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Master's Thesis in Ecology

RESPONSES OF BIRDS TO FRAGMENTATION AND REDUCTION OF WILLOW THICKET HABITATS IN THE SOUTHERN ARCTIC TUNDRA

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Abstract

The goal of this study is to estimate the association between willow thicket habitat configuration on southern Arctic tundra and abundance and species richness of birds, from the perspective that reindeer overbrowsing causes habitat fragmentation and size reduction of willow thicket areas. The study was performed in two different regions in Finnmark County, Northern Norway; The Varanger peninsula and Laksefjordvidda. The birds associated with the willow thickets were censused by point sampling method. Willow thickets were classified by 1:15 000 ortho-rectified aerial photos in raster-tiff format. Variables describing thicket area and fragmentation were derived from these photos while thicket height and density were measured in the field. The analyses were made at two spatial scales; section scale (2.2 x 2.2 km) and point scale (200 x 200 m). Effects of thicket variables were mainly detected in species expected a priori to be associated with willow thickets. On point scale thicket area emerged as an important factor explaining abundance and species richness while on section scale vertical density and height were explaining abundance and species richness of birds on southern Arctic tundra.

Key words: Habitat fragmentation; size reduction; area; willow thicket; abundance; species richness; Arctic; passerine birds; birds; scale.

1. Introduction

Biodiversity is of central importance in ecology. It is likely to play an important role for ecosystem functioning (Loreau et al. 2001), and spatial and temporal variation in biodiversity is one of the most fascinating ecological patterns to understand (Rosenzweig 1995, Gaston 2000). Recent global changes, and in particular land-use and climatic change, are likely to have strong negative impacts on biodiversity of terrestrial ecosystems (Sala et al. 2000). Consequences for Arctic ecosystems are expected to be especially large, because climatic changes are amplified in polar regions (Serreze et al. 2006) and because Arctic ecosystems may be less resilient (Callaghan et al. 2004). There are, however, relatively few studies documenting changes in diversity of Arctic terrestrial ecosystems (Callaghan et al. 2004). Willow thickets are expected to be hotspots for biodiversity in the treeless Arctic tundra, providing critical habitat for wildlife (Keigley et al. 2002). They represent areas of high conservation priority because a potentially large portion of a regional flora and fauna can be preserved within their bounds. In southern Arctic tundra willow (*Salix* spp.) thickets are common on riparian sediment plains. However intense ungulate browsing can strongly affect plant structure and limit reproduction of riparian willows (Brookshire 2002, Den Herder et al. 2004, Zimov 2005), thus reducing and fragmenting the area extent of thickets.

Over the last decades it has been claimed that the increase in density of semi-domestic reindeer has had substantial browsing impacts on the tundra (Moen and Danell 2003). Willow is an important summer food resource for the reindeer in Fennoscandia (Olofsson et al. 2001). Studies have shown that summer browsing by reindeer strongly affects willow growth and reproduction, as well as densities of herbivorous insects utilizing willows. This effect is suggested to be most evident in low-productivity tundra heaths where alternative forage plants are scarce (Den Herder et al. 2004). Even though there are some reports demonstrating changes in the vegetation being compatible with the impacts of intensified browsing (Bråthen et al. 2007), the broader implications of these changes for the structure and function of the tundra ecosystem have only partly been addressed (Ims et al. 2007, Killengreen et al. 2007).

A main premise of the present thesis is that increasing fragmentation and area reduction of willow thickets is the expected outcome of reindeer overabundance. Habitat fragmentation and habitat loss is generally seen as one important factor affecting diversity negatively (Wilcox 1980, Wilcove et al. 1986, Meffe and Carroll 1997, Sala et al. 2000). Habitat fragmentation involves reduction of habitat patch size and increased isolation of patches (Andrén 1994). Increased habitat fragmentation is also usually associated with loss of habitat area. In fragmented habitats, suitable area remains only as a remnant surrounded by deteriorated environment (Urban and Shugart 1984, Fahrig and Paloheimo 1988). Habitat patch area has emerged from many studies as an important variable positively associated with measures of abundance and richness (Zajc 2005). Population declines because areas of suitable habitat decrease (Temple and Cary 1988) or because of lower reproduction or higher mortality in remaining habitats (Robinson 1992, Porneluzi et al. 1993). The habitat edges can have greater rates of predation or parasitism (Askins 1995, Donovan et al. 1997,

Patten and Bolger 2003) and lower food availability (Burke and Nol 2000), thereby potentially reducing the effective area of the habitat patch for some species (Freemark et al. 1995, Mörtberg 2001). On the other hand, some species may be edge species in the sense that they perform better in fragmented habitats with a high amount of edges (Robbins 1979, Virkkala 1987a,b).

Birds have often been used as indicators of change in diversity. Their use of a large variety of microhabitats for nesting and foraging and their diverse roles in food chains make them suitable for monitoring structural and functional changes in ecosystems (Hausner et al. 2003). Willow thickets form a very important habitat structure for small birds on low Arctic tundra (Snow et al. 1998), many of these being insectivores. They make use of the willow in different ways - for nesting, as hiding places and for foraging. The birds of the southern Arctic tundra are mainly summer migrants. Arriving in spring and staying throughout the summer for breeding they are coming to exploit the high productivity and abundance of insects at the tundra, whilst escaping the darkness, freezing temperatures and snow cover in winter (Haftorn 1971, Hausner et al. 2002). In this study I discriminate between birds supposed to be dependant on willow thickets as their main habitat, and other birds that have a looser connection with the willow thickets.

The goal of this study is to estimate the association between willow thicket habitat configuration on southern Arctic tundra and abundance and diversity of birds, from the perspective that reindeer overbrowsing causes habitat fragmentation. I expected that; 1) A higher degree of fragmentation and decreased area of willow thickets would result in reduced abundance and richness of birds relying on willow thickets for shelter, nesting and foraging; 2) Large thickets would be associated with a higher richness of birds compared to small thickets.

2. Materials and Methods

2.1. Study area

The study was performed in two different regions in Finnmark County, Northern Norway; The Varanger peninsula and Laksefjordvidda (Fig.1). At the Varanger peninsula, the selected study sites were situated along the main river valleys of Komagdalen (70°19' N, 30°01' E) and Vestre Jakobselv (70°18' N, 29°06' E). At Laksefjordvidda the study site were situated along the mountain pass Ifjordfjellet (70°25' N 27°20' E). The bedrock geology of the study regions consists of sedimentary rocks, sandstone, shales and mudstone (Siedlecka and Roberts 1992, Ratcliffe 2005).

