University of Natural Resources
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Generalist or specialist?
About the abundance and distribution of waders in the Swedish mountains

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Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

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POPULAR ABSTRACT

Habitat selection directly affects birds, their fitness and survival. Generalist species are more flexible when selecting a habitat while specialists are more restricted to certain habitat structures and depend strongly on their availability. This study investigated habitat selection and preferences in wader species in the Swedish mountain tundra in Vindelfjällen Nature Reserve, Sweden.
Species diversity and species abundance were analysed. Relative abundance values calculated in this study mostly agree with abundance estimated in the literature. Diversity was high and evenly distributed in wetlands while highest abundance was found in dry areas. Golden Plover *Pluvialis apricaria* was the most abundant, generalist species appearing in all habitat types. Ringed Plover *Charadrius hiaticula* was found to be a specialist occupying open pioneer grounds close to open water. For the Temminck's Stint *Calidris temminckii* and the Redshank *Tringa totanus* no clear preferences could be detected. Further investigations would be necessary to get more reliable results for less frequent species as the Redshank. More diverse transects need to be surveyed to include a broader range of wader species and habitats. High efforts in fieldwork are necessary to balance low information content of remote sensing data in the Nature Reserve.

ETHICAL ASPECTS

Animals can suffer stress when getting disturbed during the breeding period. By the nature of this project, stress was inevitable to obtain the data. Results are used to improve the understanding of species ecology and conservation of the species surveyed in the area. While conducting the fieldwork for this study, observers were anxious to cause as little disturbance as possible and to avoid additional stress of any form.

ABSTRACT

Birds face a variety of biotic and abiotic constraints in their environment and habitat selection directly affects their fitness and survival. Generalist species can inhabit a broad range of different habitats, while specialists are more dependent on certain habitat structures for breeding and foraging. This study investigated habitat selection and preferences in wader species in the Swedish mountain tundra and looked into species diversity, distribution and abundance patterns within Vindelfjällen Nature Reserve.

The Swedish mountain tundra inhabits a variety of wader species in summer. Golden Plover *Pluvialis apricaria*, Ringed Plover *Charadrius hiaticula*, Temminck's Stint *Calidris temminckii* and Redshank *Tringa totanus* breed in Vindelfjällen Nature Reserve in upper Sweden and were the most common species in this study. Wetlands play an important role for waders throughout their life stages. As found in this study, wader species diversity was much higher and more evenly distributed in these areas compared to dry, short vegetated habitats like dry heath. Abundance in contrary was highest in dry heath, fresh heath and grass heath vegetation, which resulted from the high presence of the most abundant species, the Golden Plover. Mean relative abundance broadly agreed with breeding pair densities estimated in the literature, excepting the Temminck's Stint where abundance was slightly higher than expected.

The Golden Plover was the most generalist species appearing in all habitats throughout the study region. Its high abundance might affect species diversity and abundance of other waders as presumed in this study. Ringed Plover was habitat-specific and selected for open, low-vegetated pioneer grounds close to open water and streams. Because of inconsistent results, the Temminck's Stint could not be clearly assigned as generalist or specialist. Statistical results did not show any tendencies in habitat selection, while the species strongly accumulated in two certain transects which would suggest the opposite. For the fourth species analysed, the Redshank, no habitat preferences could be detected. This stays in contrast with descriptions found in the literature and its morphological appearance, which strongly relate the species to wetlands and similar habitat types. For both species, Temminck's Stint and Redshank, further investigations would be necessary if clearer statements want to be made. More diverse triangles need to be surveyed to include a broader range of wader species and habitats. Environmental maps were undetailed and high efforts in fieldwork are still necessary to balance the low information content.

In conclusion, species abundance and diversity differed strongly between habitat types and some waders showed stronger habitat selection than others.

Key words: habitat selection, habitat preferences, waders, species diversity, relative abundance, remote sensing, GLM

TABLE OF CONTENTS

INTRODUCTION

The Swedish mountain tundra is a unique ecosystem and inhabits various plant and animal species. While some species can be found all year round in the area like the endangered Arctic Fox *Vulpes lagopus*, other species appear as seasonal visitors from spring to autumn (Angerbjörn et al. 2013). Birds migrate from their Southern wintering areas to their breeding grounds in the Northern hemisphere to reproduce. Waders, like the Eurasian Golden Plover *Pluvialis apricaria,* arrive in the Swedish mountains in late spring to profit from a short, highly productive and food rich summer time in the upper mountain regions (Thompson et al. 2012).

Waders, or shorebirds as they are called in North America, inhabit wetland ecosystems and coastal areas all over the world. These habitats are vulnerable and since 1900, more than 60% of the natural wetland areas have disappeared (Davidson 2014). Habitat loss is one of the biggest threats for wader populations. Around 30% of the worlds wader populations show decreasing trends. More than 20% of them are listed as near threatened, vulnerable, endangered or critically endangered (Wetlands International 2012). In addition, migration has a big influence on the survival of many shorebird species. It is physically challenging and requires a lot of energy (Bairlein 1996). Arriving early on the breeding ground in a good condition enables birds to start breeding right away and to make best use of the short breeding season in mostly arctic regions (Tulp et al. 2009). As so-called income breeders, waders depend on good food supply in both their summering and wintering grounds to improve reproductive success (Morrison et al. 2004). Stopover sites along migration routes like the Yellow Sea in China are highly important, as they allow birds to rest and to restore their fat reserves (Lovette et al. 2016; Piersma et al. 2017).

Birds face a variety of biotic and abiotic constraints in their environment. Food availability, inter- and intraspecific competition, risk of predation etc., have direct influence on the fitness and survival of birds (Hildén 1965). These factors vary in their expression within different habitats. Additionally, birds have changing requirements to their environment according to their life history (Bairlein 1996). Habitat selection describes a hierarchical process, in which habitats offer different functions and conditions and individuals choose between these habitats according to their current needs (Fuller 2012). Following the ideal-free distribution, a habitat selection model implemented by Fretwell and Lucas (1969), fitness and reproductive success of birds should be equal in high- and low-quality habitats. High-quality habitats offer best conditions and get settled first. When density increases, individual fitness and reproductive success decrease because of stronger competition for the available resources. Individuals then start colonializing habitats with lower quality and lower densities. Following this strategy, birds are expected to have the same average success throughout different habitats (Fretwell et al. 1969; Lovette et al. 2016).

