *et al.* 1995). Sharp edges will block the movement of the Siberian flying squirrel if moving by gliding from tree to tree is prevented. However, narrow gaps are not likely to affect the space use of the species if open areas can be crossed by gliding (own observations). The effective landscape use at the local scale is enhanced if breeding habitat patches are embedded in the matrix of habitat where interpatch distances can be traversed along more or less forested habitat (V). Thus, at this scale, landscape connectivity for the Siberian flying squirrel is principally a matrix effect and the quality of matrix determines the degree of connectivity in a landscape (Table 1). However, individuals are unlikely to move along the shortest distance between two habitat patches, instead they tend to move along closed canopy forest habitat and cross narrow gaps. Therefore, interpatch distances should not be measured by using shortest Euclidean distance but by using landscape structural characteristics as a clue of landscape connectivity. This, however, provides good ecological knowledge on the species ecology. The dispersal potential of the Siberian flying squirrel ranges up to nine kilometres (Selonen & Hanski 2000), but some individuals are likely to disperse even further. The maximum dispersal distances normally cover several small and a few large habitat patches in northern Finnish forest landscapes where the species is rather abundant. Within the average dispersal distance of two kilometres there are always suitable habitat patches for the Siberian flying squirrel. Nevertheless, the role and proportion of long distance dispersers in population dynamics is not known (see Fahrig & Paloheimo 1988).

4.1.3 Landscape configuration of habitat patches

Habitat patch configuration has been considered an important structural characteristic in a landscape, but, for mammals and arboreal species in particular, landscape configuration is linked further to landscape connectivity. For the Siberian flying squirrel interpatch distances of occupied habitat patches tended to be shorter than what was observed for unoccupied ones (V). The proportion of open areas surrounding large old-growth remnants was connected to lower probabilities in occupancy (I). However, the composition of the surrounding landscape at local scales seemed to be rather similar for occupied and unoccupied habitat patches and had no significant effect on their occupancy probabilities (V). This suggests that the effect of physical arrangement of habitat patches is masked by other landscape characteristics or classification criteria of landscape elements. This may also indicate that landscape configuration was perhaps measured at the wrong spatial scale. At a local scale, structural connectivity, and the fact that most of the patches are within the dispersal range of the Siberian flying squirrel, are far more important than configuration (Table 1). Regional scale studies (I, III) did not detect any patterns in the intervening landscape, which is most likely a result of too coarse a classification or too large a spatial scale. Moreover, there are no unambiguous and satisfactory quantitative measures to characterise the dispersion and juxtaposition of habitat patches in a spatial context. Indices that describe spatial dispersion of landscape elements have often been developed in model landscapes and are therefore difficult to interpret in real landscape situations (Schumaker 1996, Hargis *et al.* 1998). Quantification of spatial arrangement of landscape elements would be important to illustrate landscape configuration more accurately. In boreal forest landscapes, local scale habitat patch configuration seems not to be very important for the Siberian flying squirrel, but at a regional scale the spatial spacing of larger landscape units such as old-growth forest areas or nature reserves is likely to have an effect on regional scale population dynamics. This suggests further that landscape configuration may be determined by long-distance dispersers and, thus, by occasional but regular interchange of individuals between subpopulations.

Table 1. Landscape characteristics at multiple scales and their importance for the Siberian flying squirrel in northern Finland.

Landscape characteristic	Scale			Study
	Home	Local	Regional	
Graininess	Very important	Important	Less important	II, (IV), V
Composition	Very important	Important	Important	I–V
Connectivity	Important	Very important	Less important	II, III, V
Configuration	Less important	Important	Very important	II, III, V