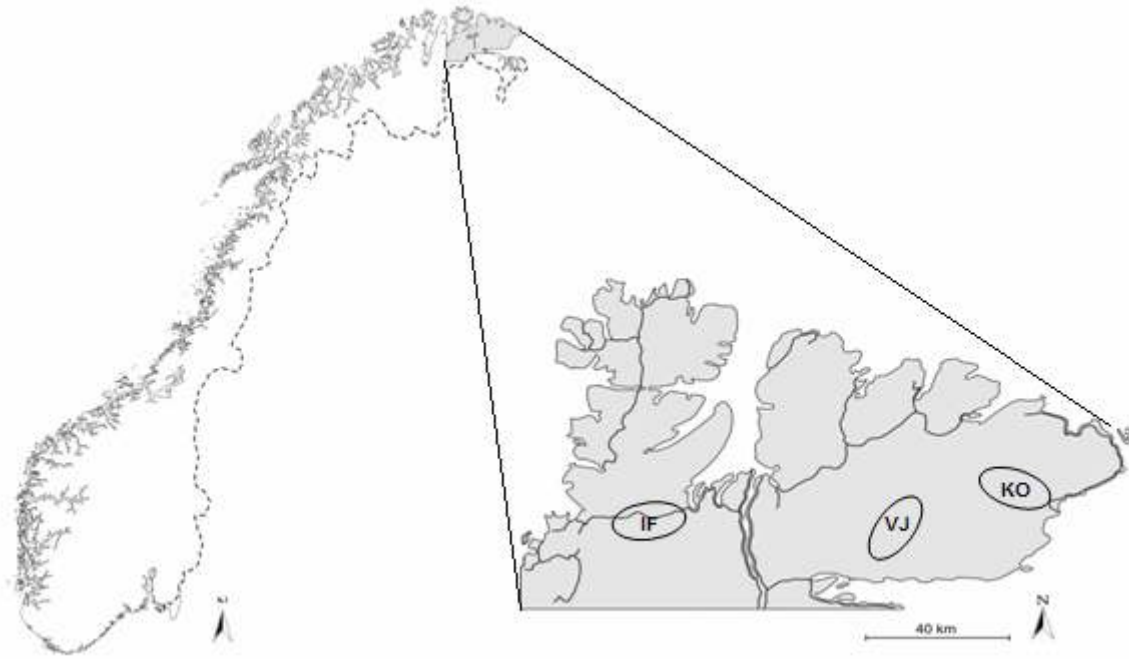


Figure 1: Study area in Norway eastern Finnmark with IF=Ifjordfjellet, VJ=Vestre Jakobselv, KO=Komagdalen.

The area is bioclimatically classified as southern Arctic tundra (Walker et al. 2005). Mean temperature in June at nearby weather stations (0-100 m asl) has a range from 7.4 °C to 8.7 °C (Meteorologisk institutt). Annual precipitation has a range from about 365 mm to 460 mm (Meteorologisk institutt). Temperatures below 0 °C both in spring (May and early June) and autumn (September) are common and low winter temperatures are typical for the study area (Ratcliffe 2005). The study was conducted at altitudes ranging from 110-290 meters above sea level at the Varanger peninsula and 260-360 meters above sea level at Laksefjordvidda. The vegetation zone according to Walker et al. (2005) and Moen et al. (1999) is mainly shrub-heaths dominated by *Empetrum hermaphroditum*, *Betula nana*, *Vaccinium spp.* and lichens (Oksanen and Virtanen 1995, Ims et al. 2007, Killengreen et al. 2007). In moist depressions, and especially on sediment plains along creeks and rivers, there are lush meadows interspersed with patches of willow thickets mainly of *Salix lapponum*, *Salix phylicifolia*, *Salix lanta* and *Salix glauca*. In heath patchy occurrence of mesic and wet vegetation with dicotyledons such as *Bistorta vivipara*, *Alchemilla alpina*, *Thalictrum alpinum*, *Viola biflora* and graminoids such as *Deschampsia flexuosa*, *Nardus stricta*, *Carex bigelowii*, *Eriophorum angustifolium*, *Agrostis capillaris* and *Deschampsia cespitosa* occur along with *Salix herbacea* (Ims et al. 2007, Killengreen et al. 2007).

Reindeer, moose, willow grouse, hare and small rodents are herbivores present in the area. Reindeer, which are semi-domestic in the area, are the dominant large herbivore. Varanger peninsula is mainly exploited as summer pastures by reindeer, while at Laksefjordvidda reindeer use the area as spring and autumn pastures. In both areas reindeer use the sediment plains with willows

intensively, and there are clear indications that the areas with willow thickets, especially at the Varanger peninsula, are shrinking due to reindeer overbrowsing.

2.2 Study design

2.2.1 Study sites, sections and points

As the study focuses on the effect of habitat size and fragmentation of willow thickets, I aimed within the three study sites to devise a hierarchical sampling design that would cover the existing variation in thicket size and degree of fragmentation. At the first level (within study sites) I selected 3-4 *sections* forming naturally adjoining willow thicket complexes. Extensive dwarf-shrub heaths surrounded the sections of willow habitat. At the next level in the hierarchy (i.e. within sections), I selected sampling *points*. Each point was associated with a willow patch at 7 meters distance perpendicular to the edge of the thicket. All selected points fulfilled the criterion of being situated on mineral soils on riparian sediments flats and where the willow thickets were imbedded in lush meadow vegetation. The distance between two adjacent points within a section was minimum 164 meters and the average nearest distance was 652 meters (SD=524 meters) to avoid spatial autocorrelation. The sample size at the various levels in the sampling design is given in table 1.

Table 1: Number of sampling points in the different sections of the two study regions Varanger peninsula and Laksefjordvidda.

Region	Study site	Section	No. of points
Varanger peninsula	Komagdalen	KO 1	5
		KO 2	5
		KO 3	2
	Vestre Jakobselv	VJ 1	4
		VJ 2	5
		VJ 3	4
Laksefjordvidda	Ifjordfjellet	IF 1	5
		IF 2	1
		IF 3	4
		IF 4	2

2.2.2 Bird count method

The birds associated with the willow thickets were censused by point sampling method (Hausner et al. 2003). Detection distances were estimated by the observer and classified into three intervals; 0-50 m, 50-100 m and >100 m. At each site, point counts were conducted during the breeding season in early July in 2005 (8/7-17/7) and 2006 (3/7-8/7). In all regions, each point was visited 3-5 times during a period of 5-7 days on days with little wind or rain. At these high latitudes the sun never sets in the period of census, and birds sing mostly in evening from 19.00 - 23.00 and in the morning

from 02.00-10.0 (Hausner et al. 2002, Ratcliffe 2005). Counting was primarily conducted in these periods. The recording period at each point was set to fifteen minutes. For each point and bird species the recording period with most observations in a year was used in the statistical analysis since this particular record probably get closest to 100% detection of birds. In this study three experienced observers did the sampling, one in each study site in 2005. In 2006 one of the observers did the sampling both in Komagdalen and Ifjordfjellet, while one of the others sampled Vestre Jakobselv.

To get an indication of the habitat preference of the different bird species, the observer noted the type of habitat in which they were detected. For this purpose the following categories were used: willow thicket, meadow, heath, water, flying over, others (e.g mire, bolder fields etc.).

2.2.3 Quantifying willow thicket area and fragmentation

Willow thickets were classified by 1:15 000 ortho-rectified aerial photos in raster-tiff format (BLOM geomatics) taken in summer of 2006. Thicket area and fragmentation were derived from these photos. The aerial photos and the elevation model had a pixel size of 0.20 m. Prior to photography white plastics (0.75*1.00 m) were placed in each corner of a square of 15x15 m to indicate location of the points. For converting the aerial photographs from tiff-format to img-format, ARC GIS-software, version 9.1 (Environmental Systems Research Institute 2002) was used. All willow thickets within the different sections were digitized manually in GRASS, version 6.1 (Grass Development Core Team 2006). Polygons were made by producing a vector file around each willow patch and then converting this to a raster file. For all sections a patch was defined as consisting of willow thicket with less than two meters of separation. These polygons were further analyzed with Fragstat, version 3.3 (McGarigal and Marks 1995) to calculate patch metrics, i.e. willow thicket area (PLAND; percent willow thicket), and two variables describing the degree of fragmentation. These variables were patch density (PD; number of patches per 100 hectare) and edge density (ED; meters of edge divided by area). Fragmentation of thickets was thus described by the three continuous predictor variables PLAND, ED, PD. The vertical structure at the willow thickets was described by the two variables willow height (Wheight) and willow density (Wdensity). Measurement of these two variables was done one meter into the thicket at four random places along a fifteen meter long line at the edge of the thicket. I used the mean of this measurement. For Wdensity the height was divided by number of hits on a stick from ground to the top of the thicket, measured at the same place as height. See table 3A for interpretation of the variables.