Bairlein (1996) further points out, that different bird species do not disperse equally throughout habitats rather than showing habitat preferences. Some species are generalists and more flexible when choosing a habitat, while others are specialized on macro habitats (habitat niches) with certain characteristics and are consequently more habitat-specific (Fuller 2012). Species diversity should increase in heterogenous habitats where more diverse macrohabitats are available and where both, generalists and specialists can find suitable habitats according to their needs (Cody 1985). Specialists show stronger habitat preferences than generalists (Bairlein 1996). Breeding birds again show stronger selection than non-breeding birds, because nesting places must meet very specific needs throughout the whole breeding season and birds are locally bound (Mills 2005). Because of their stronger dependency on certain macro habitats, specialists are more likely to be threatened by changes within their environment due to climate change, higher predation rates or intra- and interspecific concurrence (Cody 1985).

Vegetation structure is one crucial element that determines habitat suitability due to differences in vegetation height or plant species composition which then again affects food availability, shelter and availability of suitable nesting sites (Fuller 2012). The heterogenous mosaic of willow, dwarf shrubs, grass, meadow, fen and rocks that covers the Swedish mountain tundra should therefore contain a varied number of specialist and generalist wader species. Nearly all breeding wader species in the Swedish mountains are listed as generalists, excluding the Dotterel *Charadrius morinellus* which is declared as an arctic-alpine specialist (Thompson et al. 2012).

The ability of occupying various habitat types is related to behaviour patterns and morphological adaptations within species (Baker 1979). The form of a birds beak is closely related to its diet selection and feeding behaviour (Bairlein 1996). Differences in beak shape and size determine the prey species birds feed on and which habitat they prefer to live in. Long legs are destined to walk through shallow waters, while short legs are often seen in gliders which are adapted to a life in the air (Lovette et al. 2016). In waders, beak morphology and leg length are the most characteristic morphological adaptations (Colwell 2010). The Eurasian Golden Plover preys on invertebrates and berries on the ground surface of alpine tundra and mountain heaths, wherefore its beak and legs are relatively short (Béchet 2009). The Black-tailed Godwit *Limosa limosa* in comparison is a long-legged, long-necked and long-billed shorebird, that feeds on invertebrates it catches in shallow waters and muddy areas of fens and along the edge of lakes (Gejl 2017).

In the Swedish mountain tundra, little is known about wader populations, their breeding ecology and habitat preferences. Waders can form an important food source for arctic predators. Artificial nest studies investigate predation pressure on wader nests in arctic regions. Predation on wader eggs and chicks is high, especially after lemming peak years when predators are high in numbers (Machín 2012). A study of Blomqvist et al. (2002) emphasizes high predation pressure on waders in their breeding grounds in low lemming years. The breeding success of Red Knots *Calidris canutus* and Curlew Sandpipers *Calidris ferruginea* in Ottenby, Sweden decreased noticeably in those years.

In the Swedish tundra, most important aerial and terrestrial predators of wader nests and chicks are the Long-tailed Skua *Stercorarius longicaudus*, the Red Fox *Vulpes vulpes* and the Stoat *Mustela erminea* (Machín et al. 2017). Due to its low population densities and the close link to its main prey species the Norwegian Lemming *Lemmus lemmus*, the Scandinavian Arctic Fox is not stated as an important wader predator in Sweden. Yet there are hints, that the fox preys more intensively on birds in years with low rodent abundance. The amount of bird remains in its diet composition is much higher in those years (Wolfram 2013). In Canada, where the Arctic Fox appears in much higher densities, the species is declared as one of the main predators on high-arctic wader nests (McKinnon & Bêty 2009). Abundance and distribution of waders as well as their predator-prey relations in the arctic ecosystem need to be investigated further to get a better understanding of their value in the overall concept.

In Vindelfjällen Nature Reserve, where this study was performed, ground-breeding waders as the Golden Plover, the Red-necked Phalarope *Phalaropus lobatus* and the Common Snipe *Gallinago gallinago* inhabit areas along and above the treeline within a landscape consisting of grassland, wetland, open water and shrubland. A standardized, long-term study conducted by the Lund University (see http://www.luvre.org/) shows population trends for waders and other bird species for Sweden, Norway and Finland. Population trends of 24 wader species are equally distributed between increasing and decreasing populations. While species like the Ringed Plover *Charadrius hiaticula* and the Common Redshank *Tringa totanus* have positive population trends, the Common Snipe and the Ruff *Philomachus pugnax* are decreasing in numbers (Lindström et al. 2015). Rather than general trends, more detailed information on breeding ecology and habitat choice of waders in their Swedish breeding grounds is still lacking (Machín et al. 2017).

This study investigated habitat selection of waders in the mountain regions of Vindelfjällen Nature Reserve in Sweden. In a descriptive part, habitat use of the most common species was analysed and an attempt was made to assign whether species are habitat generalists or specialists within their Swedish breeding grounds. Relative species abundance and species diversity were computed to identify species rich and species poor habitats and to see how abundance and diversity correlate in these habitats. The importance of wetlands on wader abundance and diversity was discussed.

Another emphasis was placed on the methodology section. True wader densities within different habitat types were estimated using distance sampling and spatial analysis in Geographical Information System (GIS). A new modelling approach in GIS was tested to estimate relative humidity in upper mountain regions. Ecological factors and vegetation categories were worked out, analysing the influence of these factors on the occurrence of waders by using generalized linear models (GLM). Habitat availability and predicted number of wader observations per area were calculated and subsequently compared with actual observations made in the field. The objective was to test the reliability of predicted species occurrence derived from spatial analysis using GIS.

The outcome of this study should help understand the processes underlying habitat choices of waders in the Swedish mountain tundra. Learning more about driving factors on distribution and abundance of waders in the study area allows adaptations to larger regions. Thus, their influence on the overall ecosystem and their relation to predator species can be investigated further.

