Multiple scale habitat selection of the Siberian jay *Perisoreus infaustus* in a sub arctic managed forest landscape

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Abstract

Habitat selection studies are important in increasing our understanding of population patterns and processes in fragmented and spatially heterogeneous landscapes. Identification and characterisation of a species' habitat requirements are essential in guiding land-use management practices aimed at the protection of critical habitats. With such knowledge we can understand animal ecology and achieve management practices to conserve species.

Serious declines in the population of Siberian jays *Perisoreus infaustus* have been observed in recent decades in parts of Fennoscandia. These population declines have been attributed to modern forestry altering habitat from native old spruce to pine plantations and habitat fragmentation.

Through radio-tracking 8 focal birds and habitat surveying I assessed jay habitat selection and elucidated their behavioural choices at multiple-scales during autumn and winter.

Jays strongly preferred forest and avoided wooded bogs and cutovers when moving along trajectories in the homerange. At this scale they preferred intermediate densities of large spruce and pine forest avoiding forest with no spruce or too dense pine. Furthermore, jays avoided young forest preferring older, closed canopy forest with an intermediate level of vertical structure. Small scale observations showed Siberian jays had a distinct preference for food searching in spruce avoiding pine and birch in this respect. Jays also preferred to sit in spruce trees, avoided birch and used pine randomly.

These results suggest that without adequate and well planned management of old growth spruce forest, forestry is likely to result in further declines in Siberian jays in northern Sweden.

Contents

1. Introduction

1.1. Habitat selection and its management

Habitat selection can be viewed as choices an organism makes within a 'patterned' environment. Environmental patterning refers to the non-uniform, spatial and temporal distribution of resources and abiotic conditions that influence species or species interactions (Addicot *et al* 1987). Such patterning is pervasive in nature and is known or hypothesised to affect many ecological processes and phenomena, including population dynamics, life histories, dispersal, foraging behaviour, natural selection, coexistence of species, predation, and species diversity (see Addicot *et al* 1987). Therefore the study of environmental patterning and how organisms respond to it has become a central focus of current ecological research.

Several factors such as vegetation structure, quality of food and protection from predators influence habitat utilisation by vertebrates (Sjöberg & Danell 2001). Determining which resources are selected more often than others is of particular interest because it provides us with fundamental information about the nature of animals and how resources meet their requirements for survival (Manly *et al* 1993). When use of resources is disproportionate to availability use is said to be selective (Manly *et al* 1993). Selection is the process in which an animal chooses a resource, and preference is the likelihood that a resource will be selected if offered on an equal basis with others, and avoidance is the opposite (Johnson 1980). For heterogeneous patches, utilisation of the different patch types can be random, in proportion to their availability, or non-random (i.e. some patch types used higher than others relative to availability or used less). These represent fine and coarse grain responses, respectively (MacArthur & Levins 1964). Animals may select habitats according to habitat suitability in habitats not altered by man but this may not be true in disturbed habitats or in a source-sink habitat mosaic (Wiens *et al* 1987, Pulliam & Danielson 1991, Morris 1995). Human caused alterations in habitats can change their suitability as well as the proximate cues animals use to select habitats (Morris 1995, Kirsch 1996). Selection of habitat ultimately influences the survival of individuals and can enhance their reproductive success by providing food, mates and potential nesting sites (Reunanen *et al* 2002).

Declines in the abundance of old-growth forest resident birds such as Siberian jays *Perisoreus infaustus* have been observed in recent decades in parts of Fennoscandia (Järvinen & Väisänen 1979, Väisänen *et al* 1986, Virkkala 1988). Populations have declined by about two-thirds in Finland from the 1940s to the 1970s and currently jays in Sweden have near threatened red list status and are declining by 11.1 % annually (source Swedish Species Information Centre 2005). These population declines have been attributed to modern forestry altering habitat from native old spruce to pine plantations and habitat fragmentation (Virkkala 1987). Forests are the main terrestrial habitats in Sweden, and Swedish forestry is among the most efficient and technically developed in the world (Gamlin 1988, Esseen *et al* 1997). Since the Second World War proportions of mature age classes of Norway spruce *Picea abies* forest in northern Fennoscandia have been increasingly replaced with managed even aged monocultures of Scots pine *Pinus sylvestris* and young successional stages (Kouki & Väänänen 2000, Axelsson and Östlund 2001). At present 91 % of Swedish forest is being used for commercial purposes (Anon 2002), which has a large impact on the structure and function of forest ecosystems (Berg *et al* 1994). Large forestry companies own the vast majority of forest in Northern Sweden,

and only a few percent of forest is in nature reserves. Forestry thus plays a very important role in controlling the structure and function of the boreal forest ecosystem and its plant and animal communities. Cutting of old growth forest, fragmentation and other consequences of forestry have resulted in decreasing populations for several hundreds of plant and animal species (Esseen *et al* 1997).

Identification and characterisation of a species' habitat requirements are essential in guiding land-use management practices aimed at the protection of critical habitats (Kolowski & Woolf 2002). With knowledge of habitat-type selection it is possible to understand animal ecology and achieve appropriate management practices and even evaluate possible threshold conditions for the persistence of the species in fragmented landscapes (Pakkala *et al* 2002). Habitat selection of birds is proximately determined by necessary resources, such as food and safe roosting, which they require for daily activities (Reunanen *et al* 2002). Selection of habitat ultimately influences the survival of individuals and can enhance their reproductive success by providing food, mates and potential nesting sites (Reunanen *et al* 2002).

Harris (1984) suggested that the principles of island biogeography could guide us in the planning of a system for the maintenance of old-growth habitat islands, however, as a result of past intensive forestry with clear cutting and no or little attention being paid to the structure of forest surrounding the 'nature consideration area' (Mönkkönen 1999) many Fennoscandian Siberian jays are most likely to be isolated in a hostile matrix. Many workers have warned of the perils of relying entirely upon nature reserves to preserve species diversity (Järvinen & Väisänen 1979, Thiollay 1992, Andrén 1994, Virkkala *et al* 1994, Angelstam & Petterson 1997, Harrison & Bruna 1999, Mönkkönen 1999). The extent to which forestry influences habitat suitability for forest-dwelling birds has not been thoroughly explored. Analysing behaviour and habitat use in different types of forest can give insight into forest bird responses and adaptations to forest structure and composition changes. Forest structure and tree species composition are important determinants of habitat suitability for foliage gleaning birds (Holmes & Robinson 1981, Thiollay 1992, DeGraaf *et al* 1998, Artman *et al* 2001, Edenius & Meyer 2002). It is important to know what the critical densities of different tree species are (Edenius & Meyer 2002).

1.2. The importance of scale in wildlife studies

Habitat selection occurs in a hierarchical fashion from the geographical range of a species, to individual home ranges (Johnson 1980) and even down to smaller-scale selection (e.g. individual tree or tree part), and the criteria for selection may be different at each scale. Convenient but arbitrary spatial and temporal study units may be inappropriate for the processes being studied and conclusions appropriate to one scale of environmental or population patterning may be inappropriately transferred to another scale (Johnson 1980, Addicot *et al* 1987). Without a reasonable means of scaling, it is difficult to compare results from the same species in different environments (Johnson 1980, Addicot *et al* 1987) and the likelihood of detecting resource patches and understanding their distribution across a landscape is reduced (Johnson 1980, Wiens *et al* 1987, Levine 1992, Thompson & McGarigal 2002). Despite an awareness of this there remains a significant gap in the application of landscape ecology theories and scaling techniques to wildlife ecology research (Otis 1997). Most wildlife habitat research conducted either in a single spatial scale or at discrete 'micro-' and 'macro-' scales, risk missing important patterns that are readily apparent at other scales (Wiens *et al* 1987), or drawing incorrect conclusions

regarding habitat use (Orrock *et al* 2000). Habitat selection appears to be driven by multiple choices at a variety of scales and different processes in the same system may be occurring at different scales, and therefore it may not be sufficient to examine a particular system at only one spatial or temporal scale (Addicot *et al* 1987, Thompson & McGarigal 2002). The home range has to fulfil a variety of needs and a multitude of behaviours will be carried out in that home range such as resting, roosting, competitor/predator avoidance, food searching, commuting, moving etc. The overall area a foraging Siberian jay is searching at any given time is its "ecological neighbourhood", sensu Addicott *et al* (1987). The type of behaviour being studied will partly dictate the observed habitat selection pattern. I was able to distinguish between different behaviours at smaller scales of observation.

More research efforts are needed to understand the causes, processes, and ecological consequences of land use and land cover change (Wu & Hobbs 2002). Many landscape ecological problems need to be studied over large and multiple scales in a spatially explicit manner. I investigated Siberian jay habitat selection in an attempt to integrate the concepts of scale sensitive research into wildlife ecology.