2.2.4 Scale considerations

Patterns and processes in nature are sensitive to the scale on which they are viewed (Wiens 1985) and the selection of scale will have an influence on the conclusions that are reached (Karr and Freemark, 1983). Thus the patterns and strength of the relationships between birds and willow thicket features may vary depending on scale of the investigation. Optimally, the scale of a study when examining ecological relationships should be based on apriori knowledge of the ecological

processes. When the study started, I did not know what the most appropriate and relevant scale would be. For this reason I initially explored relationships at three scales. Scale 1 was a 100*100 meter quadrat centered on the middle of the point. Scale 2 was a 200*200 meter quadrat with the same center as scale 1. Scale 3 equals the average size of the willow thicket sections. The size of the quadrat encompassing scale 3 was determined by the average length of willow thicket in all sections i.e. 2.2* 2.2 km. This quadrat was centered on the middle point of the section.

Exploratory analyses conducted by Sørensen (2007, unpublished) on the willow thicket variables, showed that scale 1 and scale 2 were strongly correlated while neither scale 1 or 2 correlated strongly with scale 3. On this basis I decided to do the analysis on scale 2 and 3. These scales will hereafter be termed the scales of “point” (scale 2) and “sections” (scale 3). On the point scale bird counts in the two intervals 0-50 and 50-100m were pooled. On the section scale the counts over all points and distances were pooled. The mean and range for fragmentation variables at the two scales considered are given in table 2.

Table 2: Mean value and range of the willow thicket/habitat variables used in modelling passerine birds diversity and abundance. See table 3A for interpretation of the variables.

Variable	Ifjordfjellet		Komagdalen		Vestre Jakobselv	
	Mean	[min,max]	Mean	[min,max]	Mean	[min,max]
PLAND_Point	23.14	[7.96, 47.60]	18.72	[3.65, 54.34]	17.73	[1.37, 37.89]
PLAND_Section	2.25	[0.56, 3.45]	1.69	[0.68, 2.47]	1.63	[0.56, 3.02]
PD_Point	779.60	[100.50, 2183.70]	349.50	[125.50, 853.40]	270.40	[25.1, 502.50]
PD_Section	60.38	[15.81, 139.63]	29.97	[21.21, 35.77]	17.77	[10.81, 23.30]
ED_Point	562.50	[270.10, 1008.90]	391.30	[188.50, 703.60]	372.29	[91.66, 676.51]
ED_Section	49.76	[17.81, 80.04]	35.43	[23.61, 45.10]	28.20	[19.95, 45.10]
Wheight	117.30	[77.50, 220.00]	210.60	[145.00, 270.00]	154.60	[110.00, 220.00]
Wdensity	2.72	[1.36, 3.61]	1.33	[0.45, 5.50]	1.40	[0.14, 4.25]

2.3 Statistical analysis

The study has an observational approach focusing on willow thicket size and fragmentation as the key design variable. All statistical analyses were conducted using R (R Development Core Team 2006). Log-linear models assuming a Poisson distribution for the response variable and a logarithm link were used to estimate the dependence of bird abundance and species richness (as response variables) on willow thicket area (PLAND), fragmentation (ED and PD) and vertical structure (Wheight and Wdensity) as the key predictor variables. When using point scale data, study site and year were tied as covariates, both as additive effects and in two-way interactions with all the continuous willow thicket variables (PLAND, PD, ED). I used Akaike's Information Criterion (AICc) to select between different models (Burnham and Anderson 1998). For some species the models suffered from overdispersion and in those cases qAICc based on quasi-likelihood estimation methods was used when selecting the appropriate model as recommended by Anderson and Burnham (1994) and Johnson and Omland (2004). Irrespective of the AICc/qAICc value, the variables PDpoint, PLANDpoint, Year and Region were maintained in the model of species abundances. This made it possible to compare the effect size of these predictor variables between species, whether significant or not. For the analyses on the scale of sections, the response variable was tested

against one predictor at a time in interaction with year and region respectively. This was done because the small sample size at the largest scale made it difficult to include more variables in the model. Models with $\Delta AICc/\Delta qAICc < 2$ were considered to be indistinguishable (i.e. equally supported) and the most simple model was chosen.

For species richness the response was number of bird species observed at each point and section respectively. I included all birds in the richness analysis that from general knowledge of the species in some way were expected to exploit willow thicket, irrespectively of how many times it was observed in the point counts. For the model selection of the richness at point scale and section scale, I followed the same procedure as for relative abundance at point scale and section scale respectively, but without any variables tied in the model.

3. Results

3.1 Observed species and their abundance

A total of 37 species were observed in 2005 and 28 in 2006 (Table 3 and 1A). For 2005 and 2006 combined, a total of 1332 birds were observed (Table 3, Fig. 1A). According to available literature (Haftorn 1971, Snow et al. 1998) I classified the observed terrestrial bird species in two groups according to their expected affiliation with willow thickets. A first group of “thicket species” were supposed to have willow thicket and immediate surrounding areas as their main habitat i.e. they either were reported to preferentially breed, forage and seek shelter in thickets. This group included 7 and 8 species at point- and section scale respectively. The second group consisting of “non-thicket species” was expected at the most to be only loosely connected with the thicket and to have other preferred terrestrial habitats (meadow or heath). Birds strongly connected to open water (terns, gulls, ducks and certain shore birds) were not considered in the analyses. This apriori classification corresponded well with the actual frequencies of observations made in the different habitat categories (Table 2A).

Table 3: The overall abundance (total counts over all species) and bird species richness (total number of species) in the two study years at the three study sites.

	Komagdalen	Vestre Jakobselv	Ifjordfjellet	Total
Abundance				
2005	362	216	203	781
2006	211	133	207	551
Richness				
2005	33	21	19	37
2006	25	13	18	28

3.2 Predictors of abundance

For most species there was a decline in relative abundance from 2005 to 2006. The exceptions were White Wagtail (*Motacilla alba*), Bluethroat (*Luscinia svecica*) and Roughlegged Buzzard (*Buteo lagopus*) which had a slight increase (Fig. 1A, Table 4). In the analysis of abundance I included species that had been observed at least in 2 out of 3 study sites each year and that amounted to

more than 1 percent of the birds observed in the census (see Table 4A for species traits). For analysis of abundance 11 terrestrial species fulfilled these criteria on point scale and 14 on section scale (Table 4 and 5). Ten species obtained the lowest AICc/qAICc value with only the obligatory four predictor variables included in the model. The remaining species, Lapland bunting (*Calcaeus lapponicus*), obtained the lowest AICc/qAICc value by keeping Wdensity (Table 4). Overall abundance of the different bird species was explained by mainly four factors: year, study site, fragmentation (PDpoint) and area of willow thicket (PLANDpoint). The predictor variables EDpoint and Wheight were not selected in any model. Five thicket species at point scale had a significant area or fragmentation term in the model (Fig. 2 and 3, Table 4). All three effects of thicket area (i.e. PLANDpoint) were positive, whereas there were two effects of opposite signs for fragmentation (i.e. PDpoint) (Table 5). In non-thicket species there was one species showing significant negative relationship with thicket area and abundance.