MATERIAL & METHODS

Study area

The study area is located in Vindelfjällen Nature Reserve in Västerbotten, Sweden (65.923056°N 15.317778°E). With 5.628 km², Vindelfjällen is the largest nature reserve in Sweden and one of the largest protected areas in Europe. The densely vegetated boreal forest in the lower valleys lightens up in higher elevations and transforms into large areas of sparsely vegetated alpine tundra. The Swedish mountain tundra is characterized by cold winters with long lasting snow cover from September to June and a short vegetation period. Low productive plant communities consisting of grasses, sedges, crowberries *Empetrum nigrum*, blueberries *Vaccinium myrtillus*, heather plants, mosses and lichen cover most parts of the mountains. Areas with bare or rocky ground as well as long lasting snow patches are spread throughout the region (Staafjord 2012).

Main animal species as the Arctic Fox, the Norwegian Lemming, the Rock Ptarmigan *Lagopus muta* and the Mountain Hare *Lepus timidus* have adapted to harsh winter conditions and highly productive summer months in the Swedish mountains. Lemming population fluctuations (lemming cycles) have a huge impact on the ecosystem (Ims et al. 2005). The survival and reproductive success of the Arctic Fox is closely linked with the abundance of rodents (Angerbjörn et al. 2013). Next to this all-year present species, seasonal visitors arrive in the area in spring and stay until autumn. Songbirds, waders and raptors have their breeding grounds here and alpine meadows form important grazing grounds for semi-domesticated Reindeer *Rangifer tarandus*.

Data collection

Wildlife triangles and distance sampling

Fieldwork was performed in July 2016 and 2017. Data was collected along so-called Wildlife triangle transects. Wildlife triangles are used as a common wildlife census technique by the Finnish Game Research since 1989. A triangle consists of three transect lines with 4 kilometres length each, arranged as an equilateral triangle of 12 kilometres in total length (Lindén et al., 1996). 28 of these triangles were established throughout the area of Vindelfjällen Nature Reserve in 2004 (Figure 1). Triangle locations in the study area were chosen semi-randomly. Good accessibility, low steepness of terrain and the avoidance of spatial proximity to arctic fox dens were influencing factors (Stoessel et al. unpublished). As one triangle can comprise a high variety of habitats within 12 km, in this study triangles were split into three corner transects to reduce variation in environmental factors within a transect. The splitting further allowed to increase sample size for further analysis and it helped avoiding double counts within buffer zones implemented around transect lines (Figure 2).

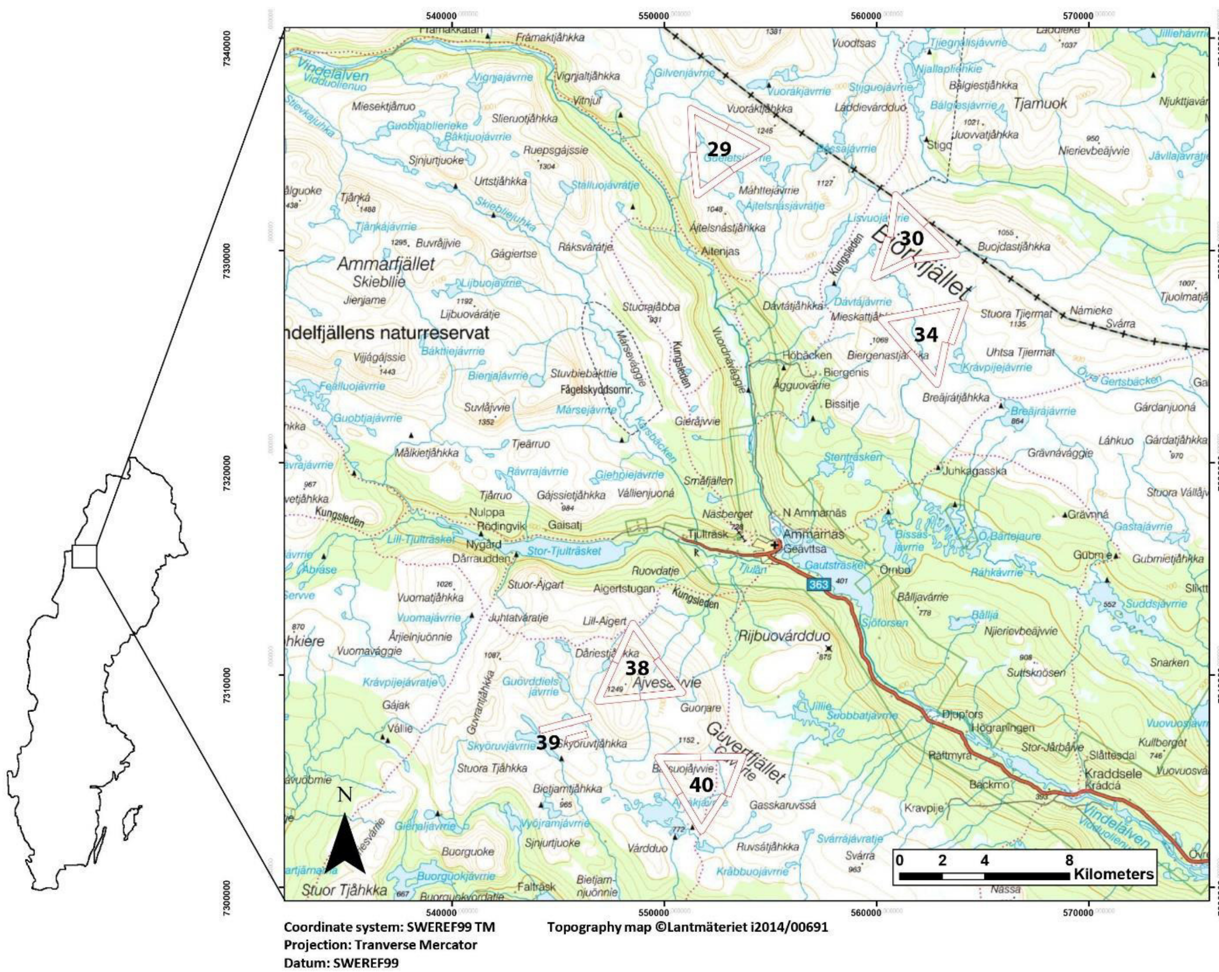

Figure 1: Overview over the study area. 28 Wildlife triangles are spread throughout the area of Vindelfjällen Nature Reserve, Sweden. The triangles pictured were surveyed in 2017. Triangle 29 was surveyed in 2016 and 2017. Map created by Marianne Stoessel, Stockholm University 2018.

