Habitat selection of Ural Owls (Strix uralensis) during the breeding season in a poor vole year

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Master Thesis 30 credits 2009

PREFACE

The process behind this thesis has been a great learning experience, and I will remember the field period with some nostalgia. The Ural Owls are really magnificent raptors, taking my breath away at several occasions.

I give a special thanks to my good friend Charlotte A. Johansen for introducing me to the Ural Owls, her guiding in field, moral support, and collaboration throughout the whole master thesis process. I thank Geir A. Sonerud for his excellent supervising, Gunnar Nyhus for teaching me how to use the GIS program, Hilde Rønning for reading and giving me feedback on my thesis, and Nils Boysen for language vetting.

Also, I would like to thank my friends in my reading room at school who made my days brighter, and managed to make me look forward to yet another day at school, and my family for supporting me.

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Ås, June 4th 2009

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ABSTRACT

Forest dwelling raptors, like the Ural Owl (*Strix uralensis)*, are considered especially sensitive to modern forestry. Previous studies on habitat selection of Ural Owls in Scandinavia have mainly been based on observations without the aid of radio telemetry. Souch observations are probably biased towards open habitats, such as large clear-cuts and bogs, because they are dependent on the visibility of Ural Owls. I investigated habitat selection in the Ural Owl during the breeding season in a Scandinavian boreal forest area, by the use of radio telemetry. Habitat use of five males and four females was compared to habitat availability within their home ranges by logistic regression. Based on point locations, the Ural Owls used medium dense or dense forest, mature forest, and moist coniferous forest more than randomly expected, and clear cut and young forest, dry coniferous forest, and mire/ bog less than randomly expected, irrespective of behaviour. Based on the habitat composition in a buffer within 25 m of the point location, the probability of the Ural Owls using a location even decreased with increasing proportion of clear-cut and young forest in the buffer. When hunting, the probability of the Ural Owls using a location increased with increasing proportion of moist coniferous forest in the buffer. Also, when disregarding the effect of behaviour, the probability of males and females using a location increased with increasing proportion of moist coniferous forest and wet coniferous forest in the buffer. The Ural Owls used buffers with a mixture of two or more vegetation types, i.e. containing an edge between vegetation types, more than randomly expected, while buffers with two or more forest age classes were used less than randomly expected. These effects of edge on habitat selection may be a result of two patterns; the Ural Owls avoiding open habitats, and wet coniferous forest often being confined to small patches. This study suggests that the Ural Owl is a mature forest raptor, for which relatively dense moist and wet coniferous forest is important, while open mires/bogs and clear-cuts and young forest are avoided. My findings contradict the current conception of modern forestry, based on clear-cutting, provides good habitat for Ural Owls, and suggest that future forest management should take precautions to preserve wet forest habitats of importance to this species.

CONTENTS

INTRODUCTION

Forest dwelling raptors are considered an especially sensitive group (Carey et al. 1992; Newton 1979). Even small changes in the procedure of forestry may have great effects on the food supply of raptors (Newton 1979). Old forest is expected to decline in the future, while the proportion of young and medium aged forest will increase (Sonerud 1991).

The Ural Owl *Strix uralensis* belongs in the taiga (Bolin et al. 1992; Lundberg 1979). In Sweden it is found in the eastern part (Svensson et al. 1999), south to approximately 60° N (Lundberg 1981). The Ural Owl is associated with medium dense and old coniferous forest with elements of deciduous birch forest, large mire/ bog areas with elements of wet forest, and large clear cut areas (Ahlén *et al.* 1972; Bolin et al. 1992; Cramp 1985; König *et al.* 1999). In Scandinavia, it resides in areas of low precipitation, and subsequent high fire rate, probably linked to it's use of chimney stacks made from fire as nest sites (Nyhus *et al.* 2003). The density of Ural Owls is suspected to be limited by the access to nest sites (Lohmus 2003; Lundberg 1981; Peterson 2002). Earlier studies indicated a need to study the significant of the occurrence of natural coniferous forest for a vital Ural Owl population (Bolin et al. 1992; Lundberg *et al.* 1984). There are approximately 3000 pairs of Ural Owl in Sweden (Cramp 1985; König et al. 1999; Peterson 2002). The population has recently increased, and this is assumed to be attributed to the adding of nest boxes, and from creation of hunting biotopes by forestry (Peterson 2002). The carrying capacity of an area to a raptors can be limited by nest-site or food availability, which ever is in shortest supply (Newton 1979).

Habitat selection affects all aspects of a bird's biology and will therefore affect all possible aspects of a bird study (Cody 1985). Selection of habitat is a hierarchical process, and use of habitat within home range is the third order of selection, and selection of geographical range and home range is designated as first and second order of selection, respectively (Johnson 1980). Usage is selective if a resource is used significantly different from its availability (Alldredge *et al.* 2006). According to Johnson (1980), "preference for a particular component is a reflection of the likelihood of that component being chosen if offered on an equal basis with others". Not all factors affecting choice of habitat will be equally important at all times. Many biological factors may effect estimated selection (Thomas *et al.* 1990). The choice of habitat may vary in accordance with demands of a season, or social and reproduction status (Cody 1985). Morphology and foraging behaviour may interact with habitat factors, such as vegetation type and vegetation cover, and influence the decision of habitat selection in raptors (Janes 1985). When foraging, a bird should spend more time in the patches that gives a higher net energy gain than the overall habitat, but as the quality of the overall habitat increases the time spent should decrease (Pyke 1984).

Ural Owls hunt by auditory clues (Norberg 1977; Peterson 2002), and mainly perch hunt in a pause-travel manner (Lundberg 1980b). The probability of hunting increased with increasing darkness and cloud cover (Johansen 2009). The Ural Owl is a prey generalist (Cramp 1985; Jaderholm 1987; Korpimaki *et al.* 1987; Mikkola 1983; Sidorovich *et al.* 2003). Nevertheless, its main prey type is voles, and vole abundance effects the distribution of Ural Owls in the landscape, as well as numbers of pair that breeds, clutch size, and survival (Brommer et al. 2003; Jaderholm 1987; Lundberg 1981; Pietiainen 1989; Sidorovich et al. 2003; Solonen 2004; Sundell et al. 2004). This means that the 3-4 year vole cycles in the mid boral zone (Hanski et al. 1991) greatly effect Ural Owl populations (Brommer et al. 2002; Korpimaki et al. 1987). The occurrence of voles in the Ural Owls' diet is positively correlated with the relative vole abundance between years (Korpimaki et al. 1990; Sidorovich et al. 2003).

In Fennoscandia, Ural Owls usually stay together with the same mate, in the same area, all their life (Cramp 1985; Hagen 1952; König et al. 1999; Lundberg 1981; Mikkola 1983; Peterson 2002; Pietiainen 1989). The Ural Owl has reversed sexual size dimorphism, and the mean body mass for male and females is 720 g and 871 g, respectively (Mikkola 1983). They produce 1-5 nestlings (Gunnar Nyhus per. comm.) The female incubates, broods and feeds during the first weeks after hatching, while the male provides the food (König et al. 1999; Lundberg 1980a). Gradually, as the nestlings grow, the females spends less time inside the nest box and more time guarding and some hunting, still dependent on food from the male (Cramp 1985). This might restrict the home range of the female, while the male may have to extend his foraging area to find enough food. For approximately two months after they have left the nest, the young are cared for and feed by their parents (König et al. 1999), then they disperse in September- November (Cramp 1985).

Radio telemetry has been used in many studies on home range and habitat selection in owls (Carey *et al.* 1995; Eldegard 1996; Fredriksson 2008; Strøm *et al.* 2001). Previous studies on the habitat selection of Ural Owls in Scandinavia have mainly been based on observations without the aid of radio telemetry, and the Ural Owl was assumed to hunt in open areas

(Cramp 1985; Lundberg 1980b; Mikkola 1983), and have an activity peak around sunset and sunrise (König et al. 1999; Lundberg 1980b). Such observations are probably biased towards open habitat, such as large clear-cuts and bogs, because they depend on the visibility of the Ural Owls. Radio telemetry provides unbiased information on use of habitat, therefore it is a very powerful tool in studies of wildlife (Aebischer et al. 1993). I have only found one published radio telemetry study on habitat selection in Ural Owls from Scandinavia (Bolin et al. 1992). This was based on one individual only and its results should therefore be regarded with caution. More studies are thus needed to validate these results. Therefore, the aim of my study was to investigate habitat selection in the Ural Owl during breeding season by the use of radio telemetry, and compare it with availability, in a Scandinavian boreal forest area. The questions I aimed to address were 1) Do Ural Owls use habitat randomly within home range? 2) Do Ural Owls show preference for any vegetation type, forest age class or edge between habitats?

METHODS

Study area

The study area covered about 382 km^2 and was situated in Torsby municipality in Värmland, Sweden (60°10`N- 60°35`N, 12°40`E- 13°38`E)(fig. 1 and 2). The area is situated in the mid boreal ecological zone with a climate in the transition between the continental and the marine (Helmfrid 1996). Forest is the most common vegetation type, and the dominating tree type is Scots Pine (*Pinus sylvestris*), Norway Spruce (*Picea abies*) and Downey Birch (*Betula pubescens*) (Nilsson 1990). The area is mostly coniferous forest intercepted by large areas of bog and mire (Nilsson 1990). The data was collected from late May to the end of July in 2008.

Radio tracking

The owls were captured and marked in may 2007 as described by Fredriksson (2008). They were equipped with radio transmitters (Biotrack, UK) mounted on as a backpack with a 6 mm Teflon tubing harness. The transmitter weight was c. 17 g for males (2.1 % of body mass)and 23 g for females (2.3 % of body mass). To track the owls a Biotrack Sika Yagi antenna and receiver were used. First, the owl's approximate location was determined from roads transecting the area, often by triangulation, and then the owl was tracked on foot. The more accurate positioning was done by homing in on the individual as described by White and Garrott (1990), and then locating it by sight. To avoid temporal clumping the time of tracking was rolled for all individuals. Each individual was attempted tracked evenly throughout the 24 hour cycle, except the two darkest hours (24.00-02.00, boreal summer time) when tracking became inefficient. Autocorrelation (dependence between positions) was avoided by making the time between successive trackings of the same individual longer than it would take the individual to cross its entire home range (Newdick 1983; Tew 1989, sited in Rooney et al 1998 p.90). There was at least six hours between successive trackings of the same individual. The annual survival rate of Ural Owls in Sweden is considered to be 90 % (Cramp 1985; Lundberg 1979), and in the current study survival from May 2007 to May 2008 was 89.5 % (Braathen 2009). Therefore, I consider the strain of our handling on the Ural Owls to be of little concern.