1.3. Siberian jay ecology and past studies

The Siberian jay is a resident, non-migratory species of the Palaearctic region, living in small groups, specialising on closed-canopy coniferous forests (Blomgren 1964, Coombs 1978, Virkkala 1988, Sklepkovych 1997b). The Siberian jay has been described as a foliage gleaning specialist member of the "northern taiga group" (Virkkala 1991). Jays are versatile in their diet selection (Virkkala 1988). Foods taken during autumn and winter primarily include: invertebrates (especially beetles living on conifers), conifer seeds, bilberry and red whortleberry (Blomgren 1964d, Andreev 1982). Collectively the northern taiga group may be considered characteristic and important representatives of the boreal taiga, and could serve as potential conservation indices. Workers have shown that old growth spruce dominated forest is a superior habitat to managed, usually pine dominated forest patches for Siberian jays (Virkkala 1988, Ekman *et al* 2001, Edenius & Meyer 2002). Various reasons have been proposed and proven for this, for example, greater species richness of invertebrates at late growth stages (Pettersson *et al* 1995) and greater forest structural complexity providing more niches for foraging and food storage (Edenius & Meyer 2002). In addition, more cover is provided from predators and competitors in late seral, structured contra managed open forest (Ekman *et al* 2001, Edenius & Meyer 2002, Eggers 2002).

The behavioural adjustments of the Siberian jay to changes in its habitat need further analysis to provide information for planning forest management strategies. This species has been reported to exploit a variety of forest habitats and food resources (see Blomgren 1964, Nilsson & Alerstam 1976, Borgos 1977, Andreev 1982, Sklepkovych 1997a, Edenius & Meyer 2002). Conclusions about habitat selection clearly depend upon the aspect of behaviour being studied, the number of observations made, scale of the study, seral stage and or level of management of forest habitat in which birds are studied.

Studies to date in northern Fennoscandia have shown that the Siberian jay has a broad feeding niche and generalised microhabitat selection and that this generalism is adaptive to a harsh winter climate (Virkkala 1988, Sklepkovych 1997b). They also show a preference for spruce trees over pine trees for foraging, resting and nesting when a choice is available (Sklepkovych 1997b, Ekman *et al* 2001, Edenius & Meyer 2002, Eggers

2002). Sklepkovych (1997 a-b) showed that selection of spruce over pine for nesting was done in a compensatory way, and benefits gained by avoidance of predators through nesting in spruce trees incurred thermoregulatory costs which could negatively influence chick rearing success.

Some studies of Siberian jays have documented small scale selection for optimal habitat and various vegetative characteristics with which jays may be associated. Nilsson & Alerstam (1976) studied jay foraging locations and did transect counts of the birds in mature pine and spruce forest. Borgos (1977) followed jays in Scots pine forest only; Virkkala (1988) concentrated on their niche forage sites concentrating on fine scale observations; Sklepkovych (1997) looked at nest site selection and Edenius & Meyer (2002) focused on the microhabitat use of these birds (e.g. individual tree). However, to my knowledge few studies have measured habitat selection and behaviour of the same selected group of Siberian jays at multiple scales ranging from landscape to micro-habitat (e.g. individual tree), and few have documented foraging and hoarding sites in a variety of habitats within a predominantly managed boreal landscape over a long period of time.

Throughout summer and autumn Siberian jays scatter hoard thousands of food items in arboreal sites and these caches are probably critical to survival during winter (Blomgren 1964, Sklepkovych 1997a). It is therefore of interest to examine habitat selection during such an important period of time, as gained knowledge could improve our understanding of the ecology of this species and help in the formation of sound management policy. A study of this nature should add to the body of knowledge that is building up about the species and its habitat requirement so that predictions can be made about types and sizes of habitats required. Additionally our understanding of the reasons why old forest stands are important to Siberian jays can be improved.

1.4. Aims of this study
This study shall focus on the behaviour and habitat use of jays in characteristic forest types in their northern range in Sweden (old spruce nature reserve, partly managed mixed woodland with remnant spruce and managed pine stands). The aim is to assess their habitat selection and elucidate their behavioural choices at multiple-scales during autumn and winter, allowing the jays to define the scale of research (Wiens 1976) in order to predict key habitat components preferred by them as well as habitats they avoid, thereby assessing their minimum requirements in a largely disturbed habitat.

I considered it likely that I would find jays to be less abundant in the mainly managed and heavily fragmented parts of the landscape and to find more family groups in the less disturbed part of the landscape. I expected to find differences in land cover composition between the low and high density areas. I predicted that jays would choose home ranges within the landscape with greater proportions of forest cover than cut over and wooded bog and for this forest cover to be older than unselected parts of the landscape.

Birds were also expected to exhibit a preference for forest over cut overs and wooded bog when moving within their home ranges. I anticipated this species to prefer mature forest with some level of vertical structural complexity when moving within their home range. I hoped to gain some indication of the Siberian jays' preferred forest type with respect to tree species and basal area of these trees in their home ranges. At the scale of trajectory vs. stopovers I expected birds to prefer Norway spruce trees to Scots pine for food search and sitting when the choice was available.

Detailed knowledge of the habitats used by Siberian jays may allow managers to predict the effects of human disturbance and habitat modification on future jay habitat use patterns, as well as the future success of a regional jay population. Habitat selection studies are important in increasing our understanding about the population patterns and processes in fragmented and spatially heterogeneous landscapes. With my study I hoped to improve understanding of a boreal vertebrate species from a conservation standpoint, and in the process contribute some information for forest management to avoid further declines of Siberian jays in Fennoscandia.

2. Method and Materials

2.1. Study area
The study took place in northern Sweden (66°18′ N, 21°37′E) 55 km north of Boden, Norrbotten, within the limits of the transition between northern boreal and middle boreal zones (sensu Ahti *et al* 1968). Siberian jays were monitored from September the 11th to December the 15th 2002 within a 57.3 km^2 area of mature reserve and managed woodland along the whole length and surrounding areas of Rissapivägen. 53 % of the study area was forest (consisting mainly of Scots pine and Norway spruce; approx 15 % was deciduous), 31 % cut-over, 9 % open mire, 6 % wooded mire and 1 % water. Jays in 8 separate locations were radio-tracked and vegetation data was gathered within and around their home ranges. Two of these jays had home areas in Blåkölens nature reserve, a continuous old spruce (age >150 yr.) covered mountain with wet boggy forest and mires at its base. Two jays were radio-tracked adjacent to and northeast of the nature reserve, in a managed area of fragmented Scots pine and Spruce forest, about one third of this area had been deforested in the last 25 years, and most pine forest showed evidence of thinning of conifer saplings preventing regeneration of an understory. The other 4 birds were located in a Scots pine dominated SCA owned area south east of Blåkölens nature reserve. This area was intensively managed, with 67 % of the forestland converted to plantations (< 60 yr) and 21 % older than 100 yr. The old forest compartments originate from natural regeneration but are devoid of very large trees due to selective dimension felling in the past. These jays had home ranges within forest with a range of connectivity, from continuous (9 % cut-over) to highly fragmented (42 % cut-over). It is worth noting that recent forest cuttings in the most intensely managed area resulted in a 22 % increase in cut-over in one home range and some bird positions had been taken prior to harvesting. 6 of the birds were followed in a Siberian jay activity and movement pattern study running parallel to this study (one of the jays in the nature reserve and one in the moderately fragmented SCA area were not followed; see Landin 2004). In general, pine dominated areas tended to have a simplified vertical structure with little understory, but small impediment areas of wooded bog and wet spruce forest remained. The majority of cut overs had trees remaining on them with basal areas values ranging from 0-4 m^2.ha^{-1}.

2.2. Vegetation survey
In order to assess what habitat was important to jays I measured a wide range of vegetation and other variables. Based upon previous data of home range sizes and boundaries of five replicated jay family groups (see Edenius & Meyer 2002) and gathered bird position and movement data during this study, an estimation was made of likely home range position. Within these areas vegetation was analysed at systematically sampled grid

points (n = 1312) each with 100 m spacing. A GPS 12 XL navigator (Garmin International, Lenexa: USA) was used to locate each grid point and then the following variables were measured – Land cover composition LCC (forest, wooded bog, open bog, water, cut-over (deforested area with tree basal area (BA) < 4 m^2 ha^{-1}). Additionally, using a relascope I measured the basal area of trees taller than 1.3 m for Scots pine, Norway spruce, birch *Betula spp.* and other deciduous trees, both over (large) and under (small) 7 m in length. Basal area may be seen as a summary of the number and the size of trees per unit area (m^2 ha^{-1}). The basal area of different tree species provided a measure of the degree to which each area was occupied by these trees and the relative proportion of each species. This enabled a comparison of Siberian jay habitat selection based on stand basal area of specific sub categories of non-correlated trees based on size and or species, and also provided data on forest vertical structure.