In Vindelfjällen, Wildlife triangles were first implemented to collect snow tracking data of Arctic foxes and other species in winter, following the protocol suggested by Lindén et al. (1996). In 2015 and 2016, first summer surveys were conducted to investigate general biodiversity patterns in summer and in 2017, the focus was laid on the abundance of waders in the upper mountain regions. Survey protocol was changed for summer surveys and distance sampling was implemented as survey method to determine species appearance.

Distance sampling is a commonly used technique to estimate abundance of plants, mammals, birds and reptiles (Thomas et al. 2006). For this study, a team of two observers surveyed the transect lines. One person walked ahead spotting and identifying individuals of interest, while a second observer followed with several metres distance filling out the protocol sheet. Species name, perpendicular distance, habitat type the individual was first seen in, weather and date were recorded for every observation. In addition, GPS points were taken for spatial reference.

Vegetation types were recorded in the field following the protocol of the Swedish Arctic Fox Project (Arctic Fox Team 2017). Most important categories were dry heath (low growing dwarf shrubs like blueberries), fresh heath (continuous plant cover, willow, junipers, grass), willow (along rivers and stands in low alpine regions), grass heath (sparse vegetation, dominated by grass species), wet heath (heterogenous, dwarf birch, willow, grass, small marshes), meadow (herb and grass species), fen (mosses, sedges) and rocky, peaty grounds.
Wader data on triangle 29 was available from studies in 2016. In 2017, six triangles (including repeated observation of triangle 29) were investigated by the observation team. Triangle 39 was aborted after 2.5 km because of a thunderstorm. A second line transect with a length of 1 km was surveyed close to the area on the way back.

Landscape features

Spatial analysis was performed in ArcGIS 10.5.1. Environmental features considered for this study were aspect, slope, vegetation type and primary productivity. Buffer zones created around each transect line formed the basic area of which landscape information was extracted (Figure 2). The width of the buffer zones was estimated using detection functions of species observed (see relative abundance section below).

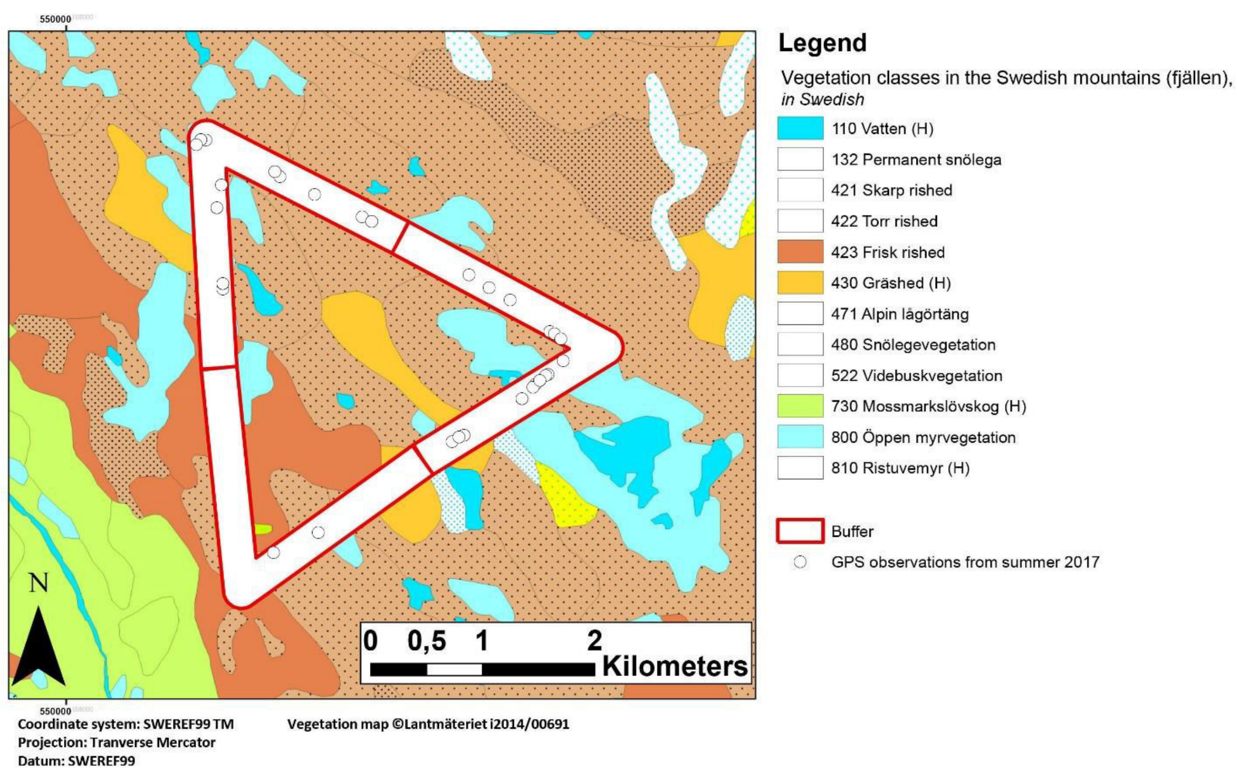

Figure 2: Decomposed Wildlife triangle 29 showing the implemented buffer zones around observed transect lines. Information of vegetation classes were exported for every buffer zone. Map created by Marianne Stoessel, Stockholm University 2018.

Topography variables such as elevation, aspect and slope derived from a digital elevation model with a 50 meters resolution (DEM, https://www.geodata.se/). Mean values for elevation and slope over the buffers were extracted. A mean aspect azimuth per buffer zone was determined, using the Python script tool “CalcZonalMeanAspect“ (Beyerhelm 2013).