Of the three thicket species showing a significant relation to thicket area at the point scale, Redpoll (*Carduelis flammea*) increased with a factor of 1.018 with an increase of one percent of area with willow thicket, while Willow Warbler (*Phylloscopus trochilus*) increased with a factor 1.045 and Redwing (*Turdus iliacus*) had an increase of 1.028 (Fig. 2). The non-thicket species Wheatear (*Oenanthe oenanthe*) decreased with a factor of 0.908 as a response to increase in willow thicket area. While area (PLANDpoint) seems to be a strong predictor of abundance at point scale, fragmentation (PDpoint) came out significant only for Bluethroat increasing with a factor of 1.07 with PD when adding one patch per hectare (while keeping area constant) and Willow Warbler decreasing with a factor of 0.890 (Fig. 3). There was one species that responded to vertical willow thicket structure on the point scale. Lapland bunting became more abundant when willow density increased.

At section scale abundance of Bluethroat was positively correlated with Wdensity, for Temminck's Stint (*Calidris temminckii*) there was a negative correlation, while Willow Warbler was positively correlated with willow height (see Table 5 for parameter estimates and CI). For the non-thicket species Long-tailed Skua (*Stercorarius longicaudus*) and Golden plover (*Pluvialis apricaria*) there was a positive connection between patch density and abundance while Wheatear had a negative association with PLANDsection, (Fig. 4).

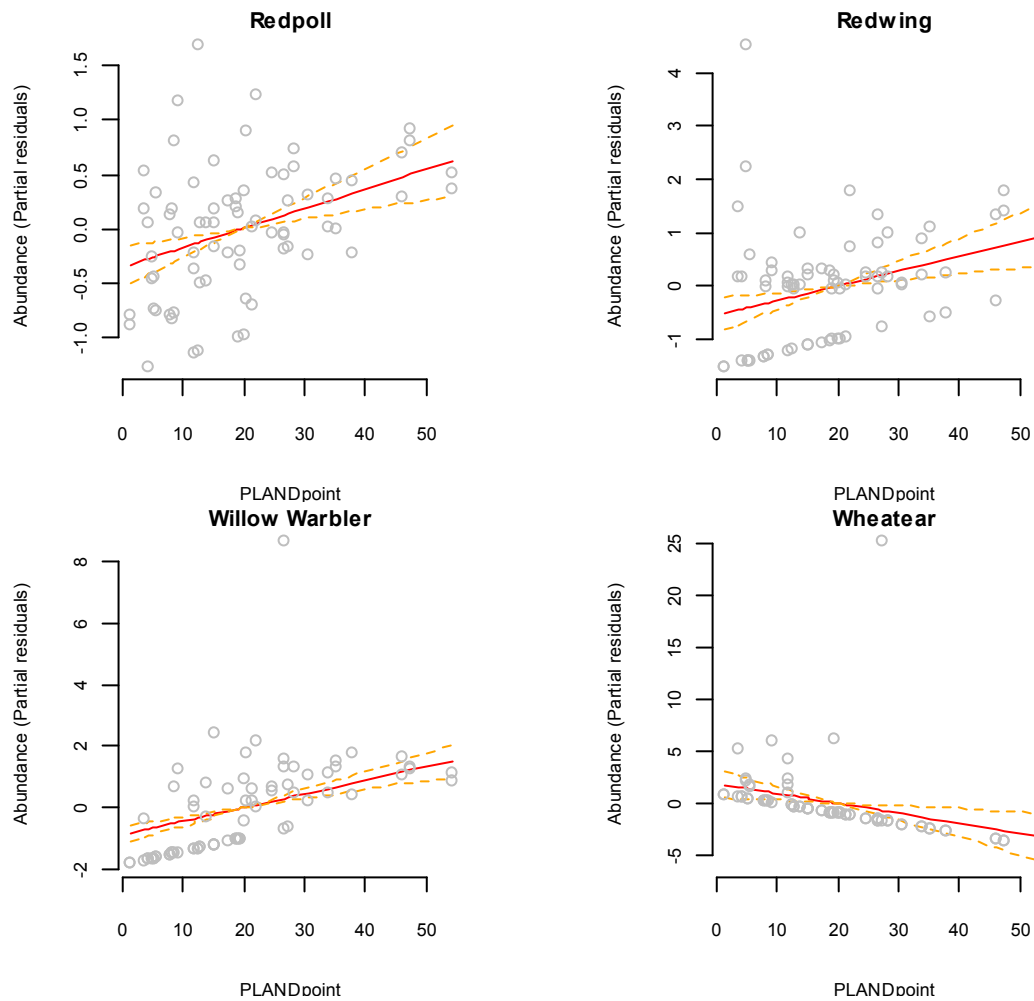


Figure 2: Effect of thicket area (PLANDpoint) on the point scale on bird abundance. Partial residuals (effects of other predictor variables removed), together with estimated linear effect (red line) and 95% confidence intervals for the mean predicted response.

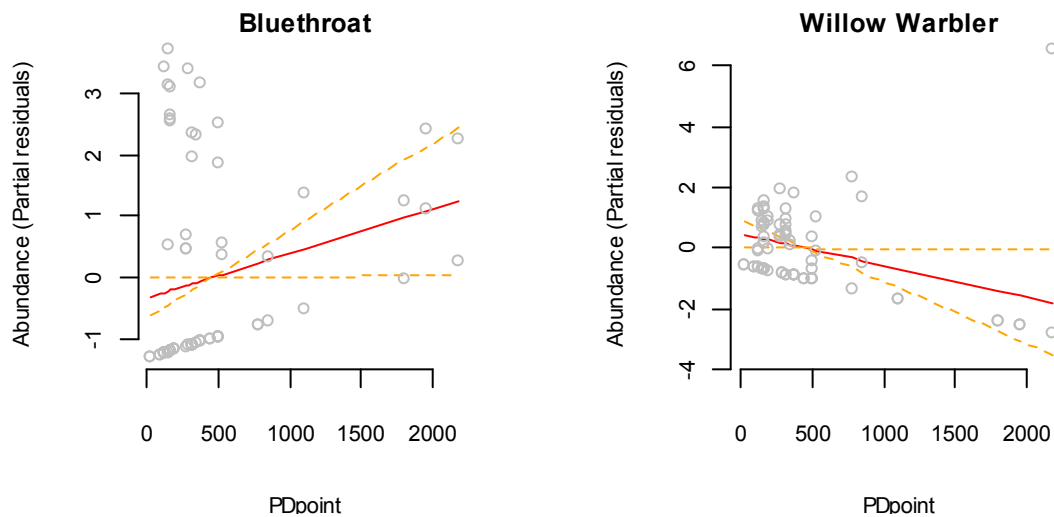


Figure 3: Significant partial effect of patch density (PDpoint) on the point scale on bird abundance.

Table 4: Results for bird abundance on point scale, R^2 is the squared correlation between the observed and predicted values. Regression coefficients with 95% C.I. n=74. Coefficients with an * were significant at $P=0.05$.