Age of the forest stand at each grid point was extracted from forestry data in ArcView GIS 3.2a database. Forest was divided into five age classes for statistical analysis, 25-50 yr, 51-75 yr, 76-100 yr, 101-125 yr, and > 125 yr, with forest over 100 yr classed as old. All collected data was transferred to ArcView for mapping and analysis.

2.3. Capturing and monitoring of Siberian jays

During September 2002 Siberian jays were attracted to feeding stations baited with tallow. We set up feeding stations in areas where jay family groups were previously known to inhabit. Feeding jays were observed through field glasses to gain an assessment of each individuals family status and level of dominance (many of these birds are identifiable by coloured plastic bands on legs placed there during previous studies, and so relatedness is somewhat known). Jays were captured in mist nets and one bird per family group was selected for attachment of a 1.8 g radio-transmitters (type BD-2G, Holohil systems Ltd, Ontario, Canada). This transmitter was fitted to the ventral side of the tail feathers on the central two retrices with dental floss and glue (Retrices are lost in the spring moult). In each case the oldest, most dominant member of the group was chosen as focal individual and fitted with the transmitter, as I expected them to exhibit typical behaviour of an adult bird in a family group. To minimise stress on jays' age estimation and sexing of most birds was not done but time permitting wing length, tail and wing feather wear and shape were recorded to assess age (Svensson 1992). All captured birds were either ring marked or their ring numbers were recorded. In order to estimate the eight Siberian jay's home range sizes and positions, and habitat selection each bird location was estimated daily. Two bird locations from separate family groups were randomly selected from observation positions of tracked birds in the side project (Landin 2004:3 Masters Thesis). In addition, when jays were spotted during vegetation analysis they were identified by their transmission frequencies using a 4-element RX 89 10 (Tele Vilt) portable receiver operating at 151 MHz. Their position was logged in GPS and later added to the pool of jay positions. Remaining locations were gathered using a car for transport, and triangulation with ≥3 bearings was obtained using an 8-element Yaggi antenna and portable receiver. Bearing triangulations were drawn onto forestry maps, and these grid reference locations were transferred to an Arc View GIS 3.2a database. In order to ensure that location gathering for each jay was independent, random numbers were generated at the start of the study to provide an order of location gathering. This order was rotated daily (e.g. day 1 order 1,2,3,4… etc; day 2 order 2,3,4…1 etc, where each number represents a focal jay in a separate home range). In all 259 locations were gathered (n ≥ 30 locations per home range). These positions were obtained between 0700 hr and 2030 hr, with 5 % constituting

night positions, 44 % between 0900-1200 hr, 30 % from 1200-1500 hr and 21 % taken between 1500 & 1800 hr.

2.4. Data analysis

All data on home range size and use were analysed using the RANGES V program. For each bird the following parameters were calculated: (1) total home range area (100 % of the point-fixes) using the convex polygon method (MCP minimum convex polygon), (2) 95 % isopleth home range size (using the kernel home range estimator, which takes the spatial patterning of the locations into consideration). (3) bi-nuclear home range area estimates based on 80 % and 50 % isopleths. (4) Flight corridors in home ranges. (5) Sitting and food search positions (behavioural observation positions) along flight corridors (trajectories). I defined all foraging, feeding or hoarding as food searching behaviour as it was difficult to distinguish between these behaviours correctly when observing birds. All habitat variable data was tested for autocorrelation before running any tests for selection of individual habitat variables by jays. Habitat variable data was log-transformed before analysis to normalise the distributions, and tested for normality (one sample Kolmogorov-Smirnov test).

Habitat selection information along flight corridors and at behavioural observation positions was based upon field observations of 6 of the study birds (Landin 2004). 2 birds were followed per study day between 2–3 hr each and observation positions were logged in GPS. Behaviour at these observation points was noted, which provided data on frequencies of jay utilisation of different tree species whilst food searching and sitting. Additionally, information on the type of habitat used by birds was obtained by transferring observation GPS positions and vegetation grid data to an ArcView GIS database.

Correlation analysis of all habitat variables was done to test for auto-correlation. There was very little auto correlation so I was able to test for jay selection of habitat variables individually. Using compositional analysis (Aebischer *et al* 1993) I compared the composition of individual home ranges to availability in the 5730 ha study area and tested log differences of habitat variable use vs. availability using a GLM, Wilks' lambda and Chi^2 tests (Systat). Wilcoxon two unmatched sample tests were used where appropriate.

The study area could be divided into two areas with distinct differences in population density, enabling a comparison of land cover composition availability, considering amount of forest, cut over and wooded bog land.

Compositional analysis was used again to assess habitat utilisation using log transformed differences for home range 95 % Kernel (available habitat) vs. jay trajectories or flight corridors (used habitat) using GLM and Wilks' lambda, Chi^2 tests rank analysis and Wilcoxon two unmatched sample tests where appropriate.

At the smallest scale of behavioural observation positions (use) I distinguished between spruce vs. pine vs. birch for arboreal food searching and sitting along trajectories (availability). Data was compared using the same statistical tests as last mentioned.

Snow depth, day length (available light) and air temperature were all recorded during the study.

3. Results

3.1. Landscape compared to home range scale

Jays were found to select home ranges within the 57.3 km^2 landscape randomly according to land cover composition when testing for forest, wooded bog and cut over (Compositional analysis, Wilks' lambda = 0.343, Approx. F= 2.189, df = 7,8, p-tail = 0.147). Forest age varied in the landscape with 15 % of forest between 25-50 years, 6 % between 51-75 years, 15 % between 76-100 years, 29 % between 101-125 years and the remaining 34 % over 125 years. Despite the variation in forest age within the landscape I did not find that forest age affected choice of jay home range location (Compositional analysis, Wilks' lambda = 0.930, Approx. F= 0.503, df = 3,20, p-tail = 0.684).

Within the study area I estimated there to be approximately 15 Siberian jay family groups, of which I was able to study 8 family groups (Table 1). Based upon my estimate of the number of family groups it was possible to deduce a clear division of the study area in terms of population density, i.e. in the north east area, containing Blåkölen nature reserve, the number of home ranges was more than 0.5 km^{-2}, whereas in the south west managed pine zone there were only 0.25 home ranges km^{-2}. These two zones had significant differences in land cover composition (Chi^2 = 39.34, df = 2, p < 0.0001; see Table 1 below) with on average 24 % more cut overs and 18 % less forest in the low density zone compared to the high density zone. Jay selection of home ranges was not influenced by land cover composition in the higher density area (Chi^2 = 0.56, df = 2, p = 0.756) yet in the low density managed area birds chose home ranges according to land cover composition preferring wooded bog land over cutovers (Chi^2 = 8.66, df = 2, p = 0.013; Wilcoxon two unmatched sample test, n = 4, W = 10, p = 0.029, rank analysis wooded bog>forest>cutover). On average home ranges here were composed of 10 % more forest than was available as well as 14 % less cut overs and 4 % more wooded bog.

I made a further test to see whether population density *per se* had an affect upon habitat selection by comparing the amount of observations of jays along trajectories in different land cover types in the two areas differing in jay density, (High density, Chi^2 = 23.12, df = 2, p <0.001; low density area Chi^2 = 59.29, df = 2, p <0.001). However, in both cases rank analysis confirmed order of use to be forest>wooded bog>cutover. Below (Table 1) is a summary of habitat variables for each home range sorted according to jay population density.

Table 1. Home range information sorted according to jay population density showing the size, tree species composition and land cover composition of each home range.

Population density	Home range ID	No. of birds in group	95 % kernel home range size (ha)	MCP home range size (ha)	Tree species composition % (pine, spruce, deciduous)	LCC composition % in home range (Cut over, forest, wooded bog)
High (0.50 home ranges/ km^2)	F 209	3	150	120	41 37 22	36 61 3
	F 269	3	205	200	39 37 24	33 57 10
	F 330	3	67	60	20 57 23	3 80 17
	F 378	4	206	174	24 52 24	11 66 24
Low (0.25 home ranges/ km^2)	F 170	3	342	228	73 9 18	42 49 9
	F 191	3	183	131	74 12 14	37 46 18
	F 230	4	178	115	74 12 14	10 80 10
	F 309	4	208	154	73 12 15	24 66 10
Mean		**3.38**	**192**	**148**	**52 29 19**	**24 63 13**
SD		**0.52**	**76**	**53**	**24 20 4**	**15 13 06**
SE		**0.18**	**27**	**19**	**9 7 2**	**5 5 2**

The home range size for jay F 170 in the most highly fragmented area was twice as large compared to the mean home range size of the other 7 focal individuals (Table 1). This was most likely because forest harvesting was taking place in this birds home range during the study thus the birds were forced to abandon parts of their existing home range area and scout out new areas. In general the low density areas were extremely pine dominated, whereas high density areas had significant components of the original spruce forest remaining (Table 1).