To assess **vegetation** and habitat distribution within the mountain region, a vegetation map derived from Lantmäteriet was imported to ArcGIS (http://www.lantmateriet.se/). The map gave an overview of habitat types appearing in the landscape such as open water, forest, shrubland and others and was used to quantify areas covered by the various habitat types within buffer zones. Habitat descriptions were similar to the protocol used by the Swedish Arctic Fox Project.

A relative Normalized Difference Vegetation Index based on aerial ortho photos (rel-$NDVI_{ortho}$) was calculated and provided by researchers from Stockholm University to determine primary productivity in the study area (Erlandsson et al. unpublished; Le Vaillant et al. 2018). This index reflects photosynthetic activity in plants. Values between -1 and 1 indicate low and high productivity. It is computed as

$$NDVI = \frac{(NIR-R)}{(NIR+R)}$$

where NIR = near infrared waves and R = red waves. For detailed information see Pettorelli (2013). A mean rel-$NDVI_{ortho}$-value per buffer zone was calculated.

Moisture regime

No information on moisture regime was available in the study area. An experimental remote sensing approach was therefore applied to get an idea of moisture regime in the upper mountain regions.

Electromagnetic waves are constantly sent to the surface of our planet. Incoming light gets absorbed, transmitted and reflected in different portions, depending on the type and condition of land cover. Thanks to high spatial resolution (ca. 0,5m in the Swedish mountains), color infrared photography is used for landscape inventories and visual interpretation where the texture, the colours and the shape of vegetation elements are analysed for mapping biotopes in high detail (Ihse 2007). Color infrared pictures contain information of green, red and near infrared light. Plants reflect in the infrared, which makes near-infrared-information useful when performing vegetation analysis. Stressed vegetation for example can be detected easily because of much lower near-infrared reflections then fast-growing plants (Statewide Mapping Advisory Committee 2011).

An experimental approach was performed to test if a color infrared picture can be used to identify automatically wetland areas within the study region. Therefore, three bands (green, red and near-infrared) from a color infrared picture were extracted. Single bands were compared with a high resolution orthophoto from the study area and interpreted visually. Evidence was found, that the grey scheme of the green band correlated with varying moisture regime (Figure 3). Open waters and fens appeared much darker than dry and rocky areas. Finally, the green band was used to generate a mean value for each corner area that represents relative humidity.

Figure 3: Green band, extracted from the original color infrared picture of the study area. Open water and fen areas appear in darker grey scales, while brighter parts can be interpreted as dry or rocky grounds with less primary productivity and moist.

Data Analysis

Relative abundance

Relative abundance was computed as number of individuals per km² and was calculated for every transect. First, the software "Distance 7.1" (http://distancesampling.org/)was used to produce detection functions for the observed species. Truncation at 160 meters gave suitable detection functions for the most common wader species. This distance was then used to implement buffer zones around each surveyed transect line using ArcGIS. Corner transects had an area of 1.26 km² each, line transects surveyed in 2016 had an area of 1.28 km² and the two shorter transect from triangle 39 had areas of 0.3 and 0.8 km².

In a next step, GPS observation points were imported in ArcGIS. Observations outside the created buffer zones or observations with missing species or habitat information were excluded from further analysis. Remaining individuals formed the basis for relative abundance calculations.

Species diversity

The Shannon Index was computed to understand species diversity and evenness in species distribution in the study area. Number of individuals and species observed in the field were used to calculate an index for every habitat type. Shannon Index values close to 0 indicate low species diversity. Evenness values close to 1 indicate balanced species distribution within a habitat type.

Habitat preferences

Statistical analysis was performed in RStudio 1.1.383. Generalized linear models (GLM) with a negative binomial distribution were used to investigate habitat preferences of wader species. Number of observations in total and number of observations per species were computed for every transect and used as dependent variables. Species with 20 observations or more were analyzed in detail. Species with less than 20 observations were included in the total amount of individuals but were not analyzed separately.

A correlation matrix was created to predict correlation between independent variables. Based on this matrix, two global models were computed. One model included environmental variables such as mean rel-$NDVI_{ortho}$, mean slope, mean relative humidity and aspect azimuth. Vegetation types derived from the vegetation map in ArcGIS were used as factors for the second model. Manual stepwise model simplification was conducted. The final models were selected according to their AICc value.

Method reliability

GIS was used to predict species occurrence within different habitat types throughout the study area. The reliability of these predictions was tested using Fisher's exact test. Habitat availability (= area covered by the different habitat types within a buffer zone) was used to calculate the number of individuals expected in certain habitats. Expected values were then compared to the number of individuals observed in the habitat during fieldwork. If $p < 0.05$, a significant difference between observed and expected situation was assumed and therefore predictions made by the GIS were not sufficiently reliable.

RESULTS

20 transect lines with a total transect length of 75.5 kilometres were surveyed during fieldwork in 2016 and 2017. 285 individuals from 9 wader species were observed: Eurasian Golden Plover, Ringed Plover, Temminck's Stint *Calidris temminckii,* Redshank, Dunlin *Calidris alpina,* Dotterel *Charadrius morinellus*, Red-necked Phalarope, Ruff and Common Snipe. Four wader species had enough samples to be analyzed in detail: Golden Plover (n = 178), Ringed Plover (n = 32), Temminck's Stint (n = 30) and Redshank (n = 22).

Relative abundance

Relative abundance was calculated per transect. Abundance varied strongly between areas and ranged from 1.6 individuals/km² up to 26.7 individuals/km². Species richness varied between 1 and 6 species per transect (Table 1).