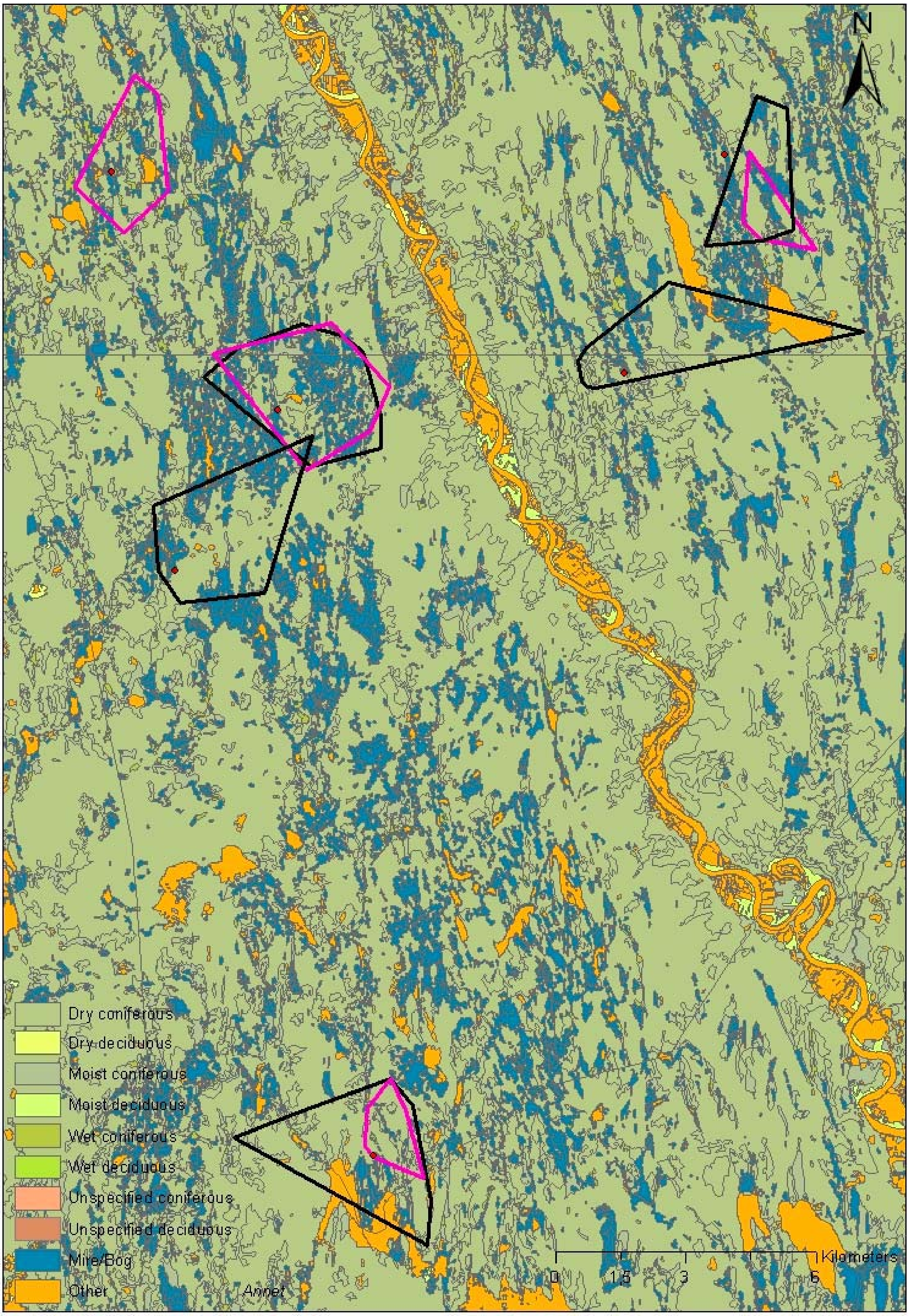

Figure 1 A map section over the study area where vegetation types are displayed. The home range (95 % MCP) of the male and female Ural Owls inVärmland county in Sweden in summer 2008 are indicated by the black and pink lines, respectively. The nest boxes are shown by the red dots.

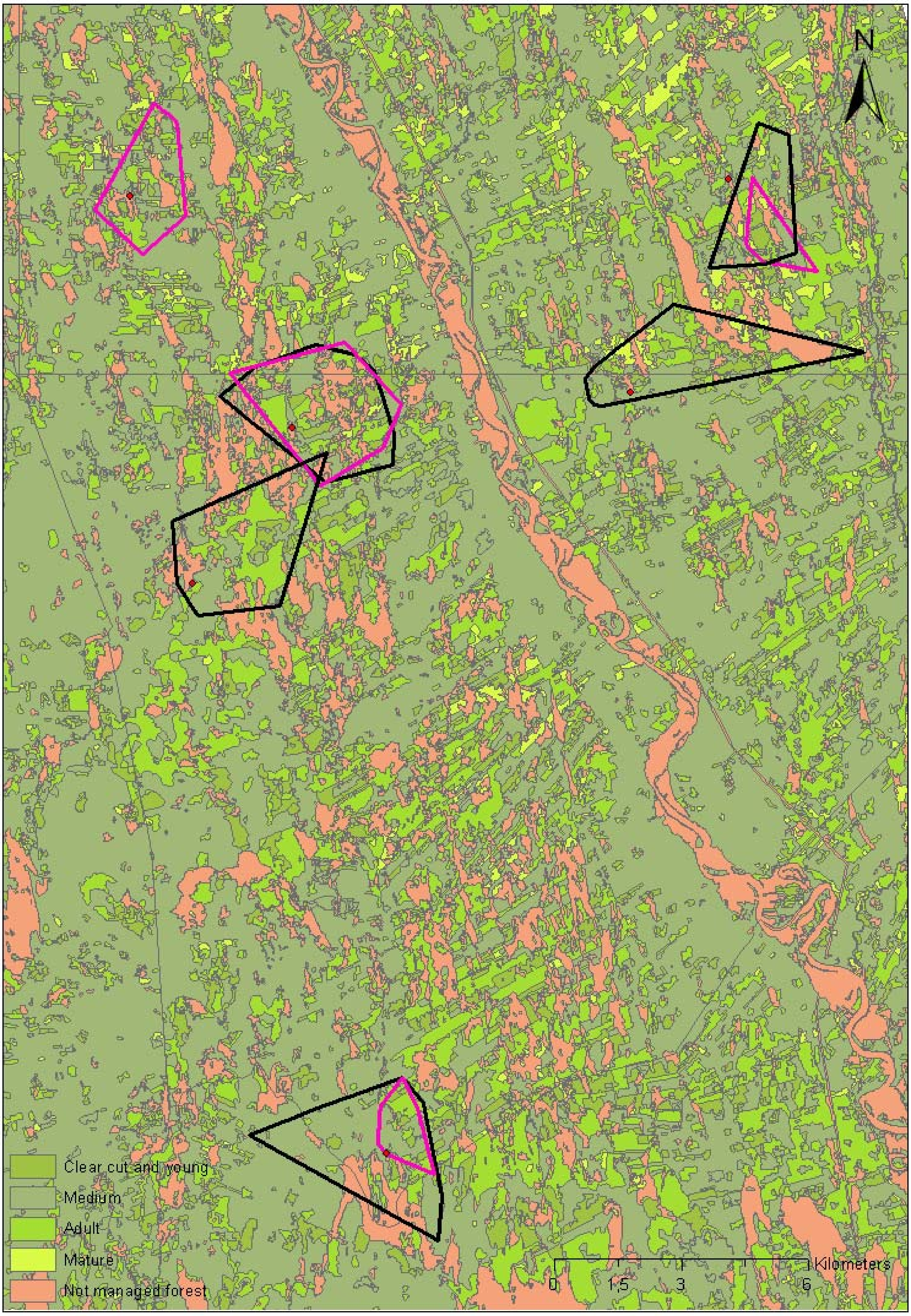

Figure 2 A map section over the study area where forest age classes are displayed. The home range (95 % MCP) of the male and female Ural Owls in inVärmland county in Sweden in summer 2008 are indicated by the black and pink lines, respectively. The nest boxes are shown by the red dots.

Data gathering

The geographical position of the located Ural Owl was recorded on a GPS (Geographical positioning system) receiver. In the cases where the owl was moving continuously or I was unable to home in on it, I positioned myself at the farthest point away from the nest box, still being between the box and the owl. This kind of plot was defined as a home range plot, and used only when making the home range estimate. If the owl was moving continuously between positions, the behaviour was defined as hunting, and if it was keeping its position it was defined as roosting. In the cases where the females were close to nest box with their young, the behaviour was defined as guarding/feeding young. If the owl was hunting when located, it was followed at distance to obtain an outer range point without interfering. On a few occasions the owl was assumed to have returned to its nest with prey, before it could be located properly. The individual was then tracked again at a later time. Information on the owl's roosting site was noted if I succeeded in spotting the owl and register its accurate position before it flew. On every observation I noted information about time, date, behaviour, habitat characteristics and weather conditions on a premade form according to defined categories (appendix).