3.2. Home range (95 % kernel) compared to trajectories
At the scale of home range compared to trajectories I showed that jays strongly selected for forest and avoided other land cover types (Compositional analysis, Wilks' lambda = 0.492 Approx. F = 10.34, df = 1, 10, p-tail = < 0.01; Wilcoxon two unmatched sample test, n = 6, W = 21 , p = 0.002, Rank analysis forest>wooded bog/cut over, Fig. 1 below).
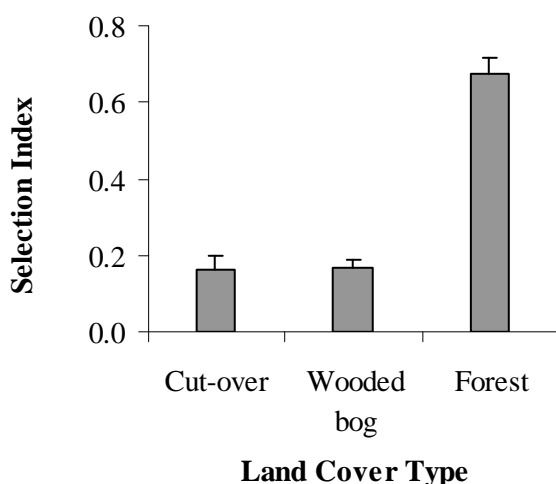
Figure 1. Selection indices of different land cover categories along trajectories in the home range.

Whilst moving in forest in their home ranges Siberian jays strongly preferred areas with large spruce basal area between 5 and 12 $m^2 ha^{-1}$ (34 % of total home range area), whereas forest without any large spruce at all (41 % of total home range area) was avoided, and the remainder of the forested territory was used according to availability with regards large spruce density (Compositional analysis, Wilks' lambda = 0.676, Approx. F = 3.189, df = 3, 20, p-tail = 0.046, Wilcoxon two unmatched sample test - 4 basal area preferred over 0 basal area n = 6, W = 21, p = 0.002; 8 basal area preferred over 0 basal area and >12 basal area n = 6, W = 27, p = 0.047 & 0.015 respectively; 12 basal area preferred over 0 basal area and 4 basal area n = 6, W = 21 & 27 respectively, p = 0.002 & 0.047 respectively; >12 basal area preferred over 0 basal area n = 6, W = 27 , p = 0.047, Fig. 2 below).
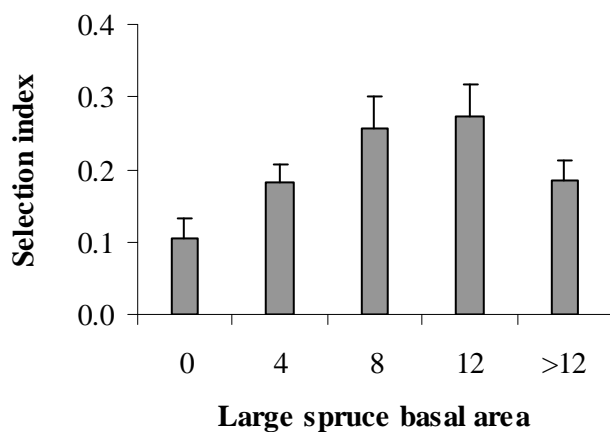
Figure 2. Selection indices of large spruce of different basal area classes along trajectories in the home range.

I found that jays preferred forest with large pine basal area between 4-10 $m^2 ha^{-1}$, avoiding > 20 $m^2 ha^{-1}$, using pine forest between 11-20 $m^2 ha^{-1}$ randomly (Compositional analysis, Wilks' lambda = 0.592, Approx. F = 4.595 df = 3, 20 p-tail = 0.013, see Table 2 below).

Table 2. Availability and selection of large pine forest along trajectories in the homerange showing Wilcoxon two unmatched sample tests.

Basal area $(m^2.ha^{-1})$	% available in homerange	Use	Wilcoxon two unmatched sample test
5	38	Preferred	Preferred to 20 and >20 basal area; n = 6, W = 27, p = 0.048
10	17	Preferred	Preferred to >20 basal area; n = 6, W = 21, p = 0.002
15	18	Random	Preferred to >20 basal area; n = 6, W = 21, p = 0.002
20	16	Random	Preferred over >20 basal area; n = 6, W = 27, p = 0.048
>20	10	Avoided	

90 % of large birch forest had a basal area value less than 5 $m^2.ha^{-1}$. Siberian jays showed no selection for large birch (Compositional analysis, Wilks' lambda = 0.744, Approx. F = 2.150, df = 4, 25, p-tail = 0.104).

On average forest in the home ranges had the following age distribution; 16 % = 50 years, 7 % = 75 years, 9 % = 100 years, 26 % = 125 years and 42 % = > 125 years. Compositional analysis of forest age showed that jays distinctly preferred forest over 100 years and avoided forest less than 51 yr when moving along trajectories. (Wilks' lambda = 0.403, Approx. F = 9.875, df = 3, 20, p-tail = 0.000, Wilcoxon two unmatched sample test 75, 100 & 125 yr. preferred over 50 yr. n = 6, W = 21, 21 & 27 respectively, p = 0.002, 0.002, 0.048 respectively; >125 yr. preferred over 50 yr. & 100 yr. n = 6, W = 21 & 27 respectively, p = 0.002 & 0.048 respectively, Fig. 3 below).
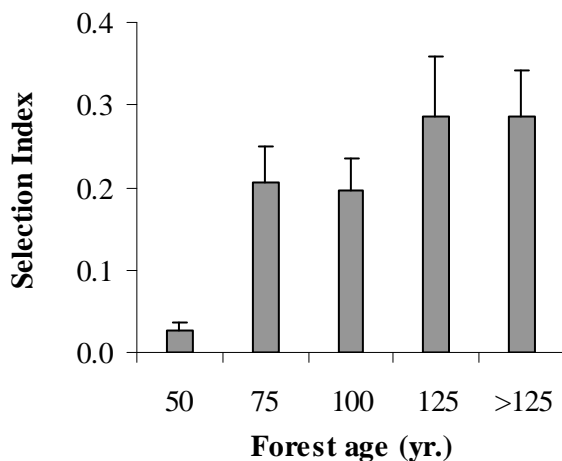
Figure 3. Selection indices of forest in different age classes along trajectories in the home range.

An assessment of understory in areas of closed canopy forest (defined as forest with a total large tree basal area > 11 m^2 ha) showed that jays strongly selected for areas with a small tree basal area between 3.5 - 4.5 m^2 ha^{-1}. Understory densities of 1.5 - 2.5 m^2 ha^{-1} were also selected but not as strongly, and 2.5 - 3.5 m^2 ha^{-1} were used in proportion to

availability. All areas of none or very little understory were avoided as were locations with dense understory (> 4 basal area small total), (Compositional analysis, Wilks' lambda = 0.799, Approx.F = 3.458 df = 4, 55, p-tail = 0.014, Wilcoxon two unmatched sample test, 0, 2, 3 & 4 small basal area over 1 small basal area (n = 6, W = 21, p = 0.002); >4 small basal area over 1 small basal area (n = 6, W = 27, p = 0.048); 2 small basal area over 1, 3 & >4 small basal area (n = 6, W = 27, p = 0.048); 4 small basal area over 3 small basal area (n = 6, W = 27, p = 0.048); see Fig. 4 below).
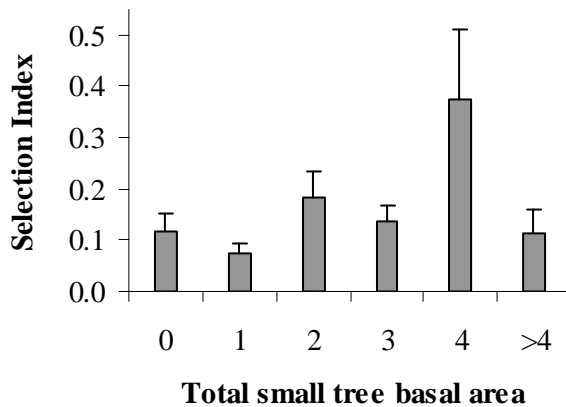

Figure 4. Understory selection in closed canopy forest along trajectories in the home range.