	R^2	Intercept			PDpoint			PLANDpoint			Wdensity			factor(year)			Study site Komag			Study site V.Jakobse		
		Coef*	1	2.5%	97.5%	Coef*	10000	2.5%	97.5%	Coef*	100	2.5%	97.5%	Coef*1	2.5%	97.5%	Coef*1	2.5%	97.5%	Coef*1	2.5%	97.5%
Thicket species																						
Bluethroat	0.138	-1.55	-2.93	-0.35	7.28*	0.35	14.43	-0.12	-3.16	2.56	-	-	-	1.25	-57.11	8.31	0.78	-1.62	1.84	-0.16	-1.37	1.09
Feldfare	0.139	-0.46	-1.78	0.72	-6.42	-20.76	3.89	0.89	-1.96	3.6	-	-	-	-3.36	-10.81	3.78	-0.22	-1.36	0.91	0.65	-0.25	1.67
Lapland bunting	0.453	-2.14	-3.91	-0.52	1.83	-2.88	6.47	-0.28	-3.14	2.5	0.96*	0.5	1.45	-6.29*	-11.9	-0.98	-0.34	-1.4	0.59	0.64	-0.23	1.5
Redpoll	0.268	0.99	0.57	1.39	-0.81	-3.75	1.94	1.81*	0.88	2.72	-	-	-	-2.18	-4.74	0.36	-0.02	-0.34	0.3	-0.16	-0.5	0.18
Redwing	0.242	-0.75	-1.54	-0.001	0.97	-4.27	5.67	2.79*	1.15	4.38	-	-	-	0.82	-3.78	5.45	0.15	-0.43	0.73	-0.08	-0.72	0.55
Temminck`s Stint	0.015	-2.5	-5.27	-0.35	-0.13	-22.51	16.04	1.48	-3.64	5.93	-	-	-	1.34	-11.64	14.69	0.75	-1.02	2.96	0.69	-1.13	2.99
Willow Warbler	0.443	-1.05	-1.83	-0.32	-10.33*	-21.64	-1.77	4.43*	2.99	5.86	-	-	-	-1.03 *	-5.51	3.42	1.04*	0.50	1.64	0.04	-0.66	0.73
Non thicket species																						
Golden Plover	0.142	-0.45	-2.21	1.05	4.84	-4.12	13.94	-4.07	-10	0.79	-	-	-	0.00	-10.47	10.47	-1.14	-3.04	0.46	-0.52	-1.97	0.95
Meadow pipit	0.24	0.93	0.43	1.4	0.37	-3.08	3.62	-0.11	-1.23	0.97	-	-	-	-3.31 *	-5.87	-0.78	0.366 *	0.037	0.704	-0.05	-0.42	0.32
Wheatear	0.291	1.42	-0.39	3.06	-35.6	-76.89	-6.81	-9.65*	-17.55	-3.7	-	-	-	-6.93	-15.96	1.28	-0.248	-1.343	0.958	-0.50	-1.64	0.74
White Wagtail	0.104	-1.46	-3.41	0.06	-1.15	-16.66	11.18	-2.95	-6.8	0.4	-	-	-	2.23	-5.34	10.02	1.01	-0.28	2.66	1.23	-0.04	2.92

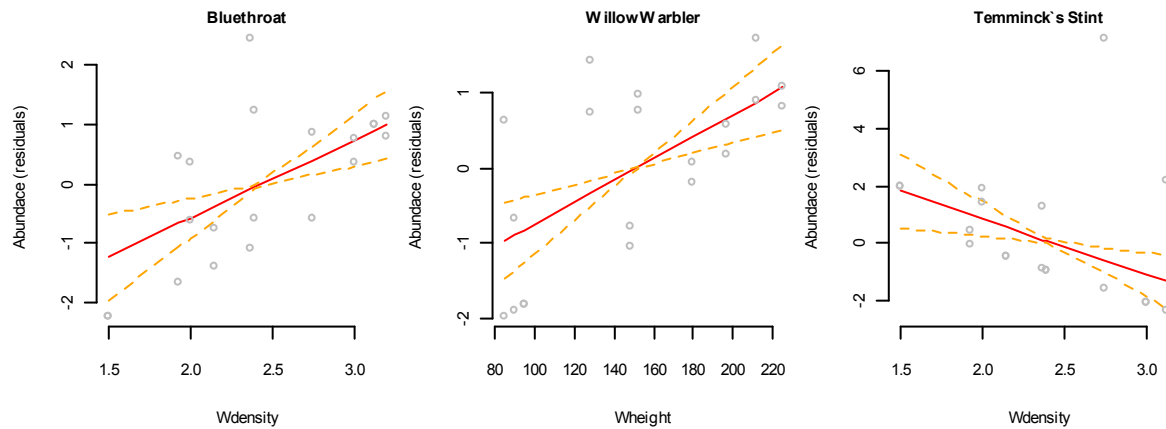


Figure 4: Significant effect of willow density and height on the section scale.

Table 5: Results for bird abundance on section scale. Coefficients with an * were significant at $P=0.05$, (95% C.I., $n=20$) Predictor 1,2 and 3 refer to predictor variables in the model in column "Predictor var" explaining abundance.

	R ²	Intercept			Predictor var	Predictor 1			Predictor 2			Predictor 3		
		coef	2.50 %	97.5 0 %		coef	2.50 %	97.5 0 %	coef	2.50 %	97.5 0 %	coef	2.50 %	97.5 0 %
Thicket species														
Redpoll	-	-	-	-	Konstant model	-	-	-	-	-	-	-	-	-
Fieldfare	0.110	1.07	-0.94	2.97	Wdensity	-0.59	-1.44	0.23	-	-	-	-	-	-
Redwing	-	-	-	-	Konstant model	-	-	-	-	-	-	-	-	-
Bluethroat	0.485	-3.99	-6.31	-2.00	Wdensity	1.32 *	0.59	2.12	-	-	-	-	-	-
Willow Warbler	0.522	-2.20	-3.74	-0.88	Wheight	0.015 *	0.007	0.023	-	-	-	-	-	-
Willow Grouse	0.241	1.92	-1.71	5.45	Wdensity	-1.54	-3.44	0.04	-	-	-	-	-	-
Temminck's Stint	0.583	3.09	0.40	5.85	Wdensity	-1.91 *	-3.38	-0.66	-	-	-	-	-	-
Laplad Bunting	0.865	-0.17	-0.71	0.30	PD3+Year+PD3:Year	0.013	0.006	0.019	-1.43	-2.59	-0.44	0.008	0.002	0.020
Non thicket species														
Long-tailed Skua	0.539	-1.93	-2.93	-1.16	PDsection	0.02 *	0.01	0.03	-	-	-	-	-	-
Rough-legged Buzzard	-	-	-	-	Konstant Model	-	-	-	-	-	-	-	-	-
Golden Plover	0.270	-0.50	-1.04	-0.02	PDsection	0.01	0.001	0.02	-	-	-	-	-	-
Meadow Pipit	-	-	-	-	Konstant Modell	-	-	-	-	-	-	-	-	-
White Wagtail	-	-	-	-	Konstant Model	-	-	-	-	-	-	-	-	-
Wheatear	0.439	0.26	-0.45	0.97	PLANDsection	-1.14	-1.93	-0.56	-	-	-	-	-	-

3.3 Species richness

Twenty-five species fulfilled the criteria to be included in the analysis of species richness (see Table 1A for list of species). At the point scale the best model explaining variation in species richness included only thicket area (PLANDpoint) which positively correlated ($R^2 = 0.035$, $b = 0.006$ 95% CI [0.001; 0.013] log scale, $P = 0.09$) with species richness (Fig. 5). Richness at the section scale was best explained by the height of willow thicket which was positively correlated with species richness ($R^2 = 0.510$, $b = 0.004$ 95% CI [0.001; 0.007] log scale, $P = 0.03$), see Fig. 5.