Data processing

The geographical positions of each owl were imported into ArcMap 9.2 (ESRI 2008) Home range was calculated according to the minimum convex polygon (MCP) method as guided by Andreassen et al. (1993), which is the most common home range estimator (Hansteen et al. 1997). A 95 % MCP was used for habitat analysis, calculated from the 100 % MCP, after the 5 % most distant locations had been removed. This was unfortunately not possible for the one female (Varmestad) who had too few plots to remove the outermost 5 % plots. The study area was defined at the population level of the study objects, as the pooled 100 % MCP. Availability within each individual's home range was estimated by the random point method, making it possible to handle several parameters simultaneously (Marcum *et al.* 1980). Within each of the individual home ranges, 100 random plots were generated. In addition, a buffer with a 25 m radius, covering1953.541 km^2, was generated around each location, both observed and random. The use of buffer composition data increases the accuracy of determining habitat selection (Rettie *et al.* 1999). Varying patch sizes, selection of habitat mosaic and spatial associations among habitat types cannot be detected using point locations only for habitat analysis. To reduce the noise derived from including habitat that is not a part of the selection process, the size of the buffer was set to a minimum size (Rettie et al. 1999).

Information on the habitat characteristics of the geographical point locations and of the area inside the generated buffers was extracted from a digital map of the area (Lantmäteriverket 2001), based on aerial photos taken after 1995, with an accuracy of 10 m. For the point location of the owls, the information registered in field was used for analysis., thereby avoiding problems with GPS location inaccuracy (Dussault et al. 2001b). The vegetation types not used by the owls were categorized as "other" and the rest was categorized into the 7 vegetation types used during the field work which were dry- moist and wet deciduous or coniferous forest, and bog/ mire. Some random locations lacked the clarification of moisture gradient in the digital map (n<10), and so this was given in the following way: The moisture categories were written on several peaces of paper which were drawn at random to determine the moisture stated in the analysis. Moisture categories had the same possibility of accruing as in the rest of the random plots. Forest four age classes were clear cut and young forest, and medium- adult- , and mature forest. When analysing the effect of forest age classes on habitat choice the areas not categorized as managed forest (NMF), i.e. not forest and natural forest. I presumed that natural forest was included in the areas not covered by any category in the digital maps, as these maps are mostly used for timber production and therefore probably focus on productive forest. The data collected was prepared for analysis in Microsoft Excel 2003 (Microsoft 2003a).

Statistical analyses

Habitat selection was analysed by stepwise logistic regression with backward elimination of variables. The individual owls were the sampling unit. I assumed that the individual birds were independent of each other, while observations of the same bird were considered as a dependent subsample, which should exclude autocorrelation as a problem (Otis *et al.* 1999). The data was pooled across individuals when analysed, but to include valid error terms, each individual was included as a random effect in all the models (Thomas *et al.* 2006). I tested for an effect of sex and behaviour on habitat use to decide if the data could be pooled. The owls' use of habitat was compared with habitat availability based on vegetation type and forest age class. This was done for point locations and buffers. Also, to look for effect of edge on habitat choice I compared used and available number of vegetation types and forest age classes in buffers. Statistics and associated graphics were done in JMP 4.0 (SAS 2000). Histograms were made in Microsoft Excel 2003 (Microsoft 2003a), and the tables in Microsoft Word 2003 (Microsoft 2003b). All reported results are significant ($\alpha \leq 0.05$) unless otherwise stated. Because of small sample size, guarding/ feeding of young was excluded from the analysis. Not all individuals tracked were included in the analysis. One female (Svarttjern) had to be excluded, because of small sample size (most of her plots were guarding/feeding young), and the home range of another female (Granberg) was not entirely covered by the digital map. Sometimes variables had to be removed from the model before analysis due to bias and unstable variables. Because of problems with overdispersion in some models for point analysis, some analyses were not feasible.

RESULTS

All data on habitat use is based on observations of five male and four female Ural Owls (N=263). The average number of observations was 36.6 ± 1.21 (SE) for males and 20± 3.51 for females, and average number of locations per individual was 29.2 ± 3.31 (range=13-40). The median number of plots per individual per 24-hour period was 1 (range= 1- 3). Among the individuals used for habitat analysis, the Fastnes male and female, and the Fäbro male were nesting. while the remaining three males and three females were non-nesting.

Vegetation type: point locations

The Ural Owls used the various vegetation types in their home range different from what was available in their respective home ranges (fig. 3). The individual male (fig. 4) and female (fig. 5) Ural Owls used the vegetation types in their home range to different degree. Not all vegetation types were used by all individuals or both sexes.

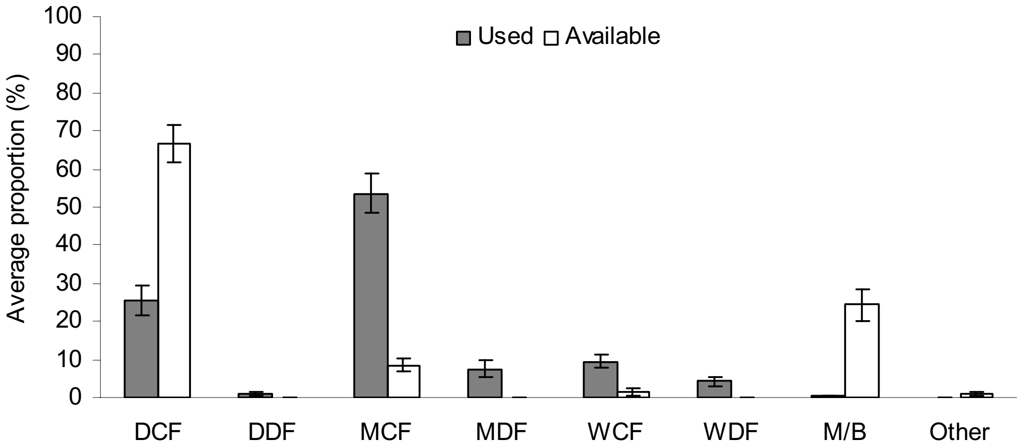

Figure 3 Proportions (%) of vegetation type used by and available to the Ural Owls ($\bar{x}$ ± SE) in Värmland in Sweden in summer 2008. DCF denotes dry coniferous forest, DDF denotes dry deciduous forest, MCF denotes moist coniferous forest, MDF denotes moist deciduous forest, WCF denotes wet coniferous forest, WDC denotes wet deciduous forest and M/B denotes mire/ bog. The category "other" includes all vegetation types and other categories in the digital map not used by any of the studied Ural Owls.

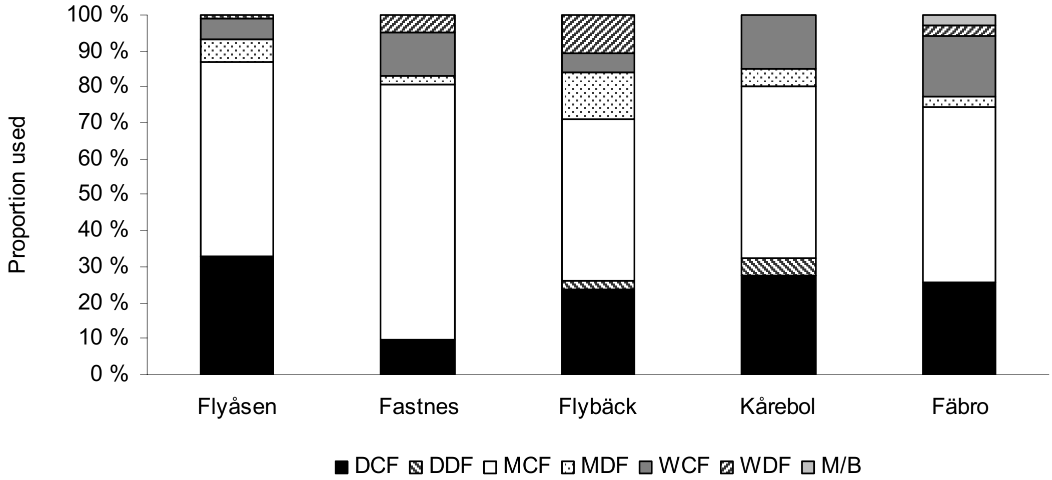

Figure 4 Proportions (%) of the vegetation types used individually by the male Ural Owls in their home ranges used in Värmland in Sweden in summer 2008. DCF denotes dry coniferous forest, DDF denotes dry deciduous forest, MCF denotes moist coniferous forest, MDF denotes moist deciduous forest, WCF denotes wet coniferous forest, WDC denotes wet deciduous forest and M/B denotes mire/ bog.

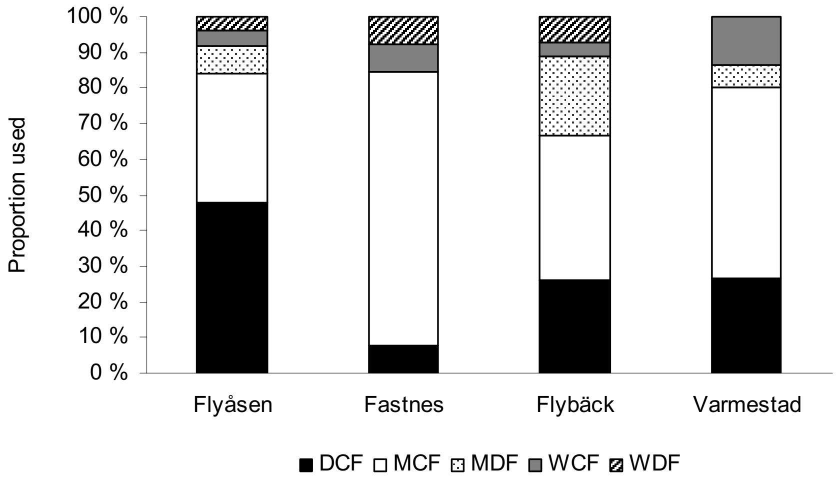

Figure 5 Proportions (%) of the vegetation types used by the female Ural Owl in their home ranges in Värmland in Sweden in summer 2008. DCF denotes dry coniferous forest, MCF denotes moist coniferous forest, MDF denotes moist deciduous forest, WCF denotes wet coniferous forest and M/B denotes mire/ bog.

The sex of a Ural Owl significantly affected its use of vegetation types based on point location (table 1). Therefore, analyses on the Ural Owls probability of use of vegetation types based on point locations were done separately for males and females.

Table 1 A logistic regression model of variables significantly affecting the probability that the Ural Owl were male or female, based on vegetation type in point locations. Whole model: N=771, X^2=3, df=8.92, P=0.030.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-0.27	0.14	3.64	0.057
Location (random)	2	0.68	0.711				
Moist coniferous forest	1	8.26	0.004	0.28	0.10	8.01	0.005

The males used three vegetation types significantly differently than randomly expected; dry coniferous forest, moist coniferous forest and mire/bog (table 2). The males used moist coniferous forest more, and dry coniferous forest and mire/bog less than randomly expected based on point locations (fig. 6).