### 3.3. Trajectories compared to stopovers

In total bird positions were recorded 2,758 times along all trajectories, with behavioural observations being possible at about half of these positions. Sitting and food search were two dominant behavioural categories with 54 % out of the total 1331 behavioural observations being sitting, and 40 % food searching. Comparing behavioural observations with positions of birds along trajectories Siberian jays showed a distinct preference for food searching in spruce and avoidance of pine and birch in this respect (Compositional analysis, Wilks' lambda = 0.621, Approx. F = 6.098 df = 1, 10, p-tail = 0.033; Wilcoxon two unmatched sample test, spruce over birch & pine n = 6, W = 27 , p = 0.048, pine over birch n = 6, W = 33 , p = 0.364, Rank analysis spruce>pine/birch, see fig. 5 below).
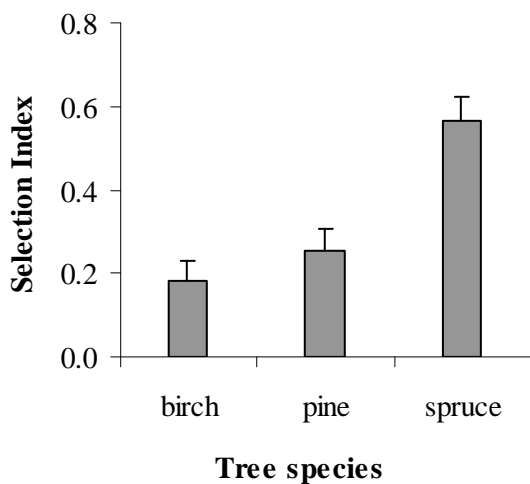
Figure 5. The use of different tree species for food searching along trajectories.

When sitting Siberian jays preferred spruce used pine randomly and avoided birch (Compositional Analysis, Wilks' lambda = 0.556, Approx. F = 8.000, df = 1, 10, p-tail = 0.018; Wilcoxon two unmatched sample test, spruce over birch n = 6, W = 21 , p = 0.002, pine over birch n = 6, W = 27 , p = 0.048, pine over spruce n = 6, W = 33, p = 0.364, Rank analysis spruce>pine>birch, see Fig. 6 below).
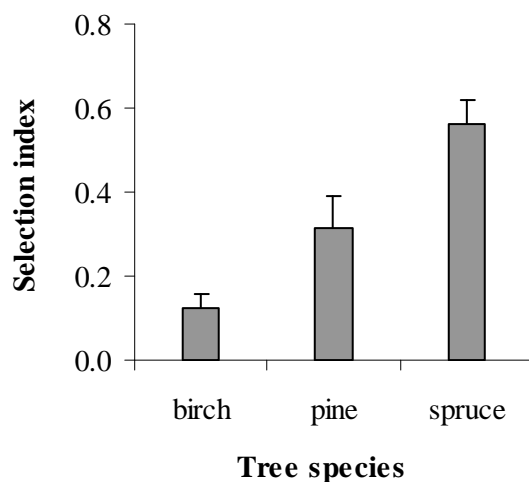
Figure 6. The use of different tree species for sitting along trajectories.

4. Discussion

In this study jays were found to select home ranges within the 57.3 km^2 landscape and within high density area randomly according to land cover composition when testing for forest, wooded bog and cut over. There was some evidence that wooded bog was preferred over cut overs in the low density area. Population density *per se* had no influence on habitat selection with regards to land cover composition. I did not find any evidence that forest age influenced selection of home ranges within the landscape; however caution for

small sample size may be warranted. At the scale of home range compared to trajectories (movement routes of focal birds) I identified that jays strongly preferred forest and avoided other land cover types. Jays also showed a preference for intermediate densities of large spruce and pine forest avoiding forest with no spruce or too dense pine and there was no significant selection of large birch forest. Furthermore, jays were found to avoid young forest preferring older, closed canopy forest with an intermediate level of vertical structure. Comparing behavioural observations with bird positions along trajectories, Siberian jays showed a distinct preference for food searching in spruce and avoidance of pine and birch in this respect. I also found that jays avoided sitting in birch, used pine randomly, preferring to sit in spruce trees.

4.1. Does land cover selection depend on jay population density*?*

Siberian jays are known to exhibit behaviours that exclude dispersing jays from preferred, high quality habitat, and juveniles will even queue for preferred habitat (Ekman *et al* 2002). Most landscapes are patchy environments and differences in habitat quality offer a range of possibilities for individuals to survive and reproduce and there is a potential for demographic differences in different habitats (Lomnicki 1980). The northern Swedish forest landscape is naturally fragmented by mires and lakes, but also by cut overs and areas of low density forest. With few areas of core habitat we can expect low abundances of "forest interior" species such as Siberian jays (Edenius & Sjöberg 1997). Inferior habitat areas can be expected to be unoccupied giving a subsequent reduced local population density in comparison to "stable" habitats (Wauters *et al* 2001). Jays exhibited different population densities in different sections of the landscape with 0.81 pairs km^{-2} in the section with significant components of spruce forest, and 0.44 pairs km^{-2} in the managed pine forest area. My density estimates are somewhat comparable to results from northern Finland where observations ranged from 2.1 pairs km^{-2} in spruce dominated forest, 1.2 pairs km^{-2} in virgin pine forest and only 0.3 pairs km^{-2} in managed pine forest (Virkkala 1988) and c1 bp km^{-2} in prime habitat (Väisänen *et al* 1986). These two zones had significant differences in land cover composition with on average 24 % more cut overs and 18 % less forest in the low density zone compared to the high density zone. Despite observed differences in population densities in my study area, I did not find population density *per se* to have an effect upon habitat selection with regards land cover composition in the low respective high density areas. In both cases birds chose forest>wooded bog>cut over when moving along trajectories in the two areas. The landscape was just over half covered with forest and yet on average 86 % of trajectory observations were made in this habitat, and despite a third of the landscape consisting of cut overs only 10 % of trajectory observations were found there.

Jay selection of home ranges was not influenced by land cover composition in the higher density area yet in the low density managed area birds chose home ranges according to land cover composition preferring wooded bog land over cutovers. Rank analysis showed order of selection to be wooded bog>forest>cut over. This is probably a result of a large area of wooded bog in the home range of bird F191 (See Table 1). Home ranges in the low density zone were composed of 10 % more forest than was available as well as 14 % less cut overs and 4 % more wooded bog.

4.2. The habitat characteristics of home ranges within the landscape

I did not find that land cover composition had any influence on jay selection of home ranges within the landscape as a whole, despite the fact that forest covered only half

of the landscape, with the rest of the landscape consisting of 1/3 cut overs and 9 % wooded bog. Lack of selection may have been a result of the managed forest landscape being predominantly fragmented by cut overs and bogs at a scale smaller than the average home range size of the jays, and thereby being fine grained (sensu Levins 1968) with respect to ranging behaviour. Thus, in general, regardless of where a home range is located in the landscape jays will inevitably have been forced to incorporate a sizeable area of cut overs and bogs into their home ranges. A typical Siberian jay's home range is relatively large, thus encompassing a variety of land cover types, including forest, wooded bog and sometimes a small bog (Blomgren 1964). Natural forest-mire ecotones are considered to be important areas providing food resources predictable in time and space (Sjöberg & Ericson 1997) which may partly explain the inclusion of none forested areas in home ranges. Sklepkovych (1997) found a higher breeding success of jays close to forest edge than in interior forest, which he attributed to forest edge springtime foraging success when autumn hoards are depleted. I believe resource limitation in late winter despite hoarding is probably only relevant to their survival in disturbed habitats, as Andreev (1982) has recorded Siberian jays surviving Siberian winters on as little food as 0.46 – 0.66 g /hr (berries and mushrooms), so daily food requirements can be very small. I do not think Sklepkovych's findings entirely question the theory of edge-sensitivity in the Siberian jay as I believe jay springtime edge foraging is a behaviour that was adapted in their native habitats where generalist predator numbers would have been low.

Jays did not select home ranges in the landscape according to forest age, probably because forest of the preferred age (excluding the nature reserve) occurred at a scale smaller than that of the home range size. Additionally, although over 60 % of the forest in the landscape was older than 100 years (as was the case in the home ranges), forest only covered about half of the landscape (mean forest cover in home ranges was 63 %).

4.3. Habitat selection along trajectories in the home range

The majority of Siberian jay home ranges in the study area were fragmented by bog land and cut overs. When I compared movement of jays along trajectories within their home ranges, they showed a strong preference for forest and avoided wooded bogs and cut overs. Landin (2004) demonstrated that despite retention of trees on the majority of cut overs in the study area Siberian jay movement in forest was directed when jays were within 150 m of a cut over edge (whereas bird directionality was random in forest interior), and that jays avoided crossing cut overs, irrespective of tree retention magnitude. Jays possibly avoid cut overs because of the higher risk of predation in open spaces, as well as greater energetic costs and poor foraging opportunities on cut overs. Previous workers have also suggested that jays are reluctant to cross open spaces (Blomgren 1964, Coombs 1978), and logging can have a great negative impact on insectivorous foliage gleaners reluctant to cross open spaces or dense second growth that separates remaining patches of undisturbed forest (Thiollay 1992).