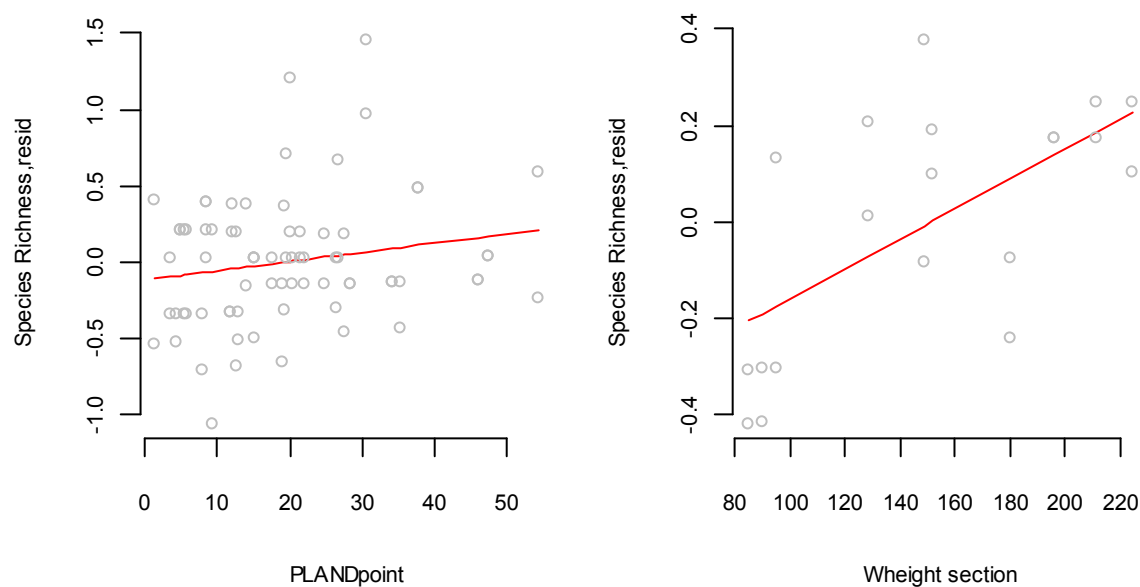


Figure 5: Relationship between species richness, thicket and height of willow thicket (Wheight) at point and section scale respectively.

4. Discussion

In this study I aimed at demonstrating impact of size and degree of fragmentation of willow thickets on abundance and richness of birds associated with willow thicket in southern Arctic tundra. Apart from Järvinen & Väisänen (1978) who did a survey of bird habitat choice in northern Norway, there are hardly only quantitative studies conducted on bird communities associated with willow thickets in this region or any other southern arctic regions. In particular, I have found no other studies that were done on responses of birds to fragmentation and size reduction of willow thickets.

For the analysis of abundance I classified birds in two groups according to their expected dependency of willow thicket; 1) strongly connected “thicket species” and 2) loosely connected “non-thicket species”. For the thicket species group at point scale there was an indication of abundance being positively affected by the area of willow thicket and a tendency of negative effect of habitat fragmentation. This is in line with other studies on small insectivorous species that were found to be area-sensitive (Saunders 1993, Watson et al. 2004). At section scale, however, abundance for species classified as thicket species was explained by the vertical structure of the thickets rather than by area and fragmentation variables. The non-thicket species responded

positively to area reduction and fragmentation of willow thicket. Species richness was positively related to the area of willow habitat at point scale while at section scale I found that height of willow thicket was explaining number of species. There were clear differences between the two years of study in the abundance of birds. High year-to-year variation in bird communities is common in northern latitudes (Järvinen 1979). Even if there was a difference in abundance between years, my predictor variables were independent of year and region.

4.1 Area and fragmentation effects

Martin (1980, 1981) and Riffell (2001) found area to be the best single predictor of abundance and species occurrence in wetland and forest birds. In my study Redpoll, Redwing and Willow Warbler had a positive relationship with percentage cover of willow thicket at point scale. The reduction of willow thicket by reindeer browsing, leading to less area of willow thicket habitat, could thus result in a decline in abundance for these species. This is not too surprising, as percentage cover provides a measure of a landscape's capacity (Vos et al. 2001) for supporting species that rely on the cover type in question. Redpolls eat mainly seeds year-round with different types of seeds in different seasons (Newton 2006). Therefore it is reasonable to expect a positive relationship between amount of willow thicket and abundance of Redpoll since seeds of willow is an important food source. Tyrväinen (1969) and Virkkala (1987a,b) found that Redwing and Willow Warbler were most common where there was a dense and continuous bush layer. A dense bush layer is important for protection when foraging on ground and concealment of a nest near or on ground. This fits well with my findings, showing that Redwing and Willow Warbler abundance increased strongly with proportion of willow thicket at point scale.

In northern Finnish bird fauna Willow Warbler and Redwing have increased due to effects of forest management. This is, however, a response to clearcutting of coniferous forest and regeneration of deciduous forest (Virkkala 1987a,b). Natural dynamics, land use patterns, and management issues differ between systems, and so too will responses to fragmentation (Haila 2002). In my study in southern Arctic tundra, however, I found that reduction of willow habitat results in decline in abundance of species dependent on willow thicket. Even though application of knowledge from other systems e.g. forest, does not provide very useful information for projecting the outcome of habitat loss and fragmentation in willow thicket in southern Arctic tundra at an individual species level, there seems to be a general pattern that species with life history traits closely connected to a habitat will be negatively affected by fragmentation of the habitat in question.

I found that fragmentation had an effect on abundance of two species; Bluethroat and Willow Warbler. Bluethroat responded positively to fragmentation at point scale. This is consistent with Järvinen and Väisänen (1978) who found that Bluethroat were most abundant on dry peatland where there was a patchy distribution of thickets of willow and dwarf birch (*Betula nana*). According to Snow et al. (1998), the Bluethroat is best adapted to forest tundra and willow shrub lands on open plains or valleys with juniper, woods of birch, shrubby wetlands or floodplains. The positive

correlation with fragmentation may be due to Bluethroat's preference for some degree of open habitat. Further Bluethroat is foraging on the ground in low vegetation (Haftorn 1971, Melhum and Sæther 1991, Snow et al. 1998) and meadows around willow thicket could thus be expected to be a good foraging habitat for Bluethroat. Willow Warbler was negatively affected by increasing patch density at point scale in my study. In a study conducted by Järvinen and Väisänen (1978) in Finnmark, Willow Warbler was more connected to birch forest than willow thicket. This may be one of the reasons why Willow Warbler responded negatively to fragmentation. Further it is an insectivorous species foraging in the thicket picking insects from leaf (Snow et al. 1998). Mehlum and Sæther (1991) states that Willow Warbler is common in the mountains and needs only a small shrub to breed. This is in contrast with this study where Willow Warbler were found to decrease when willow thicket were fragmented.

The other species analysed in this study seemed to be little affected by fragmentation expressed by patch density. There could be several explanations to this. How an organism will be affected by habitat fragmentation is determined by its vagility, its habitat requirements, and relative rates of movement through various habitats comprising landscape mosaic (With and Crist 1995). There may be a critical threshold of 10-30% of amount of habitat loss in the landscape before isolation effects, i.e. effects of spatial configuration of habitat, become apparent (Andrén 1994) and this threshold may not have been reached in the study area. Area reduction and fragmentation of willow thickets have unfortunately not been monitored over a longer time period. Further, species which are habitat generalist, i.e. species which use several habitats in the landscape, may not perceive the landscape as fragmented (Andrén 1994).

Brood parasitism rates is a factor generally expected to increase with fragmentation (Faaborg et al. 1995). Moksnes (1987) found Cuckoo (*Cuculus canorus*) to parasitize mainly Meadow Pipit (*Anthus pratensis*), Reed Bunting (*Emberiza schoeniclus*) and Lapland Bunting in subalpine birch forest in a study involving all passerine bird species in my study. However, no brood parasitism birds were observed in the study area.

Fragmentation of habitat is known to reduce number of species conifer specialist and change species composition in boreal forests (Virkkala 1987a,b, Andrén 1994). On the other hand Robbins (1979), Martin (1980,1981) and Robbins et al. (1989) found that the number of species on habitat islands to a small extent is affected by factors such as habitat heterogeneity and degree of isolation, and that vegetation structure was relatively unimportant (Faaborg et al. 1995). The species-area relationship may be one of nature's most general patterns (Lomolino 2001). My results support this pattern. I observed a small increase in species number with area of willow thicket at point scale, but the effect was not significant. This indicates that further fragmentation and area reduction of willow thicket habitat might result in a reduced capacity for species richness and abundance on the Arctic tundra.