Table 1: List of transects surveyed in 2016(*) and 2017. Transect 39A was aborted after 2.5 km because of a thunderstorm. Transect 39B was surveyed as an extra transect close to transect 39A. In total, 285 individuals from 9 different wader species were recorded in the study area (total transect length of 75.5 km). Relative abundance was computed as individuals per km².

transect name	transect length (km)	buffer zone area (km²)	number of individuals (total)	relative abundance	number of species
29A	4	1.26	2	1.6	1
29B	4	1.26	18	14.3	4
29C	4	1.26	18	14.3	6
30A	4	1.26	21	16.7	4
30B	4	1.26	12	9.5	3
30C	4	1.26	9	7.1	4
34A	4	1.26	21	16.7	5
34B	4	1.26	3	2.4	2
34C	4	1.26	17	13.5	4
38A	4	1.26	11	8.7	4
38B	4	1.26	30	23.8	4
38C	4	1.26	7	5.6	2
39A	2.5	0.8	8	10	2
39B	1	0.3	8	26.7	2
40A	4	1.26	21	16.7	3
40B	4	1.26	26	20.6	3
40C	4	1.26	4	3.2	2
29AB*	4	1.28	11	8.6	2
29BC*	4	1.28	16	12.5	4
29CA*	4	1.28	22	17.2	7

In 20 transects surveyed, Golden Plover was present in all 20 transects, Ringed Plover and Redshank were missing in 9 transects and the Temminck's Stint was not detected in 10 of 20 transects (Table 2). Golden Plover was the most abundant species and appeared all over the study area with varying relative abundance between 1.6 individuals/km² and 23.3 individuals/km². Only few individuals of Ringed Plover (n = 7) were seen in the Southern parts of the study area (triangle 38, 39 and 40) and highest relative abundance was calculated in transect 30A with 6.3 individuals/km². Most observations of Temminck's Stint were made in only two transects, 38B and 40B, which therefore had high relative abundances with 6.3 and 7.1 individuals/km². Relative abundance of Redshank was low across the study area with highest abundance calculated as 3.2 individuals/km².

Golden Plover had the highest number of individuals recorded within this study and was the dominating species in most of the transects. There were only three transects, 30A, 30C and 38A, where other species appeared in higher numbers than the Golden Plover.

Table 2: Overview of the number of individuals (white) recorded and relative abundance per km² (grey) computed per transect. Only species with more than 20 observations are listed. 178 Golden Plover, 32 Ringed Plover, 30 Temminck's Stint and 22 Redshank were used in statistical analysis.

transect name	Golden Plover		Ringed Plover		Temminck's Stint		Redshank	
29A	2	1.6	0	0	0	0	0	0
29B	11	8.7	2	1.6	0	0	4	3.2
29C	10	7.9	2	1.6	2	1.6	0	0
30A	8	6.3	8	6.3	4	3.2	0	0
30B	6	4.8	5	4.0	0	0	1	0.8
30C	2	1.6	3	2.4	2	1.6	0	0
34A	15	11.9	0	0	1	0.8	2	1.6
34B	2	1.6	1	0.8	0	0	0	0
34C	13	10.3	1	0.8	0	0	2	1.6
38A	3	2.4	5	4	1	0.8	0	0
38B	19	15.1	2	1.6	8	6.3	0	0
38C	5	4	0	0	0	0	2	1.6
39A	7	8.8	0	0	0	0	1	1.3
39B	7	23.3	0	0	1	0.8	0	0
40A	15	11.9	0	0	0	0	3	2.4
40B	15	11.9	0	0	9	7.1	2	1.6
40C	3	2.4	0	0	0	0	0	0
29AB*	9	7	0	0	0	0	2	1.6
29BC*	12	9.4	1	0.8	1	0.8	2	1.6
29CA*	14	10.9	2	1.6	1	0.8	1	0.8

Observed habitat types

During fieldwork habitat type an individual was first seen in was recorded. Habitat types used by the four most common wader species is visualized in Figure 4. More than 60% of Golden Plover occurred in dry heath (> 60%), while 64% of Redshank were found in wet areas like wet heath and fen. Temminck's Stint was distributed equally throughout different habitat types. Most Ringed Plover were seen in dry heath (41%), grass heath (25%) and rock/peat areas (16%).

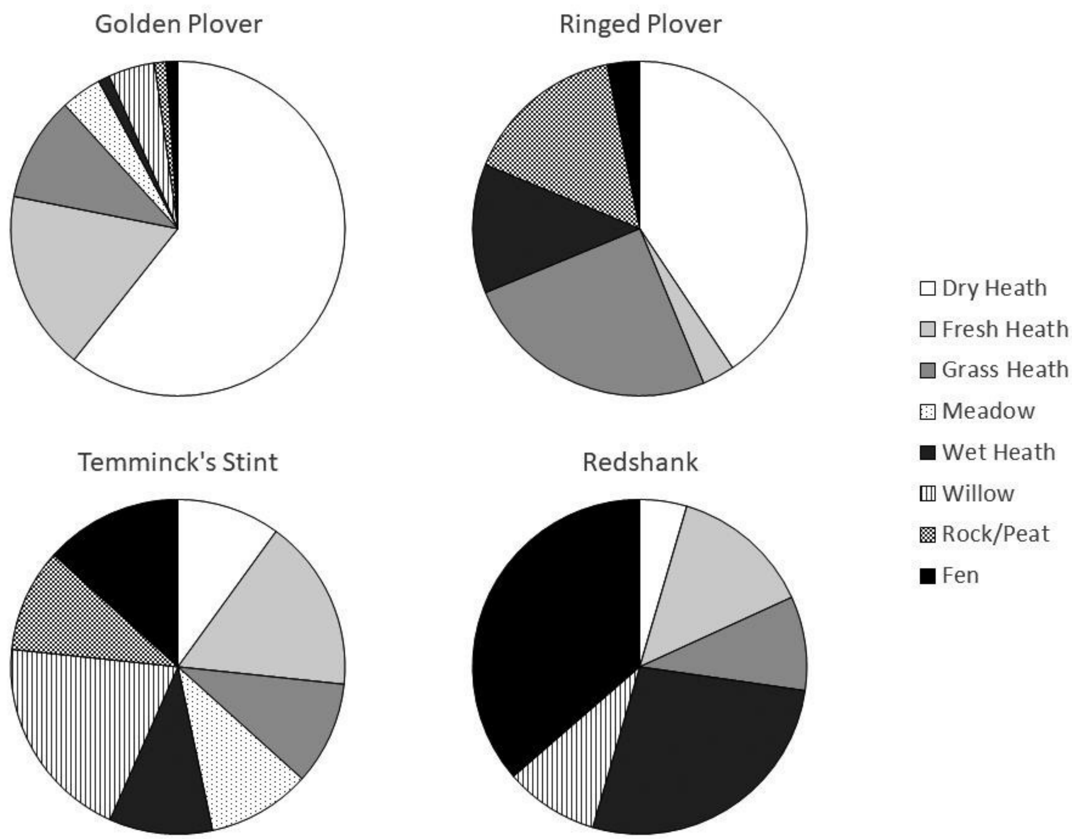

Figure 4: The pie charts give an overview of habitat types used by the four most common wader species in the study area. Habitat type is defined as the habitat an individual was first seen in when surveying a transect. 178 Golden Plover, 32 Ringed Plover, 30 Temminck's Stint and 22 Redshank were observed on 20 transects.