The avoidance of wooded bog implies that it is unsuitable habitat during autumn and winter for jays. Wooded bogs in the study area were mainly covered with large pine or spruce trees at densities < 6 basal area. Boggy forest impediments, irrespective of age, are of little benefit to jays outside of spring, and should not in my opinion qualify as old tree patches in management planning.

Thompson & McGarigal (2002) believed that avoidance of disturbance at finer spatial scale and acceptance at coarser scale indicates some degree of tolerance of disturbance, in exchange for e.g. foraging success. Despite some jays appearing to tolerate fragmentation

of the landscape by deforestation, we cannot simply assume tolerance will ensure persistence of the population without assurances from long term monitoring of population trends along with patterns of habitat use and suitability. This is especially true in disturbed systems, as populations here may be declining despite appropriate habitat use (Kirsch 1996). Patterns of habitat use that match habitat suitability may not lead to population persistence for example when habitat suitability has been reduced below that required for population maintenance because of human disturbance or when habitat suitability is naturally low, and immigration from source areas maintains the population (Pulliam & Danielson 1991, Wiens *et al* 1987). Uimaniemi *et al.* (unpublished) proved that the jays I studied were part of a sink metapopulation, providing clear evidence that despite avoidance of disturbance at a finer spatial scale and acceptance at a larger scale, persistence of jays in this landscape cannot automatically be assumed, and in fact the contrary is more likely.

If jays are to remain a part of Nordic forest biodiversity we must ascertain how large an area of forest a jay group needs (Edenius & Sjöberg 1997). To preserve and enhance biodiversity, retention of small (<1 ha) patches of old forest has been advocated, e.g. by the Forestry Act during the 1990s. However, Edenius & Sjöberg (1997) showed that in the north of Sweden, such small patches do not provide habitat for more than some generalist bird species and the maintenance of a diverse bird fauna requires the retention of forest patches >10 ha. As the majority of jays in my study had 50 % core areas ranging from 15-30 ha I similarly believe in the retention of larger patches of old forest.

Jays avoided forest in their home ranges without any large spruce at all (41 % of total home range area) strongly preferring areas with large spruce densities between 5 and 12 $m^2 ha^{-1}$ (24 % of total home range area). The remainder of the forested territory was used according to availability with regards to large spruce density. Forest structure and tree species composition are important determinants of habitat suitability for foliage gleaning birds (Holmes & Robinson 1981, Thiollay 1992, DeGraaf *et al* 1998, Artman *et al* 2001, Edenius & Meyer 2002). Various tree species can provide different foraging opportunities for birds, which in turn could influence the presence and or abundance of certain bird species and thus bird community patterns and removal of conifers can result in the elimination of some specialised birds (Holmes & Robinson 1981). Similar to Holmes & Robinson (1981) and Edenius & Meyer (2002), I believe, based on my results that removal of spruce trees from industrial forests will result in the elimination of Siberian jays from the bird community. That jays showed a preference for forest with large pine trees at low densities is perhaps not surprising when considering the fact that over half of the forest in the total home range area consisted of large pines with densities < 11 $m^2 ha^{-1}$. Jays used all other forest with large pine randomly except the most dense pine forest which was avoided despite existing in 10 % of the home range.

Jays clearly preferred 'old' forest over 100 yr. which existed in 68 % of the total home range area. The remaining young (less than 51 yr.) and maturing forest (51-100 yr.) existed in equal proportions (16 % availability) and were respectively avoided and utilised randomly. Many workers have shown that old growth spruce dominated forest is a superior habitat to managed forest patches for Siberian jay (Virkkala 1988, Angelstam & Petterson 1997, Ekman *et al* 2001, Edenius & Meyer 2002). This could be because of greater species richness and abundance of invertebrates at late growth stages (Pettersson *et al* 1995, Esseen *et al* 1997) and greater structural complexity. Structural complexity can be in the form of older, rough-barked trees, with abundant crevices or an abundant cover

of lichens. Such structurally complex habitats provide a greater supply of arthropods to birds because of more niches for foraging (Borgos 1977, Morrison *et al* 1985, Esseen *et al* 1997, Edenius & Meyer 2002) but additionally there are greater opportunities for food storage which is very important for jay winter survival. Although other factors are important in Siberian jay declines in Fennoscandia, a reduction in availability of suitable foraging and hoarding sites is clearly fundamental, especially when considering food limitation in winter time. Current forest cutting rotations occur too rapidly for structurally complex habitats to develop and so the invertebrate prey of passerine birds may be reduced (Pettersson *et al* 1995). Forestry may therefore represent yet an additional deleterious effect on boreal bird populations beyond that of habitat destruction and forest fragmentation (Pettersson *et al* 1995).

Another aspect of structural complexity that may influence Siberian jay habitat selection is the vertical structure of forests. Some level of vertical structure is most likely in old growth boreal forest (Hofgaard 1993, Engelmark *et al* 1994, Linder *et al* 1997), the native habitat of jays. Studies have illustrated that a change in habitat structure can potentially provide significant benefits in terms of reducing predation risk and enhancing foraging rates in birds; too much cover can hinder detection of predators, whereas too little offers poor protection (Whittingham & Evans 2004). My results indicated that an intermediate level of vertical structure was preferred by jays, whereas they were probably precluded from areas with an overly dense or lack of understory. The preferred forest with understory 2-4 m^2 ha^{-1} existed in 38 % of forest in the home ranges on average. A likely reason for the use of forest areas with intermediate understory is that the risk of predation from goshawks (*Accipiter gentilis*) may be less in closed-canopied, uneven sized forest stands (Edenius & Meyer 2002). When foraging within home ranges goshawks select sites with moderately dense, mature forests where they can use their maneuverability to capture prey (Kenward 1982, Beier & Drennan 1996, Drennan & Beier 2003). However during winter in N. Sweden there are few raptors about so risk of predation is less then, although perceived predation risk may also influence habitat selection (Whittingham & Evans 2004). Vertical structure in forest could also provide superior foraging opportunities and reduced energetic costs and there is reduced competition from generalists such as jays (*Garrulus glandarius*) in such forest (Edenius & Meyer 2002, Eggers 2002).

4.4. Does the Siberian jay specialise on spruce when foraging and sitting?
I found that jays strongly preferred spruce for food searching along trajectories whereas other tree species were avoided, suggesting that jays are spruce specialists. Jay preference for foraging on Norway spruce as opposed to Scots pine could be linked to spruce having a denser cover of foliage and branches and shorter but more abundant needles along branches which grow from nearly the whole length of the trunk. Preferred tree species may provide more abundant food resources and or offer a set of substrates which are more easily searched, or on which prey are more readily detected and captured (Holmes & Robinson 1981). Additionally, as stated above, the greater structural complexity in a spruce tree compared to a pine tree offers jays more opportunities for foraging and hoarding. During autumn Siberian jays hoard food in a small part of the home range; a so called *pantry*; to meet their winter needs. Food items are hoarded in arboreal sites, such as under bark crevices, in lichen clumps and needle clusters (Sklepkovych 1997a). During winter these hoards are investigated along with holes and splits in bark for potential over-wintering invertebrates (Blomgren 1964). It seems reasonable to assume that areas where birds prefer to food search are richer in niches and have greater food availability thus

offering maximum fitness benefits, and that this type of habitat is more common in old growth spruce forest.

There is much in the habitat use of Siberian jays' that leads me to suspect that they have a specialised ancestry. For example, they clearly prefer old forest, avoid cut overs and bogs in the home range, and use spruce preferentially for food search and sitting. Although jays have a varied diet I do not believe this dispels the idea that they are spruce specialists; a species cannot afford to be overspecialised if it is to obtain enough food to survive long intensely cold winters. The Nordic boreal forest biota has been more severely eliminated, fragmented, and floristically modified during ongoing ice ages than its Palaearctic equivalent producing a more ecologically plastic bird assemblage, less specialised than their Nearctic counterparts (Greenberg *et al* 1999). The Nearctic foliage-gleaning bird assemblages consist of more species that are specialised on the foliage substrate, and strongly associated with coniferous vegetation (Greenberg *et al* 1999). By examining the ecology of specialised Nearctic foliage gleaners it may be possible to gain some clues as to whether Siberian jays are Spruce specialists that may have evolved from a more specialised assemblage from around the time of the last ice age. Foliage gleaning birds in New England have strong preferences for tree species upon which they foraged for insect prey, with preferred tree species providing sites where food resources are more abundant and or insect prey is more easily detectable or accessible (Holmes & Robinson 1981). Similarly insectivorous foliage gleaning birds of the Guianan rain forest may have special foraging strategies and rather narrow adaptations to the dim light and stable microclimate conditions of the forest interior (Thiollay 1992).