Table 2 A logistic regression model of variables significantly affecting the probability that male Ural Owls used habitats different than randomly expected, based on use of vegetation types compared to availability in point locations. Whole model: N=682, df=7, X^2=318.43, P<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-3.640	0.60	36.44	<0.001
Individual(random)	4	1.83	0.766				
Dry coniferous forest	1	122.17	<0.001	2.022	0.24	73.95	<0.001
Moist coniferous forest	1	4.75	0.029	0.487	0.24	4.10	0.043
Mire/ bog	1	140.42	<0.001	3.377	0.55	37.77	<0.001

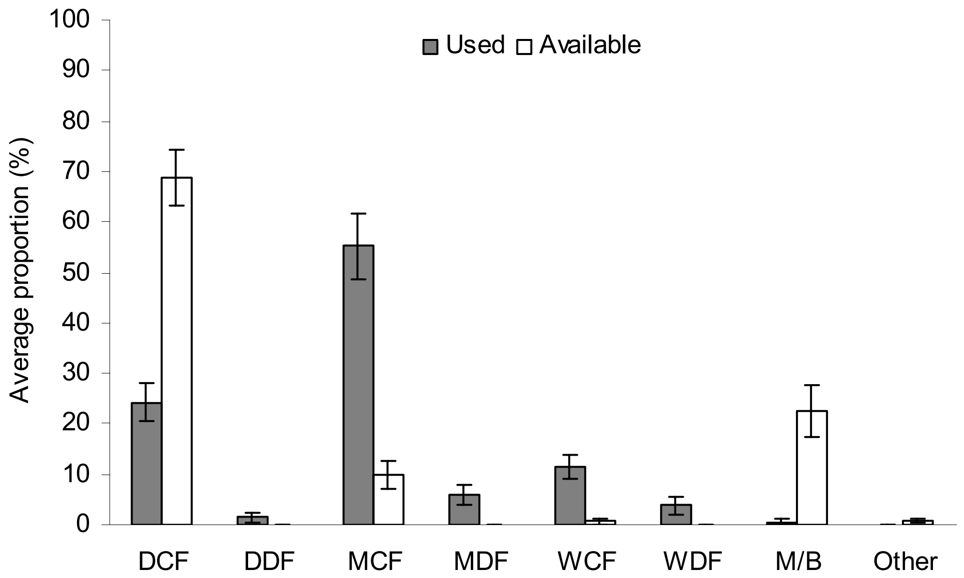

Figure 6 Proportions (%) of habitat used by and available to the male Ural Owls' in their home ranges ($\bar{x}$ ± SE) in Värmland in Sweden in summer 2008. DCF denotes dry coniferous forest, DDF denotes dry deciduous forest, MCF denotes moist coniferous forest, MDF denotes moist deciduous forest, WCF denotes wet coniferous forest, WDC denotes wet deciduous forest and M/B denotes mire/ bog. The category "other" includes all vegetation types and other categories in the digital map not used by any of the studied Ural Owls.

The females used three vegetation types especially different than randomly expected; dry coniferous forest, moist coniferous forest and mire/bog. The females used moist coniferous forest more, and dry coniferous forest and mire/bog less than randomly expected based on point locations (fig. 7). Because of problems with overdispersion (test value= 3.98), it was not possible to test the data for significance, and so the results must be regarded with caution.

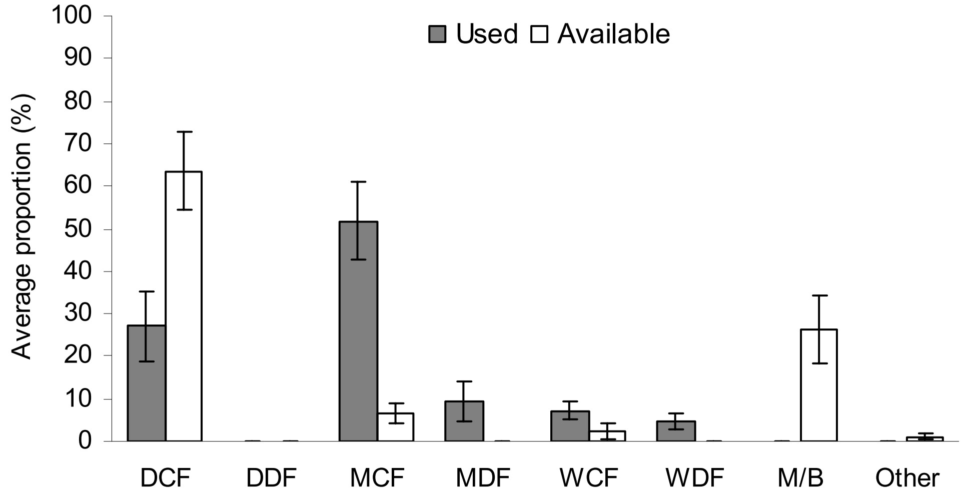

Figure 7 Proportions (%) of habitat used by and available to the female Ural Owls in their home ranges ($\bar{x} \pm$ SE) in Värmland in Sweden in summer 2008. DCF denotes dry coniferous forest, DDF denotes dry deciduous forest, MCF denotes moist coniferous forest, MDF denotes moist deciduous forest, WCF denotes wet coniferous forest, WDC denotes wet deciduous forest and M/B denotes mire/ bog. The category "other" includes all vegetation types and other categories in the digital map not used by any of the studied Ural Owls.

Vegetation type: buffer

The sex of the a Ural Owl did not significantly affect its use of vegetation type based on the proportion of vegetation types in the buffer around each location. Therefore, sexes were pooled in the analysis of the probability that the Ural Owls used habitat different than randomly expected based on vegetation types in the buffer. The behaviour of a Ural Owl significantly affected its use of habitat, based on the proportion of vegetation types in the buffer around each location (table 3). Hence, analysis of the probability that the Ural Owls used habitat different than randomly expected based on vegetation types in the buffer around each location were done separately for roosting and hunting.

Table 3 A nominal logistic regression model of variables significantly effecting the probability that the Ural Owls were roosting or hunting, based on the proportion of vegetation types in the buffer around each location. Whole model: N=173, X^2=4, df=15.08, P=0.005.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				0.51769	0.31653	2.68	0.102
Location(random)	2	10.60	0.005				
Sex	1	1.15	0.283	0.18958	0.17796	1.13	0.283
Dry coniferous forest	1	3.95	0.047	0.00045	0.00023	3.87	0.049

Whether a location was used by a Ural Owl, when roosting, or was randomly selected was significantly affected by the proportion of dry coniferous forest, moist coniferous forest and wet coniferous forest in the buffer around the location (table 4). The probability that a point was used by a Ural Owl, when roosting, rather than randomly selected increased significantly with the area of dry coniferous forest, moist coniferous forest and wet coniferous forest in the buffer around the point (fig. 8).

Table 4 A logistic regression model of variables significantly affecting the probability that the Ural Owls used habitats different than randomly expected when roosting, based on the proportion of vegetation types in the buffer around each location. Whole model: N=1071, df=11, X^2=43.51, P=<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-2.1445	0.3266	43.10	<0.001
Individual(random)	8	27.19	0.007				
Dry coniferous forest	1	6.62	0.010	0.0004	0.0002	6.13	0.013
Moist coniferous forest	1	10.39	0.001	0.0007	0.0002	10.79	0.001
Wet coniferous forest	1	10.86	0.001	0.0013	0.0004	12.38	<0.001