4.2 Spatial scaling for the Siberian flying squirrel

Siberian flying squirrels may respond to habitat and landscape structure at three hierarchical levels. The amount of spruce forest habitat in a landscape is likely to correlate with the spatial distribution of the species (III). However, the density of the species may depend more on the qualitative characteristics of the habitat patches (IV, V). Home ranges typically consist of one or more deciduous-rich forest sites on which the activity of individuals is concentrated during the breeding season (IV). This particular habitat provides required resources for successful breeding and survival and, therefore, constitutes the lowest scale for the species. At a local scale, the annual habitat use of individuals varies and they exploit a variety of forested habitats but roosting and seasonal foraging patches are located most frequently in spruce dominated habitat patches (Selonen *et al.* 2001, own observations). This indicates the next scale of perception for the Siberian flying squirrel. Dispersal ability of the species determines the scale of population interactions and avoidance of mating with closely related individuals. The extent of this scale is influenced by the landscape structure (I, III). Short-distance dispersers are likely to be responsible for local population dynamics, whereas long-distance dispersal entails the exchange of individuals and genes between spatially separate subpopulations.

4.3 Theoretical aspects

Patterns in randomly fragmented neutral model landscapes have exemplified the process of habitat loss and its consequences to landscape structure. Independent of the criteria of how model landscapes are subdivided, three main stages in fragmentation process are common. First, structural connectivity breaks down, then the patch sizes decrease and their number increases rapidly, and, finally, the isolation of patches is a direct consequence of the reduced patch sizes. Because neutral models eliminate all biological interactions and natural processes in order to produce a random pattern (Caswell 1976), they serve as an important reference background to real landscape studies (With & King 1997). Real landscapes, however, are often naturally fragmented in terms of target habitat and, therefore, e.g. the estimation of critical thresholds in proportion of the original habitat or in habitat isolation is difficult to conclude from the basis of neutral models only. The original pattern and landscape composition in real landscapes should be incorporated in these neutral models as a starting point to determine thresholds for the landscape structure. However, this presumes that the observed landscape structure supports a dynamic population under natural conditions. These conclusions are, on the one hand, species-specific and have to be assessed on the basis of species ecology and plasticity to respond to spatial changes in the landscape structure.

The boreal forest landscape is structurally heterogeneous and from the perspective of the Siberian flying squirrel it is naturally fragmented to some degree. The species inhabits forest sites that are temporary in boreal forest ecosystem (Spies & Franklin 1996) and it encounters habitats that are unsuitable for breeding or dispersing at a local scale (see Tiebout & Anderson 1997). This suggests that the Siberian flying squirrel has adapted to

live in a habitat mosaic and use the landscape matrix for colonising novel forest areas. Habitat loss and the amount and extent of totally useless habitat types, however, pose a risk to its local and regional persistence. Habitat loss effect is obvious, but the role of pure isolation effect remains relative. If habitats are isolated by wide open areas or sapling stands, isolation may be effective, but in case habitat patches are connected by forested habitat (Henein & Merriam 1990, III) even long interpatch distances are traversed and habitat patch networks function as an operative demographic unit.

4.4 Management of the forest landscapes for the Siberian flying squirrel

More than one third of the total number of endangered species in Finland is dependent on forest habitat (Rassi *et al.* 2000). This being the case, management of biological diversity in forests or even a single forest-dwelling species has shown to be a difficult task for conservationists and landscape managers. This is mainly due to a limited knowledge on species ecology, their regional distribution, and local abundances. It is also clear that very detailed guidelining can hardly be provided because landscape patterns and ecological conditions change significantly among regions and, therefore, management recommendations tend to be general by nature. Yet, one has to bear in mind that if there is no long-term data on population fluctuation or trends in the region, conclusions concerning practical rules for management have to be drawn with caution. For instance, if a population is declining and management recommendations are based only on one season study, the results may be spurious providing limited use as a sound basis for sustainable management.