Some and perhaps most of these preferences shown by birds represent species-specific adaptations predisposing them to choose certain kinds of trees in which to forage and a bird's ability to forage may differ depending on foliage structure (Holmes & Robinson 1981). Such tree species characteristics as branching patterns and positioning of leaves in relation to twigs and branches may influence how birds move through and search vegetation and how easily they can perceive and capture prey (Holmes & Robinson 1981). Positioning of needles along the branch/twig or only at the end of branch/twig may differentially affect the jays' ability to glean pine vs. spruce. Birds which are adapted for gleaning prey from nearby substrates might be expected to forage more readily in spruce than pine since they can search many needles without leaving a twig or branch and remain on the same tree longer without resorting to flight (this is a typical behaviour I observed in the jays studied). Virkkala (1988) working in northern Finland (68°N) found that jays foraged mostly from conifer trees during summer, predominantly on the mid-parts of branches along the whole length of the tree, feeding mainly on the twigs-needles when on spruce (43 %), whereas when on pine trees they only used twigs-needles 16 % of the time, which suggests that jays may be more adapted to gleaning spruce twigs-needles than pine. Virkkala (1988) concluded that decreases of old coniferous trees would be disadvantageous to the foraging of Siberian jays.

Sitting is also an important behaviour in birds whereby they can for example avoid detection by predators, rest and conserve energy during winter. Jays strongly preferred Norway spruce for sitting in, Scots pine was used randomly and birch was greatly avoided, further evidence of the Siberian jay's strong association with Norway spruce and the potentially detrimental effects of removal of spruce from their habitat. Spruce trees perhaps offer greater cover and thermoregulatory benefits than pine and birch during winter. Jays in my study sat for half of the time they were observed during early

December with temperatures averaging around -8 °C and day length 3.5 h. In Siberia they have been recorded roosting up to 20.5 h.d^{-1} mid winter at temperatures between – 40 °C and –57 °C (Andreev 1982). Further evidence of the Siberian jays' specialisation on spruce was provided by Sklepkovych (1997a) who showed that jays favoured nesting in spruces relative to pine trees. Only when spruce availability was < 20 % was pine selected. Nests producing nothing at all were more common in pine than spruce trees, which implies that reproductive success of individuals in the managed part of the landscape in my study is likely to be worse as spruce constituted less than 20 % of home ranges there.

5. Conclusions

A primary goal of biological conservation is to preserve the natural diversity of plants and animals in communities where natural processes are working (Esseen *et al* 1992, Berg *et al* 1994). Forest reserves are important for many forest plants and animals in Sweden, however the total protected forest area in Sweden is probably too small to preserve natural diversity (Esseen *et al* 1992, Nilsson & Götmark 1992). Most reserves are small and doubtless insufficient for plants and animals requiring large areas, such as Siberian jays. The persistence of the Siberian jay in larger regions requires that the quality of the industrial forest landscape exceeds a certain threshold. The species is likely to be completely missing from a region where high quality sites occur so sparsely that the landscape level condition is not met. My results provide information on the type of habitat Siberian jays require and supply relevant quantitative data for a vertebrate species showing that landscape goals have not been met for the maintenance of a viable population. Furthermore, I clearly demonstrate the importance of selecting an appropriate scale for studying Siberian jay habitat use, without which important habitat selection patterns would have been missed, possibly leading to some wrong conclusions.

5.1. Recommendations to managers
The jay population studied is non viable as it was a fragmented sink population which implies that dispersal is not enhanced, and population density in the highly managed area was low. Recent deforestation of some few remaining old forest patches close to the nature reserve has taken place since this study. I would expect Siberian jay numbers to decrease in the managed pine area if fragmentation and habitat loss continues at its current rate, and if remaining patches of old spruce forest outside the reserve are harvested I would expect to see declines in jay numbers even in the higher density area, leading inevitably to only a few groups surviving in the reserve. Mönkkönen (1999) warned that natural old growth forests, the native habitat of Siberian jays comprise an ever decreasing fraction of the total land area in Fennoscandia, and that this was a sheer challenge for forest management. A likely scenario for forestry in the future in Sweden is one in which large forestry companies buy up much of the currently remaining older forest from private land owners because of timber shortages leaving the only prime habitats available to jays in reserves and key habitats (P-A. Lindgren & J. Wester, pers. com. 2005). If population declines as witnessed in Finland are to be avoided in the rest of Fennoscandia then clearly a better type of management is required at and beyond the landscape scale. Forestry management must move away from maintaining isolated small patches of old forest, towards the new vision of an integrated landscape. Nature reserves are nothing more than habitat islands in a managed landscape and research has shown that it is not sufficient to simply conserve small patches of old forest in the landscape. Physical edge effects may render fragments hundreds of hectares in size virtually all edge and there is the risk of

penetration of remnant habitats by aggressive competitors or predators (Harrison & Bruna 1999). Despite the importance of protected areas for many species, the majority of Siberian jay individuals most likely live outside reserves (Järvinen & Väisänen 1979, Virkkala *et al* 1994), and therefore the type of forest management outside the protected areas is especially important. I believe the retention of high quality habitat patches (> 10 ha of old spruce forest) is needed if Siberian jays are to remain a part of the diversity, and these patches must not be too distant from each other because of their poor dispersal ability. This could possibly be achieved if a more conservation orientated, combined forestry management strategy was in place, with long-rotation forest islands in a matrix with several types of replacement successions whilst managing for dispersal with corridors and stepping stones (see Angelstam & Petterson 1997, Mönkkönen 1999).

5.2. Sources of error, improvements and suggestions for future studies
Limited time, personnel and transmitters restricted the amount of birds that could be studied. We followed approximately half of the local jay population. Had two jays not lost transmitters then the size of the population studied would be closer to 70 %. Our selection of jays along forestry roads in the study landscape may be a source of bias as habitat selection may be altered in disturbed habitats (Wiens *et al* 1987, Pulliam & Danielson 1991, Morris 1995). Additionally site fidelity and group adherence are behavioural traits that may cause birds to remain in unsuitable sites even when superior sites are available (Kirsch 1996). An estimation of foliage volume of large trees would perhaps be a better predictor of Siberian jay habitat selection than tree basal area alone (DeGraaf *et al* 1998).

My results have highlighted several areas that require further investigation.

(1) As jays clearly prefer spruce for food searching and sitting, below what density of large spruce in a managed pine forest do jays stop showing preference for spruce when doing these behaviours? This may give an indication of critical thresholds needed for survival of jays in the managed landscape. (2) To what extent does the spatial configuration of available habitat influence habitat usage. (3) Do jays compensate for poor tree foraging habitat in their home ranges with food searching more on the ground? This may entail increased predation risk. (4) Do jays behave less vigilantly when foraging in closed canopy forest with preferred understory levels? (5) There is a need to census Siberian jays beyond landscape scale and make an analysis of the level and type of isolation and how to increase metapopulation connectivity. Remote sensing satellite maps for old forest could be useful in focusing census activities in areas with suitable jay habitat, as well as identifying potential dispersal corridors/stepping stones.

6. Acknowledgements

7. References

Addicot, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S. & Soluk, D. A. 1987: Ecological neighbourhoods: scaling environmental patterns. -Oikos 49: 340-346.

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993: Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. - Ecology 74(5): 1313–1325.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in Northwestern Europe, - Ann. Bot. Fenn. 5: 169-211.

Andreev, A.V. 1982: Winter ecology of the Siberian Jay and Nutcracker in the region of North East Siberia. – Ornitugija 17: 72-81.

Andrén, H. 1994: Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. - Oikos 71: 355-366.

Angelstam, P. & Petterson, B. 1997: Principles of present Swedish forest biodiversity management. - Ecological Bulletin 46: 191-203.

Anon. 2002: Skogsstatistisk årsbok. Sveriges official statistik. Skogsstyrelsen.

Artman, V. L., Sutherland, E. K. & Downhower, J. F. 2001: Prescribed burning to restore mixed-oak communities in southern Ohio: Effects on breeding-bird populations. - Conservation Biology 15: 1423-1434.

Axelsson, A.-L. & Östlund, L. 2001: Retrospective gap analysis in a Swedish boreal forest landscape using historical data. - For. Ecol. Manage. 147: 109-122.

Beier, P. & Drennan, J. E. 1996: Forest structure and prey abundance in foraging areas of Northern Goshawks. - Ecological Applications 7(2): 564–571.

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. 1994: Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. – Conservation Biology 8: 718- 731.

Blomgren, A. 1964: Lavskrikan. Alb. Bonniers boktryckeri, Stockholm.

Borgos, G. 1977: Hamstring hos lavskrike (Perisoreus infaustus I.,L.). Hovedoppgave i zoologi, Universitetet i Trondheim.