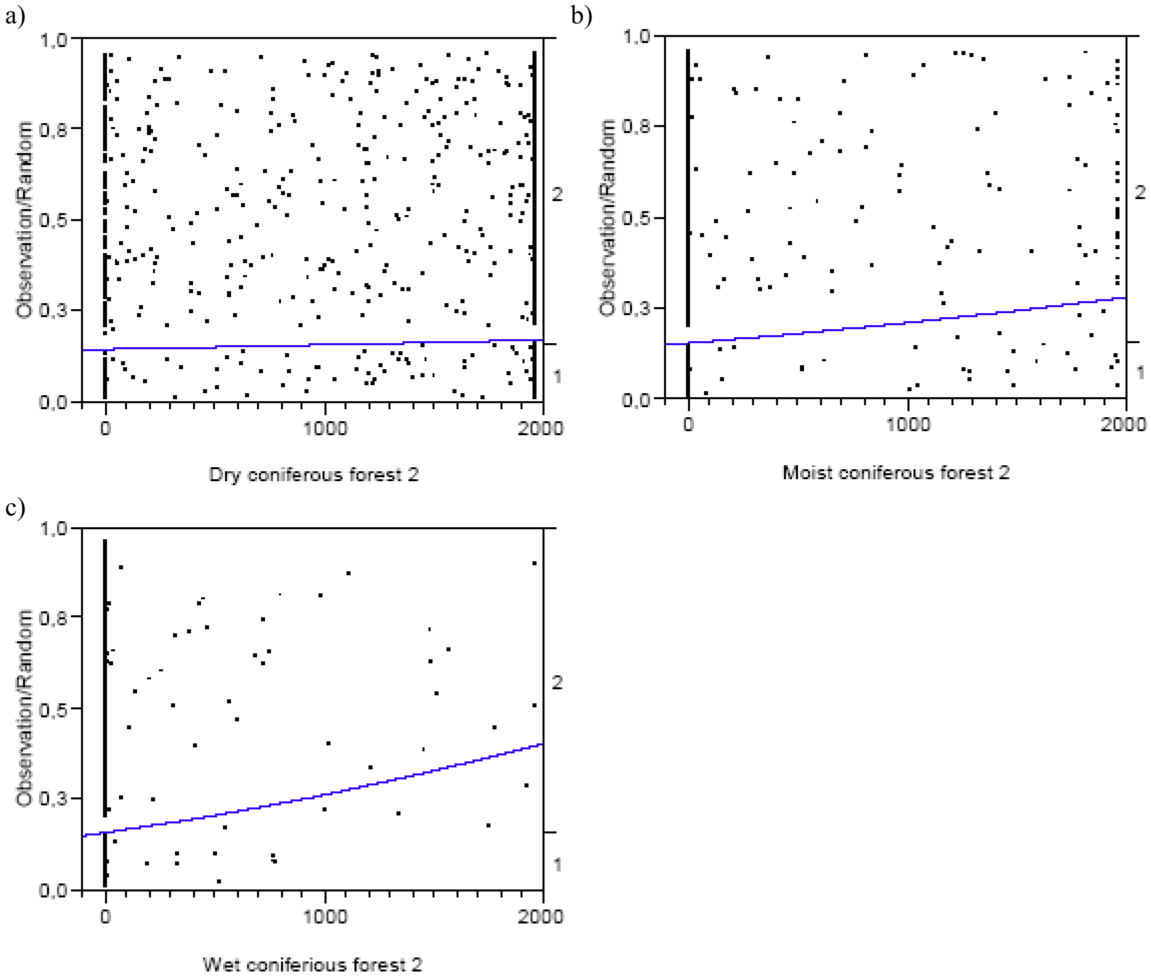

Figure 8 The probability that a location had been used by the Ural Owls, when roosting, rather than being randomly selected within the owls' home range, as a function of the proportion of a) dry coniferous forest (N=1071, df=1, X^2=0.88, P=0.348), b) moist coniferous forest (N=1071, df=1, X^2=4.98, P=0.026) and c) wet coniferous forest (N=1071, df=1, X^2=3.29, P=0.070) in the buffer around the location. The curve describes the logistic regression model, and is not corrected for individual ID.

Whether a location was used by a Ural Owl, when hunting, or was randomly selected was significantly affected by the proportion of moist coniferous forest in the buffer around the location (table 5). The probability that a location was used by a Ural Owl rather than randomly selected significantly increased with the proportion of moist coniferous forest in the buffer around the point (fig. 9).

Table 5 A logistic regression model of variables significantly affecting the probability that the Ural Owls used habitats different than randomly expected when hunting, based on the proportion of vegetation types in the buffer around each location. Whole model: N=988, df=9, X^2=22.84, P=0.007.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-1.94291	0.27860	48.63	<0.001
Individual(random)	8	16.10	0.041				
Moist coniferous forest	1	5.88	0.015	0.00053	0.00020	6.73	0.010

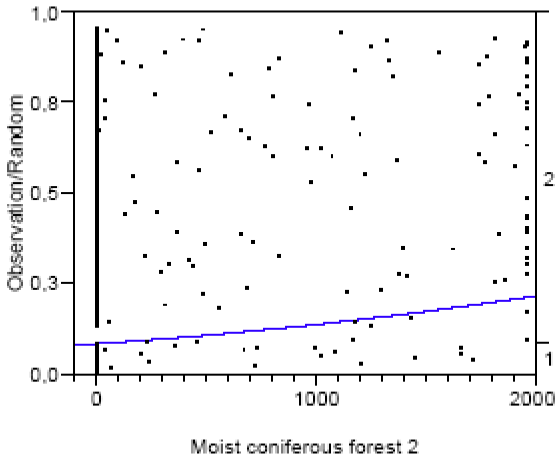

Figure 9 The probability that a location had been used by the Ural Owls, when hunting, rather than being randomly selected within the owls' home range, as a function of the proportion of moist coniferous forest (N=988, df=1, X^2=6.74, P=0.009) in the buffer around the location. The curve describes the logistic regression model, and is not corrected for individual ID.

When behaviour was pooled, whether a location was used by a Ural Owl or randomly selected was significantly affected by the proportion of moist coniferous forest and wet coniferous forest in the buffer around the location (table 6). The probability that a point was used by an Ural Owl rather than randomly selected increased significantly with the area of moist coniferous forest and wet coniferous forest in the buffer around the point (fig. 10).

Table 6 A logistic regression model of variables significantly affecting the probability that the Ural Owls pooled used habitats different than randomly expected, based on the proportion of vegetation types in the buffer around each location. Whole model: N=1161, df=10, X^2=38.17, P=<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-1.08796	0.19750	30.36	<0.001
Individual(random)	8	26.12	0.001				
Moist coniferous forest	1	9.85	0.002	0.00047	0.00014	10.41	0.001
Wet coniferous forest	1	5.28	0.022	0.00082	0.00034	5.75	0.017

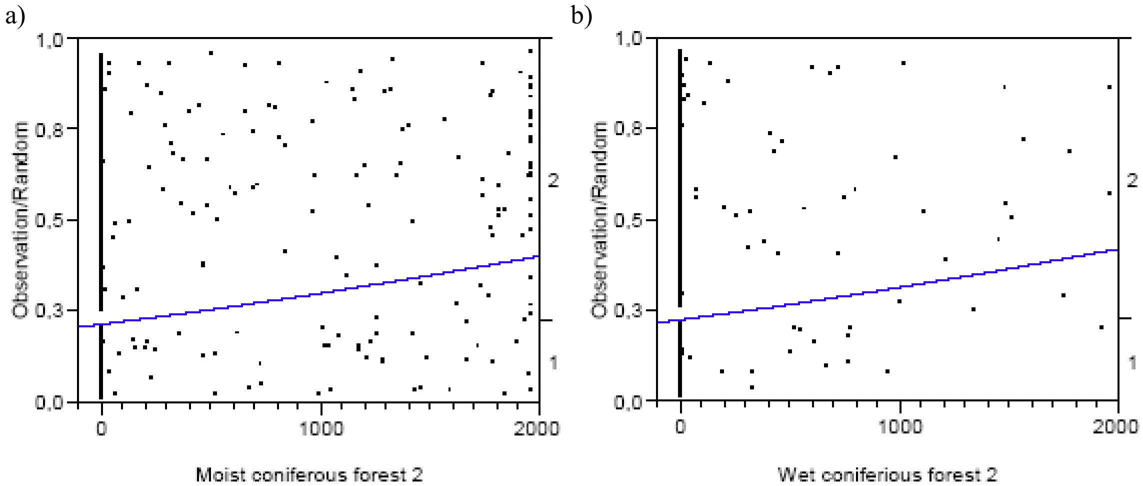

Figure 10 The probability that a location had been used by the Ural Owls rather than being randomly selected within the owls' home range, as a function of the proportion of a) moist coniferous forest (N=1161, df=1, X^2=9.88, P=0.002), and b) wet coniferous forest (N=1161, df=1, X^2=1.95, P=0.162) in the buffer around the location. The curve describes the logistic regression model, and is not corrected for individual ID.

Vegetation type: edge

As a measure of the amount of edge between habitats in a buffer, I used the number of vegetation types. The number ranged from 1-3. The sex of the Ural Owls significantly affected their use of habitat, based on the number of vegetation types in the buffer around each location when including "other" as a category (table 7). Hence, analysis of the probability that the Ural Owls used habitat different than randomly expected based on the number of vegetation types in the buffer around each location were done separately for males and females.

Table 7 A nominal logistic regression model of edge significantly affecting the probability that a Ural Owl was male or female, based on the number of vegetation types in the buffer around each location. Whole model: N=771, df=4, X^2=7.085, P=0.132.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				0.019	0.15	0.02	0.900
Location (random)	2	1.19	0.551				
Edge	2	6.42	0.040				
Edge (2-1)				-0.055	0.16	0.12	0.727
Edge (3-2)				-0.884	0.39	5.06	0.025

Whether a location was used by male Ural Owl or was randomly selected was significantly affected by the number of vegetation type in the buffer around the location when including "other" as a category (table 8). Locations in buffers with only one vegetation type were used significantly less than expected from random, while buffers with two or three vegetation types were used more than expected (fig. 11). The females showed no such significant difference in use from availability.

Table 8 A logistic regression model of edge significantly affecting the probability that male Ural Owls used habitats different than randomly expected, based on the number of vegetation types in the buffer around each location. Whole model: N=683, df=6, X^2=12.00, P=0.062.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-1.21	0.21	33.87	<0.001
Individual(random)	4	1.20	0.878				
Edge	2	11.41	0.003				
Edge (2-1)				0.47	0.19	6.34	0.012
Edge (3-2)				0.62	0.39	2.50	0.114

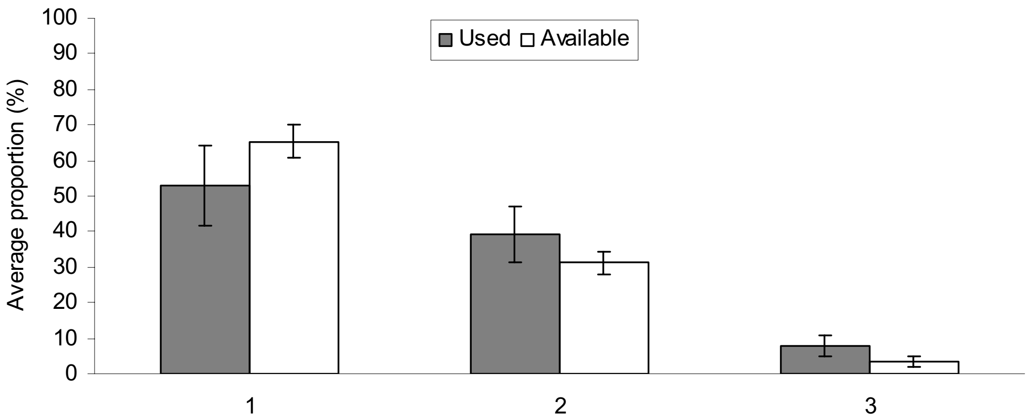

Figure 11 Proportion (%) of buffers with one, two or three vegetation types for buffers used by and available to the male Ural Owls in their home ranges ($\bar{x}$ ± SE) in Värmland in Sweden in summer 2008, when including the category "other" to the buffers.

Whether a location was used by the Ural Owls or randomly selected was significantly affected by the number of vegetation type in the buffer around the location when excluding "other" as a category (table 9). Locations in buffers with only one vegetation type were used significantly less than expected from random, while buffers with two or three vegetation types were used more than expected (fig. 12).