This study suggests some general, but presumably applicable instructions for forest managers. The main findings emphasise the importance of the landscape structure and context at separate spatial scales as a whole: the entire landscape being a management unit not just single stands as discrete entities (see also Åberg 2000). The use of satellite images enables the visualisation of the spatial dispersion of potential habitat patches for the Siberian flying squirrel and provides an estimate of their quality. Knowledge regarding species ecological requirements and landscape models help to rank habitat patches and, hence, to set preferences for strategic planning. Because of failing to predict the presence of the Siberian flying squirrel accurately, forest stands need to be checked in the field prior to forest cutting. Landscape connectivity can be mapped and likely dispersal routes illustrated. Spatio-temporal development of connecting habitat type, which often consists of managed stands can be foreseen from forest stand files. Landscape management can be directed to improve landscape connectivity and forested linkages among habitat patches or to avoid harvesting existing routes. In forest management coarse grain structure should be preferred to subdivision of the remaining old-growth areas into small fragments. These studies propose that a forest landscape where the Siberian flying squirrel persists in northern Finland should contain 20–40 % habitat suitable for dispersal. The spatial arrangement of this habitat is important for landscape connectivity and it should physically bridge spruce-dominated forest patches. Proportion of spruce-dominated forests is more difficult to estimate due to different

classification criteria used in the present studies. Nevertheless, the proportion of this habitat should range from 15 to 20 %. In regions where the Siberian flying squirrel is relatively abundant in northern Finland, the amount of deciduous-tree-rich habitat ranges between 2–4 % (Table 2). Given proportions are always relative to the landscape context in that particular region. This type of study, however, does not provide any unambiguous clue for operative planning as to how to manage deciduous forest sites at stand level in northern Finnish boreal forests. But it suggests that these, often relatively small habitats, should be preserved as key biotopes not only for the Siberian flying squirrel, but also because of their overall biodiversity values.

Table 2. Landscape composition and spatial context of different habitat types that are necessary for the persistence of the Siberian flying squirrel at a local scale in northern Finland.

Habitat type	Amount of habitat (%)	Spatial context
Breeding habitat	2–4	Within spruce-dominated forest habitat patches
Spruce-dominated forest habitat	15–20	Embedded in dispersal habitat
Dispersal habitat	20–40	Should structurally connect suitable forest habitat patches

5 Concluding remarks

In the era of sophisticated remote sensing methodology and advanced GIS techniques the applicability of this potential in ecological research is an interesting challenge. For this kind of landscape ecological study, the Siberian flying squirrel seems to be an optimal guinea pig. The species' habitat use and appropriate landscape patterns are to a great extent detectable from satellite images. This was partly confirmed by tracking radio-collared individuals. The species is neither a specialist nor a generalist in habitat use, which is an advantage in using satellite imagery data. Spruce-dominated habitat patches can be distinguished in managed forest landscapes and qualitative aspects inside these habitat patches even at a home range scale are possible to discriminate. However, detailed small-scale information on habitat characteristics are beyond the highest resolution of these techniques. At a local and regional scale the resolution is accurate enough to distinguish functionally important landscape characteristics.

Findings of these studies are ecologically meaningful and in line with more detailed studies on habitat and landscape use of radio-collared individuals. The advantage of using satellite images and GIS in landscape ecological research is that the scale of observation can be expanded over large areas and it allows the examination of landscape patterns of different habitat types simultaneously. Additionally, landscape patterns can be mapped and visualised for practical forest management and biodiversity conservation planning. However, a more detailed quantification of a landscape structure in landscape ecological research requires a more accurate discrimination of deciduous trees from satellite images than in present study. Also, new landscape metrics are needed to quantify the spatial arrangement of habitat patches in heterogeneous environments.

Future prospects of the landscape ecological research of the Siberian flying squirrel call for direct or indirect methods to assess the density of the species in a habitat patch or in a forest area, but also estimates of temporal dynamics in patch occupancy patterns are needed. Instead of correlating presence/absence data with a number of landscape variables, density estimates would provide more information regarding the role of particular habitat patches. This, however, presumes relative large-scale sampling of habitat patches to derive reliable population density estimates. In order to understand large-scale patch dynamics and the role of spatial characteristics for the Siberian flying squirrel in the long term, structurally different landscapes should be compared along a

gradient to test whether the findings proposed in this thesis are valid. The advantage of modern remote sensing techniques and GIS methods in landscape ecological study and management of overall biodiversity are undeniable. An important future challenge in this field will be to broaden the domain of this approach and develop its use as an everyday tool for ecologists and landscape managers.

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