Species diversity

Shannon Index values differed broadly between habitat types (Table 3). Dry heath covered 47% of the study area but had the lowest diversity index ($H_S = 0.66$) and the lowest evenness value ($E_H = 0.37$) while containing highest species abundance (~45% of all observations). Only 12% of the area was covered by fen. Though, the habitat showed the highest diversity (H_S = 1.79) and evenness in species distribution (E_H = 0.91) as well as the highest number of species detected in general. The categories rock and wet heath were not available in the vegetation map used. Still, they inhabit around 9% of individuals observed, wet heath contained the third highest species diversity (H_S = 1.31) and species are evenly distributed throughout the two habitat types (E_H = 0.94 in both categories).

Table 3: Shannon Index was used to calculate species diversity (H_S) and evenness (E_H) per habitat type. Low values indicate low diversity and low evenness in species distribution. The number of species (N) and number of individuals counted within habitats are given. Habitats are listed according to the percentage of area covered. Categories rock and wet heath were missing in the vegetation map and percentages could not be listed (= n.a.).

habitat type	area covered (%)	number of individuals	number of species (N)	diversity (H_S)	eveness (E_H)
dry heath	47	130	6	0.66	0.37
grass heath	18	35	6	1.37	0.76
fen	12	23	7	1.76	0.91
fresh heath	10	43	5	0.95	0.59
meadow	8	12	3	0.96	0.87
willow	1	17	4	1.14	0.82
wet heath	n.a.	15	4	1.31	0.94
rock/peat	n.a.	10	3	1.03	0.94

Habitat preferences

For the two GLM's, the total amount of individuals counted per transect and the four most common species were used as dependent variables. Explanatory variables used in the first model were productivity measured as mean rel-$NDVI_{ortho}$, mean slope, mean relative humidity and aspect azimuth. The vegetation model included the following habitats as independent factors: dry heath, fresh heath, grass heath, meadow, fen and open water (overview of model variables and results see Table 4). The total number of individuals increased with an increasing amount of dry heath ($p < 0.05$), meadow ($p < 0.05$) and fen ($p < 0.01$) in buffer zones, while no relation could be found for any environmental variable. Golden Plover were significantly related to fen areas ($p < 0.001$). The higher the amount of fen within a buffer zone, the more individuals were observed. In case of the Ringed Plover, open areas such as dry heath ($p < 0.01$), grass heath ($p < 0.01$), meadow ($p < 0.01$) and open water ($p < 0.05$) were positively influencing its occurrence. It was the only species with significant results in the environmental model. Ringed Plover were less frequent in steep areas ($p < 0.05$) and in areas with high primary productivity ($p < 0.01$). Northern orientation ($p < 0.05$) on the contrary seemed to have a positive effect on Ringed Plover appearance. No trends could be detected for Temminck's Stint and Redshank. Also, mean relative humidity had no influence on species occurrence.

Table 4: The table shows the results of the two generalized linear models: the vegetation model (white) and the model with the environmental variables tested (grey). The columns represent the dependent variables, where "total" gives the number of individuals (n=285) of all species (n=9) observed on the transects. Only four species had enough observations to be analyzed in a GLM: Golden Plover (n=178), Ringed Plover (n=32), Temminck's Stint (n=30), Redshank (n=22). Significant results are marked as "*" ($p < 0.01$), "**" ($p < 0.05$) and "***" ($p < 0.001$ = highly significant).

	total	Golden Plover	Ringed Plover	Temminck's Stint	Redshank
dry heath	*		**		
grass heath			**		
fresh heath					
meadow	*		**		
fen	**	***			
water			*		
relative humidity (mean)					
slope (mean)			* (-)		
rel-NDVI$_{ortho}$ (mean)			** (-)		
aspect			*		

Method reliability

Fisher's exact test was used to check on the independency between the number of individuals observed and the number of individuals expected in different habitat types. The Golden Plover (*$p < 0.001$*), the Temminck's Stint (*$p < 0.001$*) and the Redshank (*$p < 0.01$*) showed significant differences between observed and expected values, while the Ringed Plover did not.

DISCUSSION

Relative abundance

Relative abundance differed widely between the wader species as demonstrated in Table 2. Some transects like transect 29A or 30C were sparsely inhabited by waders while in other areas like 38B and 40A and B waders occurred rather frequently.

Golden Plover was detected in every transect and other studies confirm the species to be one of the most abundant wader species of the last decade with increasing population trends in Sweden (Svensson & Andersson 2013, Lindström et al. 2015). Its typical density is estimated of 3 to 4 breeding pairs per km² in large mountain areas in Sweden (Svensson 2006). In this study, relative abundance was calculated for single individuals rather than breeding pairs, although most individuals appeared in pairs during fieldwork (pers. obs.). Even though relative abundance varied broadly between areas (1.6 to 23.3 individuals/km²), mean relative abundance of 8.1 individuals/km² computed in this study agrees with the breeding pair density of 4 pairs/km² estimated by Svensson (2006).

Ringed Plover populations increased rapidly after the year 2000 (Svensson & Andersson 2013). Svensson (2006) rates breeding pair density of Ringed Plover in Sweden on 0 to 0.2 pairs/km². In this study the relative abundance average at 1.3 individuals/km² which is slightly higher. Ringed Plover prefer to breed in higher altitudes (Svensson 2006) and the surveyed Wildlife triangles were established in higher latitudes than transects observed by Svensson in his study. The slightly higher occurrence values calculated in this study might derive from a more suitable breeding habitat for the species found in higher regions.