Table 9 A logistic regression model of edge significantly affecting the probability that the Ural Owls used habitats different than randomly expected, based on the number of vegetation types in the buffer around each location. Whole model: N=1157, df=10, X^2=38.64, P=<0.0001

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-1.23	0.21	36.04	<0.001
Individual(random)	8	24.39	0.002				
Edge	2	15.71	<0.001				
Edge (2-1)				0.56	0.15	13.67	<0.001
Edge (3-2)				0.20	0.34	0.33	0.564

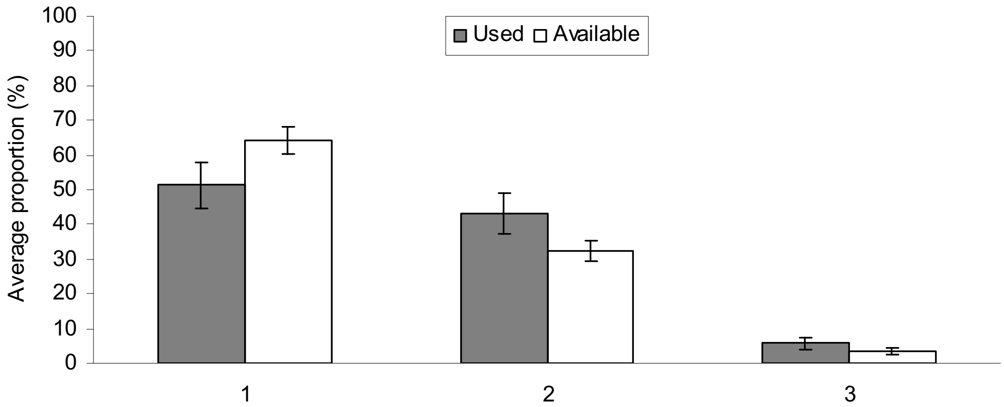

Figure 12 Proportion (%)of buffers with one, two or three vegetation types for buffers used by and available to the Ural Owls in their home ranges ($\bar{x}$ ± SE) in Värmland in Sweden in summer 2008, when excluding the category "other" to the buffers.

Forest age class: point locations

Based on the observations, the Ural Owls used 6.5 % open forest, 54.4 % medium dense forests and 39.2 % dense forests. The individual male (fig. 13) and female (fig. 14) Ural Owls used the forest age classes in their home ranges to different degree.

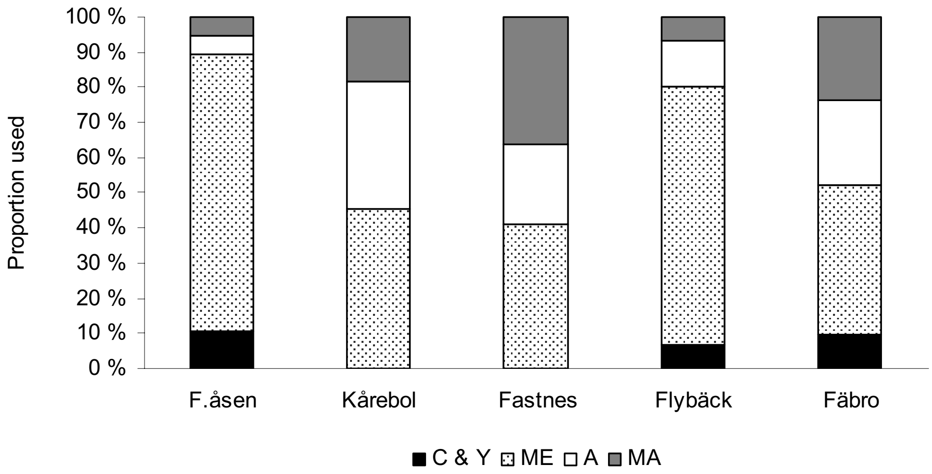

Figure 13 Proportions (%) of the forest age classes used by the male Ural Owls in their home range in Värmland in Sweden in summer 2008. C & Y denotes clear-cuts and young forest up to first thinning, ME denotes medium forest age, A denotes adult forest, and MA denotes mature forest. NMF denotes not managed forest. Not all forest age classes were used by all individuals or by both sexes.

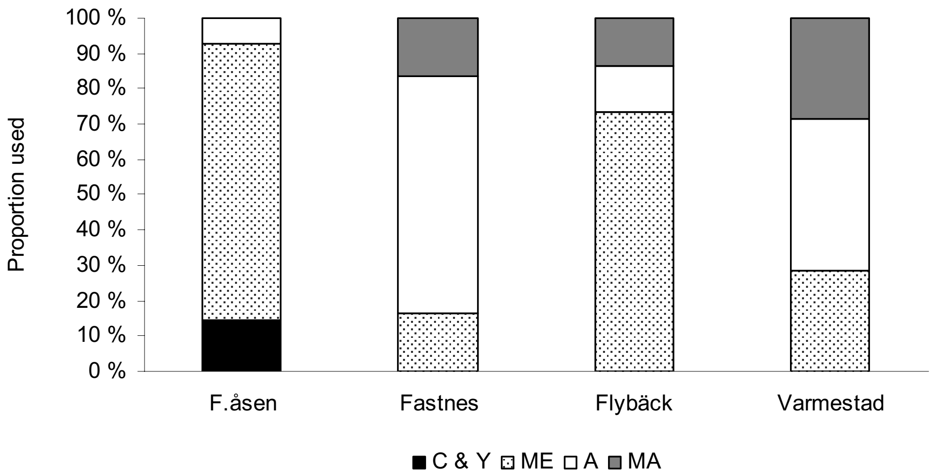

Figure 14 Proportions (%) of the forest age classes used by the female Ural Owls in their home range in Värmland in Sweden in summer 2008. C & Y denotes clear-cuts and young forest up to first thinning, ME denotes medium forest age, A denotes adult forest, and MA denotes mature forest. NMF denotes not managed forest. Not all forest age classes were used by all individuals or by both sexes.

Based on point locations, there was no significant difference in use of forest age class between males and females, nor between hunting and roosting. The Ural Owls used two forest age classes especially different than expected from random; mature forest more, and clear-cut and young forest less than expected from random (fig 15). Because of problems with overdispersion (test value= 2.40), it was not possible to test these data for significance, and so the results must be regarded with caution.

The proportion reported as used not managed forest (NMF) in figure 13 belongs in reality to the mature forest age class, but since it is not managed, e.g. natural forest, it could not be included in the analyses. Nevertheless, it is the most used forest age class and would have constituted 84 % of the mature forest age class had it been included.

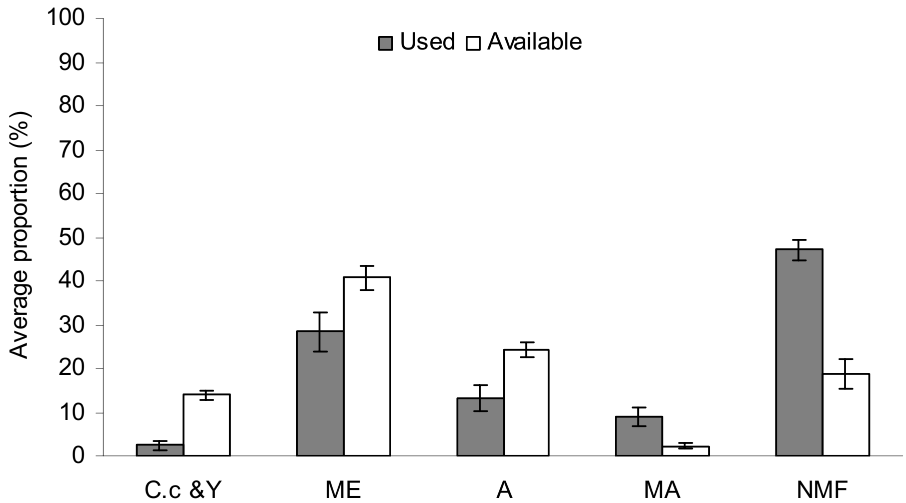

Figure 15 Proportions (%) of forest age classes used by and available to the male and female Ural Owls pooled ($\bar{x} \pm$ SE) in Värmland in Sweden in summer 2008. C & Y denotes clear-cuts and young forest up to first thinning, ME denotes medium forest age, A denotes adult forest, and MA denotes mature forest. NMF denotes not managed forest.

Forest age class: buffer

The probability that Ural Owls used forested habitat differently than randomly expected, based on the proportion of forest age class in the buffer around each location, was significantly affected by sex (table 10) and behaviour (table 11). Hence, analysis of the probability that the Ural Owls used habitat different than randomly expected based on forest age class in the buffer around each location, were done separately for males and females, and for roosting and hunting.

Table 10 A logistic regression model of variables significantly affecting the probability that a Ural Owls was male or female, based on the proportion of forest age classes in the buffer around each location. Whole model: N=729, df=6, X^2=19.19, P=0.004.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				9.847	5.143	3.67	0.056
Location (random)	2	0.150	0.928				
C.c and young	1	12.596	<0.001	-0.102	0.052	3.93	0.047
Medium	1	12.042	<0.001	-0.101	0.052	3.82	0.051
Adult	1	10.993	<0.001	-0.099	0.052	3.65	0.056
Mature	1	7.594	0.006	-0.090	0.052	3.01	0.083

Table 11 A logistic regression model of variables significantly affecting the probability a Ural Owls was roosting or hunting, based on the proportion of forest age classes in the buffer around each location. Whole model: N=171, X^2=4, df=21.48, P=<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				0.344	0.3127	1.21	0.271
Location (random)	2	7.89	0.0194				
Sex	1	0.90	0.3429	0.170	0.1803	0.89	0.346
Medium	1	9.35	0.0022	0.011	0.0038	9.08	0.003

Whether a location was used by male Ural Owls, when roosting (table 12) or hunting (table 13), or was randomly selected was significantly affected by the proportion of clear-cut and young forest in the buffer around the location. The probability that a point was used by a male Ural Owl rather than randomly selected decreased significantly with the area of clear-cut and young forest in the buffer around the point in all cases, but to a different degree depending on behaviour (fig. 16). The probability of use decreased the least when they hunted.