4.2 Vertical structure and habitat selection

The height (Wheight) and vertical density (Wdensity) of willows emerged as important for abundance at section scale for the thicket species. Increasing vertical willow density (Wdensity) had a positive effect on abundance of Bluethroat and a negative effect on Temminck's Stint. At section scale vertical willow density affected abundance of Bluethroat positively. Dense willow thicket may be important since Bluethroat is hatching on ground under shrub vegetation (Haftorn 1971, Snow et al. 1998). Temminck's Stint breeds near water on meadows with low and sparse vegetation (Rönkä 1996). In my study most observations were done in the meadow. Temminck's Stint obtain information about an approaching predator visually and the better visibility from the nest, the longer the flushing distance. Koivula and Rönkä (1998) found a lower chance of predation with good visibility. At section scale there was a significant negative correlation between abundance of Temminck's Stint and vertical willow density which might be due to poor visibility caused by dense willow thickets. Willow Warbler was positively affected by increasing willow height (Wheight). According to Järvinen and Väisänen (1978) Willow Warbler is mainly expected to be found in subalpine birch forests. Protection against predators is important (Arvidsson and Klaesson 1986) and high and dense willow thickets might also provide safe nesting sites and cover for Willow Warbler.

Foliage height diversity is found to be positive correlated with bird species richness (Mac Arthur 1965, Recher 1969). At section scale I found a significant effect of height of willow thicket (Wheight) on the number of species present. This differs from others studies of low stature habitats such as grasslands or shrublands (Wiens 1974, Roth 1976) where patch fragmentation was found important for predicting bird species richness.

4.3 Effect of spatial scaling

Not knowing what the most appropriate and relevant scale for the study would be, I initially chose to consider area- and fragmentation effects on different scales in an exploratory manner. The results indicate that the association between willow thicket habitat configuration and abundance and richness of birds, which was the main aim of this study, is most evident on point scale. However, the study also showed interesting results on section scale which was related to the vertical structure of the thickets rather than the two dimensional configuration.

Different organisms operate at different scales therefore every organism should be studied in connection with a species-specific spatial and temporal scale, called ecological neighbourhood (Addicott et al. 1987). In North American shrubsteppe birds reacted differently to habitat characteristics at large biogeography, regional and local scales (Wiens et al. 1987). In my study different scales were chosen to capture the actual scale where fragmentation of willow thicket affected species richness and abundance. According to Klopfer and Ganzhorn (1985) it appears that habitat choice may consist of a sequence of choices, with different selection criteria at each scale. If habitat selection does proceed in a stepwise fashion, with the evaluation of different criteria at

different stages, with differing temporal components at each stage, one could reconcile the differences often reported in correlations of particular species with particular features of their habitat (Wiens and Rotenberry 1979). It is apparent that the scale of analysis did make a difference in my study, as different patterns were expressed for thicket species at point- and section scale which might indicate a stepwise habitat selection for birds in the area.

Conclusion

In this study I have shown that thicket area is an important factor explaining abundance of thicket-associated species and species richness on point scale, while on section scale vertical density and height were explaining abundance and species richness of birds in southern Arctic tundra. My results indicate that further fragmentation and size reduction of willow thicket habitats may result in reduced richness and abundance of bird species in this ecosystem. This emphasizes the need for a management strategy that prevents further fragmentation and size reduction of willow thicket habitat on the southern Arctic tundra. To assist management and preservation of biodiversity of bird species in the area, more research is needed, monitoring birds and willow thicket habitats over a longer period.

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Appendix

Table 1A: Species observed in the study.

Species in abundance analysis	Additionally species in diversity analysis	Species observed in census but not used in any analysis
Bluethroat <i>Luscinia svecica</i>	Brambling <i>Fringilla montifringilla</i>	Arctic Skua <i>Stercorarius parasiticus</i>
Fieldfare <i>Turdus Pilaris</i>	Common sandpiper <i>Actitis hypoleucos</i>	Arctic Tern <i>Sterna paradisaea</i>
Golden Plover <i>Pluvialis apricaria</i>	Crossbill <i>Loxia curvirostra</i>	Black-throated Diver <i>Gavia arctica</i>
Lapland Bunting <i>Calcarius lapponicus</i>	Merlin <i>Falco columbarius</i>	Common Gull <i>Larus canus</i>
Long-tailed Skua <i>Stercorarius longicaudus</i>	Dunlin <i>Calidris alpina</i>	Golden Eagle <i>Aquila chrysaetos</i>
Meadow pipit <i>Anthus pratensis</i>	Redshank <i>Tringa totanus</i>	Goosander <i>Mergus merganser</i>
Redpoll <i>Carduelis flammea</i>	Red-throated Pipit <i>Anthus cervinus</i>	Hooded Crow <i>Corvus corone</i>
Redwing <i>Turdus iliacus</i>	Reed Bunting <i>Emberiza schoeniclus</i>	Long-tailed Duck <i>Clangula hyemalis</i>
Roughlegged Buzzard <i>Buteo lagopus</i>	Ringed Plover <i>Chardrius hiaticula</i>	Red-breasted Merganser <i>Mergus serrator</i>
Temminck`s Stint <i>Calidris temminckii</i>	Snipe <i>Gallinago gallinago</i>	Red-necked Phalarope <i>Phalaropus lobatus</i>
Wheatear <i>Oenanthe oenanthe</i>	Wood Sandpiper <i>Tringa glareola</i>	Teal <i>Anas crecca</i>
White Wagtail <i>Motacilla alba</i>		
Willow Grouse <i>Lagopus lagopus</i>		
Willow Warbler <i>Phylloscopus trochilus</i>		

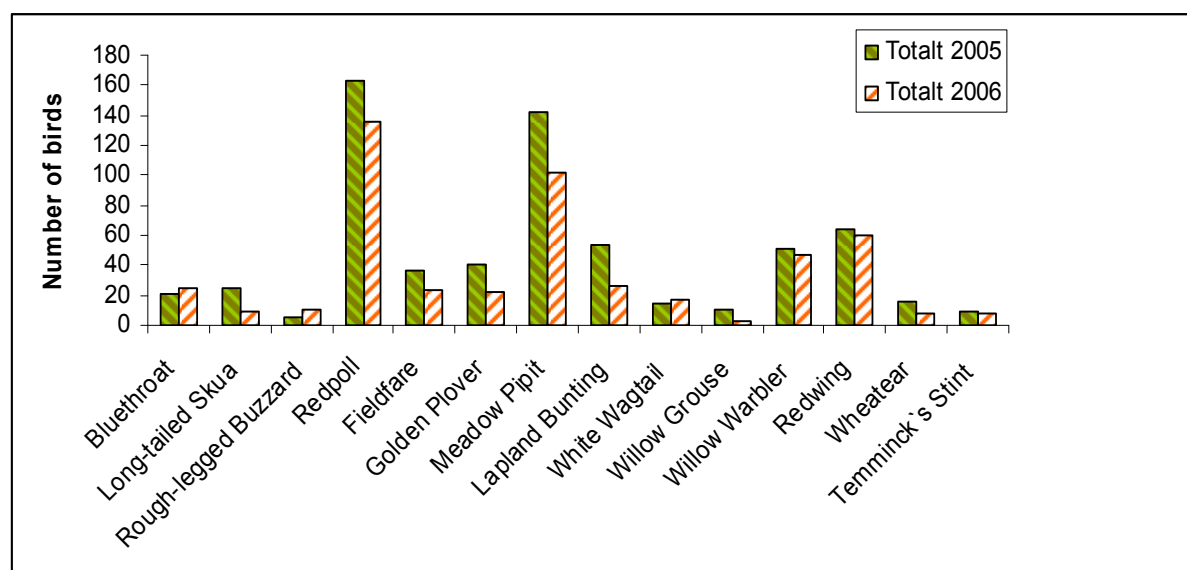


Figure 1A: Number of species for 2005 and 2006.