Coombs, F. 1978: The crows: A Study of the Corvids of Europe. B.T. Batsford Ltd, London.

DeGraaf, R. M., Hestbeck, J. B., & Yamasaki, M. 1998: Association between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine, USA. – Forest Ecology and Management 103: 217-233.

Drennan, J. E. & Beier, P. 2003: Goshawk prey and foraging habitat in winter. - J. Wildl. Manage. 67(1): 177-185.

Edenius, L. & Meyer, C. 2002: Activity budgets and microhabitat use in the Siberian Jay *Perisoreus infaustus* in managed and unmanaged forests. - Ornis Fennica. 79: 1-8.

Edenius, L. & Sjöberg, K. 1997: Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. – Ecography 20: 425-431.

Eggers, S. 2002: Behaviour and Life-History Responses to Chick Provisioning under Risk of Nest Predation. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science & Technology 773. Acta Universitatis Upsaliensis.

Ekman, J., Eggers, S., Griesser, M. & Tegelström, H. 2001: Queuing for preferred territories: delayed dispersal of Siberian jays. - J. Anim. Ecol. 70: 317-324.

Ekman, J., Eggers, S., Griesser, M. 2002: Fighting to stay: the role of sibling rivalry for delayed dispersal. – Anim. Behav. 64: 453-459.

Engelmark, O., Kullman, L. & Bergeron, Y. 1994: Fire and age structure of Scots pine and Norway spruce in northern Sweden during the past 700 years – New Phytol. 126: 163-168.

Esseen, P-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997: Boreal Forests. - Ecological Bulletin 46: 16-47.

Gamlin, L. 1988: Sweden's factory forests. – New Scientist 1597: 41- 44.

Greenberg, R., Pravosudov, V., Sterling, J., Kozlenko, A. & Kontorschilov V. 1999: Divergence in foraging behaviour of foliage-gleaning birds of Canadian and Russian boreal forests. - Oecologia 120: 451-462.

Harris, L. D. 1984: The fragmented forest. Island biogeography theory and the preservation of biotic diversity. – University of Chicago press.

Harrison, S. & Bruna, E. 1999: Habitat fragmentation and large-scale conservation: What do we know for sure? – Ecography 22: 225-232.

Hofgaard, A. 1993: Structure and regeneration patterns in a Virgin *Picea abies* forest in northern Sweden. – J. Veg. Sci. 4: 601-608.

Holmes, R. T. & Robinson, S. K. 1981: Tree species preferences of foraging insectivorous birds in a northern hardwood forest. - Oecologia 48: 31-35.

Johnson, D. H. 1980: The comparison of usage and availability measurements for evaluating resource preferences. – Ecology 61: 65-71.

Järvinen, O. & Väisänen, R.A. 1979: Changes in bird populations as criteria of environmental changes. - Holarct. Ecol. 2: 75-80.

Kenward, R. E. 1982: Goshawk hunting behaviour, and range size as a function of food and habitat availability. - Journal of Animal Ecology 51: 69-80.

Kirsch, E. M. 1996: Habitat selection and productivity of least terns on the Lower Platte River, Nebraska. - Wildlife Monographs 132: 6-42

Kolowski, J.M. & Woolf, A. 2002: Microhabitat use by bobcats in Southern Illinois. – Journal of Wildlife Management 66: 822-832.

Kouki, J & Väänänen, A. 2000: Impoverishment of resident old-growth forest bird assemblages along an isolated gradient of protected areas in eastern Finland. - Ornis Fennica.77: 145–154.

Landin, J. E. 2004.3: Activity and movement patterns of the Siberian jay (*Perisoreus infaustus*) in relation to habitat fragmentation at the home range scale. MSc thesis, University of Agricultural Sciences, Sweden, 20p.

Levine, S. A. 1992: The problem of pattern and scale in ecology. - Ecology 73: 1943-1967.

Linder, P., Elfving, B. & Zackrisson, O. 1997: Stand structure and successional trends in virgin boreal forest reserves in Sweden. – Forest Ecology and Management 98: 17-33.

Lomnicki, A. 1980: Regulation of population density due to individual differences and patchy environment. – Oikos 35: 185-193.

MacArthur, R. H. & Levins, R. 1964: Competition, habitat selection and character displacement in a patchy environment. - Proc. Natl. Acad. Sci. USA 51: 1207-1210.

Manly, B. F. J., McDonald, L. L. & Thomas, D. L. 1993: Resource selection by animals; statistical design and analysis for field studies. - Chapman & Hall, London pp 177.

Mönkkönen, M. 1999: Managing Nordic boreal forested landscapes for biodiversity: ecological and economic perspectives. - Biodiversity and Conservation 8: 85-99.

Morris, D. W. 1995: Mosaic landscapes and ecological processes. - Chapman & Hall, London.

Nilsson, S.G. & Alerstam, T. 1976: Resource division among birds in North Finnish coniferous forest in autumn. - Ornis Fennica 53: 15-27.

Nilsson, C. & Götmark, F. 1992: Protected areas in Sweden: is natural variety adequately represented? - Conservation Biology 6: 232-242.

Orrock, J. L., Pagels, J. F., McShea, W. J. & Harper, E. K. 2000: Predicting presence and abundance of small mammal species: the effect of scale and resolution. – Ecological Applications 10: 1356-1366.

Otis, D. L. 1997: Analysis of habitat selection studies with multiple patches within cover types. - Journal of Wildlife Management 61: 1016-1022.

Pakkala, T., Hanski, I. & Tomppo, E. 2002: spatial ecology of the three-toed woodpecker in managed forest landscapes. - Silva Fennica 36: 279-288.

Pettersson R. B., Ball, J. P., Renhorn, K-E., Esseen, P-A. and Sjöberg, K. 1995: Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. - Biol. Cons. 74: 57-63.

Pulliam, H. R. & Danielson, B. J. 1991: Sources sinks, and habitat selection - A landscape perspective on population dynamics - American Naturalist 137: 50-66.

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 Zoologica 39: 7-20.

Sjöberg, K. & Danell, K. 2001: Introduction of Lodgepole pine in Sweden - ecological relevance for vertebrates - Forest ecology and Management 141 (1-2): 143-153.

Sjöberg, K. & Ericson, L. 1997: Mosaic boreal landscapes with open and forested wetlands - Ecological Bulletins 46: 48-60.

Sklepkovych, B. O. 1997a: Kinship and conflict: Resource Competition in the Siberian Jay. Doctoral dissertation, Univ.Sthlm.

Sklepkovych, B. O. 1997b: The influence of kinship on foraging competition in Siberian jays. - Behav ecol. Sociobiology. 40: 287-296.

Svensson, L. 1992: Identification guide to European passerines. - Stockholm.

Thiollay, J-M. 1992: Influence of selective logging on bird species diversity in a Guianan rain forest. – Conservation Biology 6: 47-63.

Thompson, C. M. & McGarigal, K. 2002: The influence of research scale on bald eagle habitat selection along Hudson River, New York (USA). – Landscape Ecology 17: 569-586.

Uimaniemi, L. 2004: Maintenance of genetic diversity in four Taiga specialists. unpublished Doctoral dissertation, Univ.Oulu.

Virkkala, R. 1987: Effects of forest management on birds breeding in northern Finland. - Ann.Zool.Fenn. 24: 281-294.

Virkkala, R. 1988: Foraging niches of foliage-gleaning birds in the northernmost taiga in Finland. - Ornis Fennica. 65: 104–113.

Virkkala, R. 1991: Population trends of forest birds in Finnish Lapland landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? - Biol. Conservation. 56: 223-240.

Virkkala, R., Rajasärkkä, A., Väisänen R, A,. Vickholm, M., & Virolainen, E. 1994: The significance of protected areas for the land birds of southern Finland. - Conservation Biology 8: 532-544.

Väisänen, R. A., Järvinen, O. & Rauhala, P. 1986: How are extensive, human-caused habitat alterations expressed on the scale of local populations in boreal forests? - Ornis Scand. 17: 282-292.

Wauters, L. A., Gurnell, J., Preatoni, D., & Tosi, G. 2001: Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. - Ecography 24: 525-538.

Whittingham, M.J. & Evans, K.L. 2004: The effects of habitat structure on predation risk of birds in agricultural landscapes. - Ibis 146: 210-220.

Wiens, J. A.1976: Population response to patchy environments. - Annual Review of Ecological Systems 7: 81-120.

Wiens, J. A., Rotenberry, J. T. & Van Horne, B. 1987: Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. – Oikos 48: 132-147.

Wu, J. & Hobbs, R. 2002: Key issues and research priorities in landscape ecology: An idiosyncratic synthesis. - Landscape Ecology 17: 355-365.

Personal comments
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