Table 12 A logistic regression model of variables significantly affecting the probability that when roosting, the male Ural Owls used forest age classes different than randomly expected, based on the proportion of forest age classes in the buffer around each location. Whole model: N=583, df=5, X^2=52.65, P=<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-1.378	0.264	27.34	<0.001
Individual (random)	4	3.55	0.471				
C. c and young	1	46.45	<0.001	-0.057	0.020	8.24	0.004

Table 13 A logistic regression model of variables significantly affecting the probability that when hunting, the male Ural Owls used forest age classes different than randomly expected, based on the proportion of forest age classes in the buffer around each location. Whole model: N=524, df=5, X^2=22.56, P=<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-1.733	0.3007	33.22	<0.001
Individual (random)	4	7.77	0.101				
C. c and young	1	16.59	<0.001	-0.025	0.0087	8.54	0.004

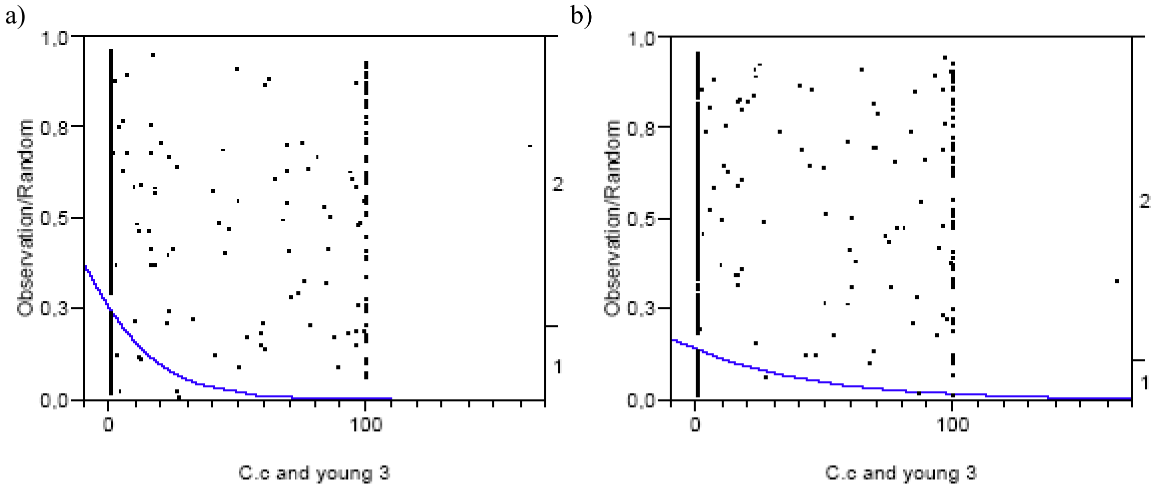

Figure 16 Proportion of clear-cut and young forest in buffer. The probability that a location had been used by the male Ural Owls rather than being randomly selected within the owls' home range, as a function of the proportion of forest age classes in the buffer around the location. The curve describes the logistic regression model, when the owls a) roosted (N=583, df=1, X^2=49.10, P=<0.001) and b) hunted (N=524, df=1, X^2=14.79, P=<0.001), and is not corrected for individual ID.

Whether a location was used by female Ural Owls, when roosting (tab 14) or hunting (tab 15), or randomly selected was significantly affected by the proportion of clear-cut and young forest and adult forest in the buffer around the location. The probability that a location was used by a female Ural Owl rather than randomly selected decreased significantly with the proportion of clear-cut and young forest, and with the proportion of adult forest in the buffer around the point when the owl was roosting (fig 17), and it decreased with the proportion of clear-cut and young in the buffer when the owl was hunting (fig 18).

Table 14 A logistic regression model of variables significantly affecting the probability that when roosting, the female Ural Owls used forest age classes different than randomly expected, based on the proportion of forest age classes in the buffer around each location. Whole model: N=416, df=5, X^2=26.46, P=<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-2.1787	0.4042	29.05	<0.001
Individual (random)	3	7.80	0.050				
C. c and young	1	16.33	<0.001	-0.0313	0.0122	6.56	0.011
Adult	1	6.65	0.010	-0.0094	0.0039	5.94	0.015

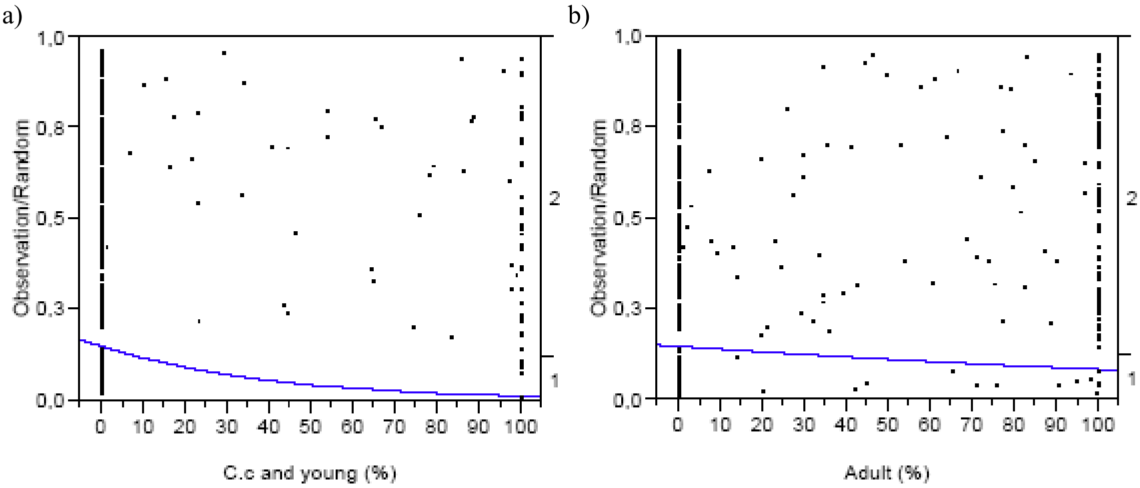

Figure 17 The probability that a location had been used by the female Urals Owls rather than being randomly selected within the owls' home range, as a function of the proportion of) clear-cuts and young forest (N=416, df=1, X^2=12.56, P=<0.001) and b) adult forest(N=416, df=1, X^2=3.043, P=0.081) in the buffer around the location. The curve describes the logistic regression model, and is not corrected for individual ID.

Table 15 A logistic regression model of variables significantly affecting the probability that when hunting, the female Ural Owls used forest age classes different than randomly expected, based on the proportion of forest age classes in the buffer around each location. Whole model: N=391, df=4, X^2=11.88, P=0.018.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-2.456	0.395	38.73	<0.001
Individual (random)	3	7.20	0.066				
C. c and young	1	4.69	0.030	-0.019	0.012	2.74	0.098

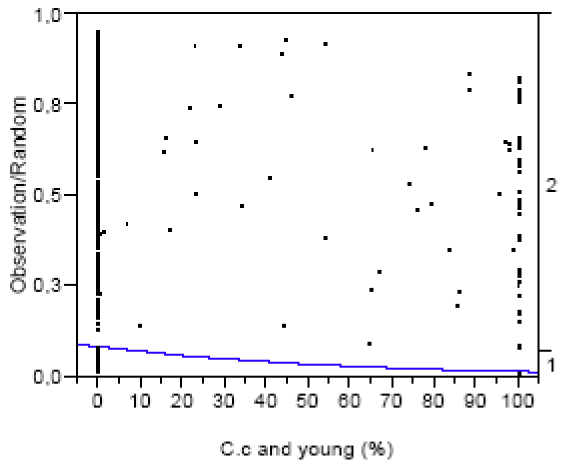

Figure 18 The probability that a location had been used by the female Ural Owls, when hunting, rather than randomly selected within the owls' home range, as a function of the proportion of clear-cut and young forest (N=391, df=1, X^2=4.67, P=0.031) in the buffer around the location. The curve describes the logistic regression model, and is not corrected for individual ID.

Forest age class: edge

As a measure of the amount of edge between habitats in a buffer, I used the number of forest age classes. The number ranged from 1-3. Whether a location was used by the Ural Owls or randomly selected was significantly affected by the number of forest age classes in the buffer around the location when including not managed forest (NMF) (tab 16). Locations in buffers with only one forest age class were used significantly more than expected from random, while buffers with two or three forest age classes were used less than expected from availability (fig 19).

Table 16 A logistic regression model of edge significantly affecting the probability that the Ural Owls used habitats different than randomly expected, based on the number of forest age classes in the buffer around each location. Whole model: N=1084, df=10, X^2=42.95, P=<0.001.

	Whole model			Parameter estimate			
Variable	df	X^2	P	β	SE	X^2	P
Intercept				-0.84	0.21	15.34	<0.001
Individual(random)	8	24.84	0.002				
Edge	2	18.79	<0.001				
Edge (2-1)				-0.84	0.21	16.23	<0.001
Edge (3-2)				0.34	0.59	0.33	0.566

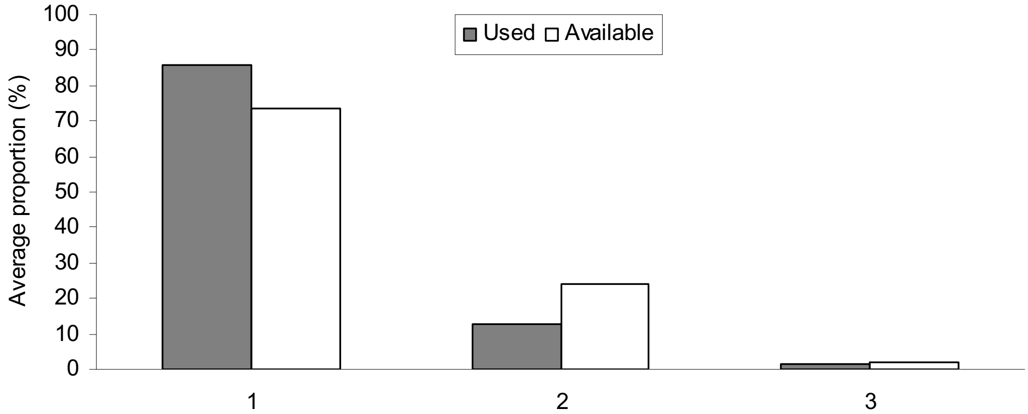

Figure 19 Proportion (%) of buffers with one, two or three forest age classes for buffers used by and available to the Ural Owls in their home ranges ($\bar{x}$ ± SE) in Värmland in Sweden in summer 2008, when excluding the category not managed forest (NMF).