Table 2A: Perferrable habitat of birds observed in the study area in percent. Predominant habitat for the respective birds are in bold (other= bog, bolder fields etc and over are birds observed in the air above observer).

Species	Meadow	Other	Heath	Thicket	Over	Water
Bluethroat	3.23	0.00	3.23	88.71	3.23	1.64
Fieldfare	5.21	0.00	10.42	76.04	8.33	0.00
Golden Plover	5.62	1.12	87.64	3.37	0.00	2.25
Lapland Bunting	6.61	0.00	30.58	62.81	0.00	0.00
Long-tailed Skua	2.56	0.00	84.61	0.00	12.82	0.00
Meadow pipit	18.07	0.00	51.57	29.64	0.01	0.00
Redpoll	0.01	0.02	0.03	64.70	29.60	0.00
Redwing	0.00	0.01	7.53	89.78	0.01	0.00
Roughlegged Buzzard	7.69	0.00	76.92	7.69	7.69	0.00
Temminck`s Stint	61.90	14.29	0.00	0.05	0.10	0.10
Wheatear	6.25	0.00	93.75	0.00	0.00	0.00
White Wagtail	6.06	0.00	33.33	27.27	18.18	15.15
Willow Grouse	27.27	9.09	9.09	45.45	9.09	0.00
Willow Warbler	0.00	1.85	0.01	96.91	0.01	0.00

Table 3A: Description of landscape metrics measured. For details on the computation of PLAND, PD and ED, se McGarigal and Marks (1995) and the FRAGSTATS 3.3 Software.

Landscape metric	Scale	Range	Unit	Intepretation
Percentage of landscape, PLANDpoint	point scale(200*200m)	0<PLANDpoint≤100	%	PLANDpoint = 0 if willow does not occur in the landscape. PLANDpoint = 100 if the entire landscape is comprised of willow
Percentage of landscape, PLANDsection	section scale(2*2km)	0<PLANDsection≤100	%	PLANDsection = 0 if willow does not occur in the landscape. PLAND section= 100 if the entire landscape is comprised of willow
Patch density, PDpoint	point scale(200*200m)	0<PDpoint≤ maximum number of patches per 100 hectare		PDpoint = number of patches per 100 hectare on point scale.
Patch density, PDsection	section scale(2*2km)	0<PDsection≤ maximum number of patches per 100 hectare		PDsection = number of patches per 100 hectare on section scale.
Edge density, EDpoint	point scale(200*200m)	0<EDpoint≤ maximum number of meter edge per hectare		EDpoint= meters edge per hectare on pointscale.
Edge density, EDsection	section scale(2*2km)	0<EDsection≤ maximum number of meter edge per hectare		EDsection= meters edge per hectare on section scale.
Wheight	Local	0<maximum height	Cm	Mean of 4 height measures per sampling point.
Wdensity	Local	0<maximum number of hits	Hits	Mean of 4 shrub density measures per point corrected For willow height (Wdensity/Wheight).

Tabell 4A: Species traits for birds in the abundance analysis from Snow et al. (1998), focusing on attributes when found in tundra.

Common Name	Species	Habitat (when breeding)	Nest	Size	Food	Use of Willow thicket
Bluethroat	<i>Luscinia svecica</i>	Floodplains and banks of rivers and lakes in dense but low woody vegetation	Ground in dense vegetation or tussock	14 cm Wing-span 20-22,5cm	Terrestrial invertebrates, insects, in autumn some seeds and fruits. Feed on ground. Also take insects from low vegetation and catch insects in the air	Food, Nest,
Fieldfare	<i>Turdus pilaris</i>	Middle and higher latitudes. Above 1000m where juniper and dwarf birch afford sufficient shelter slopes with a few straggling bushes	When above tree line in the shrub	25,5 cm Wing-span 39-42 cm.	Invertebrates, fruit on ground bushes and trees. Scratch earth, etc to take food beneath	Shelter, food, nest
Golden Plover	<i>Pluvialis apricaria</i>	Mainly higher latitudes in arctic-alpine and boreal tundra	Ground. With only low vegetation 2-3cm	26-29cm Wing-span 67 - 76cm	Invertebrates, berries, seed and grasses	Seldom
Lapland Bunting	<i>Calciarius lapponicus</i>	Low shrubby tundra and damp hummocky moss-tundra with dwarf birch, willow, and heath plants	Ground between crowberry and dwarf birch. Nest protected by overhanging twigs of e.g. willow twigs	15-16 cm Wing-span 25.5-28 cm	Invertebrates (flies Diptera) seeds of grasses and low herbs. Near ground	Occasionally foraging bushes. Shelter, nest
Long-tailed Skua	<i>Stercorarius longicaudus</i>	Low and high Arctic tundra in willow- and lichen regions	Ground	48-53 cm Wing-span 105-117cm	Mainly small rodents	Hunting small rodents at edge.
Meadow Pipit	<i>Anthus pratensis</i>	Breeds in arctic climatic zones, accepting rainy, windy and chilly conditions	By or in tussock or hidden in vegetation. On ground	14.5 cm Wing-span: 22-25cm	Invertebrates, some seeds in winter. Feed on ground. Picking invertebrates from leaves and plant stems	Resting, nest close to thicket, feeding.
Redpoll	<i>Carduelis flammea</i>	Willow thicket when above tree line	In shrub or on ground in shrub	11.5-14.5 cm Wing-span 7.1-7.8cm	Small seeds, in tree(thicket) or on ground when fallen. Invertebrates in breeding season	Breeding, food
Redwing	<i>Turdus iliacus</i>	In thickets of scrub birch, dwarf willow, and juniper,	Shrub or on ground	21 cm Wing-span 33-34.5 cm	Invertebrates, and berries in autumn and winter. On ground	Breeding, feeding

		preferably on swampy ground				
Roughlegged Buzzard	<i>Buteo lagopus</i>	Ranging over large sub arctic and arctic tundra areas	Cliff	50-60 cm Wing-span 120-150cm	Mainly small mammals, voles and lemming most important in breeding season	Hunting small rodents at edge
Temminck`s Stint	<i>Calidris temminckii</i>	Willow region in mountain areas	On ground in open low vegetation	13-15cm Wing-span 34-37 cm	Invertebrates	Shelter
Wheatear	<i>Oenanthe oenanthe</i>	From sea to alpine mountain. Open rocky terrain	Ground under stone	14.5-15.5 cm Wing-span 26-32 cm	Invertebrates	Some food search (Perching)
White Wagtail	<i>Motacilla alba</i>	Up to 1500 absl. Related to human buildings, water, streams and rivers. Open area	Under a stone or otter hollows. Dense bush	18 cm Wing-span 25-30 cm	Small invertebrates. Picking, run-picking and flycatching. On ground	Roosting, nest
Willow Grouse	<i>Lagopus lagopus</i>	Follows distribution of birch and willow	Ground	37-42cm Wing-span 55-66cm	Herbivorous. Seeds, berries, newly grown leaves of deciduous plans	Feeding, nest
Willow Warbler	<i>Phylloscopus trochilus</i>	Breeds on tundra in glades among willows	Ground (in vegetation) or in shrub	10.5-11.5 cm Wing-span 16.5-22.	Insects and spiders; berries in autumn. Picking from leaves, twigs, and branches; flycatching	Feeding, nest