DISCUSSION

Evaluation of method: data gathering

Several of the variables collected in field were based on subjective measurements and may therefore not represent the real variable as it was. Also, the data was collected by Charlotte A. Johansen and my self. Consequently, it is likely that there are some divergences in perception of the variables in field that is passed on to the data collection. This could have been tested for by including observer as a variable in the analyses. I will in the following section discuss some of the sources of error encountered in field that I consided most important for my part of this study.

Distinguishing between when the Ural Owls were roosting and hunting based on movement while tracking may lead to misinterpretations, especially in years of low vole abundance. According to Andersson (1981) perch time is longer when prey abundance is low, as long as it not so low that they switch prey species (Redpath 1995).

Moisture was used as a measure of determining vegetation type, in addition to the dominant tree species. This was to adjust the vegetation categories to the ones used in the digital map of the study area. Moisture was supposed to represent ground cover vegetation, like moss or lichen dominated vegetation. This was sometimes hard to decide during what was perceived as a particularly dry period. The bogs and mires were very dry, and most areas could easily be crossed dry shod. Therefore, sometime I based my classifications on ground vegetation and dominating tree species alone, irrespective of the actual moisture at that time. Nevertheless, there were probably some underestimations of moist and wet forest.

Sometimes I got the feeling that I was missing out on a lot of information when filling out the premade form, and hindsight and reading up on literature increased this impression. There are variables that would have given a better understanding of the location, for instance are the distance to other kind of habitat, not only open and wet, the degrees of the surrounding area covered by other habitats and the canopy cover of the perch tree.

Evaluation of method: data processing

The data are based on digital maps with an accuracy of 10 m, which may be large enough to miss out on important information. This may have had an effect on buffers around used point locations. Dussault et al (2001a) found that misclassification of forest habitat variables are common, but less so on simple classification of stands of coniferous forest, which is the most common forest stand type in this study. There were a lot of forestry activity in the study area, and in the 7 years time between the map was made and the field registrations was conducted some habitat variables might have changed, most likely in forest age class (Dussault et al. 2001a).

Evaluation of method: statistical analyses

During the statistical analysing of point locations I encountered problems with overdispersion that I was not capable of overcoming, and so the data interpretation had to be done on basis of counts presented in bar graphs. This might lead to erroneous inference. Some vegetation types were especially abundant in use and others in availability, and may have caused unit-sum constraints.

Evaluation and interpretation of the results

Based on point locations, the Ural Owls used medium dense or dense forest, mature forest, and moist coniferous forest more than expected from random, and clear-cut and young forest, dry coniferous forest, and mire/ bog were used less than randomly expected, irrespective of behaviour. This is in accordance with other findings that the Ural Owls selectively use areas of medium dense, mature and moist coniferous forest (Hagen 1952; König et al. 1999; Peterson 2002). On the other hand, the results contradicted earlier findings that the Ural Owls extensively use open areas like clear cuts and mire/bog (Cramp 1985; Lundberg 1980b; Mikkola 1983). In my study, the probability of a Ural Owl using a location even decreased with increasing proportion of clear-cut and young forest in the buffer. When hunting, the probability of the Ural Owls using a location increased with increasing proportion of moist coniferous forest in the buffer. Also, when disregarding the effect of behaviour, the probability of the Ural Owls using a location increased with increasing proportion of moist coniferous forest and wet coniferous forest in the buffer. Mature forest was not very abundant in the study area, and the owls were very mobile, so the use of mature habitat within home range for hunting and roosting was hardly affected by the owls' use of old forest for nesting.

The females' probability of using a location decreased with the proportion of adult forest in the buffer, which might be an effect of tree density and their larger size.

Selection of vegetation type and forest age classes in accordance with food abundance has been seen in several habitat selection studies on owls. Prey-based habitat selection was found in Spotted Owls (*Strix occidentalis*) and Northern Spotted Owls (*S. occidentalis caurina*), which selected primarily mature forest for both hunting and roosting (Carey et al. 1990; Carey et al. 1992; Carey et al. 1995). Cover of mature forest was important in survival of male Tengmalm's Owls (*Aegolius funereus*), because it provided bank voles (*Myodes glareolus*) and alternative prey (Hakkarainen et al. 2008). Raptor habitat selection influenced by the habitat selection of their prey is especially evident in areas where prey diversity is low and when they are unevenly distributed between habitats (Janes 1985). The preferred habitat to a raptor may vary between years (Lõhmus 2003). In my study area the proportion of bank vole in Ural Owls' diet of the in a year of low vole abundance (2005), and in a year of high vole abundance (2006), was constantly high at 33% and 32 %, respectively (G. Nyhus & G.A. Sonerud pers.comm; Rønning 2007). The proportion of field vole (*Microtus agrestis*), on the other hand, increased from nine to 15 % between the two years (Rønning 2007). Bank voles occur in a wide range of forest habitat, but attain the highest density in moist or wet older spruce forest, while field voles are most abundant in open areas like clear cuts and fields (Hansson 1968; Henttonen *et al.* 1977; Larsson *et al.* 1977; Sonerud 1986).

It is important to ask why a home range is selected (Thomas et al. 1990), and that a resource is used less than available within home range may not reflect the true importance of the resource, because the home range may have been chosen on the basis of the abundance of this resource (Johnson 1980). Based on the same data as used in this study, Johansen (2009) showed that the home ranges increased as the proportion of clear cut and young decreased. Low abundance of voles in 2008 probably made the owls more influenced by the distribution of alternative prey when choosing foraging habitat (Hakkarainen et al. 1996). Large clear-cuts have a positive effect on owls by providing more field voles (Hakkarainen et al. 1997; Lõhmus 2003; Sidorovich et al. 2008). In an experiment in captivity the Ural Owls prey utilization was not selective, but rather influenced by prey susceptibility (Nishimura *et al.* 1988). Field vole is slower than bank vole (Sonerud, pers. comm.), so they are easier to catch. The apparent effect of clear-cut area on home range size contradicts with the homologous study from the previous year (Fredriksson 2008), the findings in this habitat selection study and that field voles in the diet decreased in a previous pore vole year. A more plausible explanation is that the effect is connected to the Ural Owls preferring forest areas of good productivity that also are attractive for forestry.

The Ural Owls in my study used buffer with a mixture of two or more vegetation types, i.e. containing an edge between vegetation types, more than randomly expected, while buffers with two or more forest age classes were used less than randomly expected. Other findings in habitat use of the Ural Owls have pointed out a preference for a mixture of habitats; elements of wet forest and deciduous forest, and forest areas near large open mires and clear cuts (Ahlén et al. 1972; Cramp 1985; Hagen 1952; König et al. 1999; Mikkola 1983; Peterson 2002; Svensson et al. 1999). That the Ural Owls selected for wet coniferous forest probably had an effect on the selection of mixed habitat, considering that this kind of habitat often were confined to small patches, often border on mire/bog. According to Lundberg (1979) the proportion of birds and amphibians in the diet of Ural Owls were inversely linked to the proportion of voles. I would expect more amphibians in the edge to wet forest and mire/bog, also making edge attractive for foraging. That the Ural Owls used a mixture of forest age classes less than expected does not ascertain that edges between forest age classes are not important for foraging, because it is possible that the buffer with a 25 m radius is not enough to detect edge, since it might be broader than that. Edge provides perch sites, making it possible to hunt in the outer range of open areas (Sonerud 1986; Sonerud 1997). Breeding Hooded Crows used edge to open areas more when availability increased, and used it more than available as long as the proportion was <0.40 (Smedshaug et al. 2002).

When roosting, the probability of the Ural Owls using a location increased with increasing proportion of coniferous forest in the buffer, and the Ural Owls in my study seemed indifferent to degree of moisture. Roosting sites may be chosen based on thermal conditions or shelter (Janes 1985). Other studies have suggested that the canopy cover and the height of the roost tree is the most important variables when owls choose roosting locations (Call et al. 1992; Cooke et al. 2002; Ganey et al. 1999). Coniferous trees are generally denser than deciduous trees, and hence, they provide better cover. Another possible explanation for the selection of all three types of coniferous forest is that it might be the outcome of unit-sum constraint from avoidance of mire (Aebischer et al. 1993).

When separating habitat into categories, important information on the basis of selection by the animal may be missed out, since they may be seeking a mixture of habitats, or a certain habitat patch size or shape (Alldredge et al. 2006). Which structural variable the birds respond to can be difficult to interpret even if one is able to correlate a structural feature to abundance (Cody 1985). Also, a habitat may have different importance for an animal's fitness than reflected by the time spent there, for example a habitat used extensively for resting may be much less important for fitness than another habitat used infrequently for other purposes (Alldredge et al. 2006). Hooded Crows spent little time in crop areas, but it might have been enough to fulfil its needs (Smedshaug et al. 2002). Important resources may not be needed in large quantity or often, and may therefore used less (Johnson 1980).

Conclusion

This study suggests that the Ural Owl is a mature forest raptor, for which relatively dense moist and wet coniferous forest is particularly important, while open mires/bogs and clear-cuts and young forest are avoided. My findings contradict the current conception of modern forestry, based on clear-cutting provides good habitat for Ural Owls, and suggest that future forest management should take precautions to preserve wet forest habitats of importance to this species.

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APPENDIX

Variables noted in field on a premade form:

Serial number

Date

Time

Individual

Sex

Coordinates

Plot type: Habitat plot or range plot

Temperature

Wind: No wind, some wind, windy

Cloud cover: Clear, 50 % cloud cover, cloudy

Precipitation: No rain, some rain, heavy rainfall

Behaviour: Rosting, hunting, guarding/feeding young

Sitting post

Sitting height

Fright distance

Vegetation type

Dominating tree

Forest height

Forest age class

Forest density: Open, medium dense, dense

Distance to open habitat

Distance to wet habitat

Comments