The **Temminck's Stint** had the most inhomogeneous number of observations within this study. Population trends for this species are hard to generate because of the small amount of data available for the relatively uncommon breeding bird in Sweden (Lindström et al. 2015). Typical Swedish breeding pair densities are expected to range between 0.1 and 0.4 pairs/km² (Svensson 2006), where the average relative abundance generated in this study was 1.3 individuals/km². Even though Temminck's Stint occurrence is still low, nearly as much Temminck's Stint as Ringed Plover were recorded in the study area and the wader does not seem to be as uncommon as stated by the literature.

Despite the general increase of **Redshank** in Sweden, Southern populations are decreasing, most likely because of habitat loss and higher predation rates in the these lower parts (Svensson & Andersson 2013). According to Svensson (2006), typical densities of Redshank amount from 0 to 0.1 breeding pairs/km². Redshank had the lowest relative abundance values within the analysed waders. The mean relative abundance of 0.9 individuals/km² computed in this study is slightly higher than estimated by the literature but still matches the overall low-density trends of Redshank in its breeding grounds.

Species diversity

As stated in the introduction, wetlands are important for wading birds. In this study they had a strong effect on species diversity. Even though individuals appeared less frequently in fen habitat (n = 23) and the habitat was less available than others (12% of area covered by fen), species diversity was high and species distribution was evenly balanced (H_s = 1.76, E_H = 0.91). Red-necked Phalarope and the Common Snipe only appeared in fen structures and together with Dunlin and Redshank they are known to breed and raise their young within these wetland habitats (Gejl 2017). By offering habitat niches and proper food supply for many waders and their chicks, wetlands make an important contribution to biodiversity in the Swedish mountains.

On the contrary, dry heath was the most common habitat (47% of area covered in total) and held the highest number of individuals observed (n = 130) while at the same time species diversity was low ($H_s = 0.66$) and species ratio was strongly biased ($E_H = 0.37$). Reason for the unbalanced ratio in dry heath habitat was the Golden Plover. With the highest abundance detected in this study (8.1 individuals/km²), the Golden Plover occurred in all habitats and dominated most of them. The most generalist species in this study showed highest dominance in dry heath, fresh heath and meadow in which it made up 83, 72 and 58% of all observations. These were also the habitats where lowest species diversity was measured ($H_s = 0.66$, 0.95 and 0.96). By contrast, habitat types where Golden Plover was rare like fen and wet heath (9 and 13% of all observations) showed much higher diversity and evenness values ($H_s = 1.76$ and 1.31, $E_H = 0.91$ and 0.94). Other species occurred in higher numbers within these avoided zones. Ringed Plover dominated the rock habitat (50% of all observations) and the Redshank was most abundant in wet habitats like fen and wet heath (> 35% of all observations). In conclusion, occurrence of Golden Plover affected species diversity within different habitats in Vindelfjällen Nature Reserve. Habitats with lower Golden Plover abundance were more balanced in species composition and diversity.

Habitat preferences

Landscape features

Environmental variables had no effect on species abundance, excepting for the Ringed Plover. Explanatory power of environmental variables depends on the quality and resolution of maps used in GIS. It was hard to find high quality map material for the area of Vindelfjällen Nature Reserve. A digital elevation model with a 50 metres resolution only provides rough information. The primary productivity map had a higher resolution (2 metres) and was therefore chosen to be included in the GLM rather than information on elevation. The vegetation map was undetailed and some categories such as willow and wet heath needed to be removed from statistical analysis because they were missing in most transects surveyed. Information on the availability of bare ground and rocks in the study area was not available. Thus, individuals were observed repeatedly in these habitat types. Fisher's Exact test supports the assumption that the predicted distribution of waders derived from habitat availability did not fit with species occurrence observed in the field (Golden Plover $p < 0.001$), Temminck's Stint $p < 0.001$ and Redshank $p < 0.01$). Quality of remote sensing data must be enhanced to improve power of implemented analysis. As it is now, the low information content on environmental and vegetational features in the study area must be balanced by high efforts in conducting fieldwork.

Mean relative humidity derived from the extracted green band of the color infrared ortho picture had no effect on any species, even though wetlands are known to be closely related to wading birds. The use of the green band was an experimental approach implemented because information of moisture regime was missing. It was not possible to collect ground-truth data in scope of this work. This would have been necessary to test and to ensure the reliability of the method.

Golden Plover

Regarding the broad distribution range of Golden Plover throughout all habitat types, the species might be considered a generalist which is flexible enough to occupy various habitat types. Availability of fen was found to be an important factor for increasing numbers of Golden Plover in the study area (Table 4), although individuals were observed mainly in dry heath rather than fen habitat (Figure 4). Several reasons need to be considered when explaining these contradictory statements.

Only adult individuals were seen during fieldwork. Golden Plover breed in humid (alpine) tundra regions, peatlands and highland bogs where they prefer nesting on short vegetation (< 15 cm) like lichen, mosses or low-growing shrubs (del Hoyo et al. 1996; Pearce-Higgins et al. 2006; Ratcliffe 1976). They are solitary breeders, accompanying their young in the first 30 days before leaving them to migrate South (Gejl 2017). Golden Plover chicks are precocial and parents lead their chicks to habitats close to the nest where they can find suitable food supply and vegetation structures (Whittingham et al. 2001). A study in Great Britain found out, that adults stayed close to their chicks and foraged in the same habitats as their young (Whittingham et al. 2000). A recent study conducted in Vindelfjällen proved a habitat shift in Golden Plover chicks, where they switched from dry heathland to wet willow shrub habitat within the first weeks after hatching (Machín et al. 2017). Abundance of their favourite prey species, accessibility of the habitat due to limited movement ability of young chicks and protection from predators are the main factors that drive habitat selection in Golden Plover chicks (Whittingham et al. 2001, Machín et al. 2017). Wetlands and shrubby habitats meet these needs. Therefore, the habitat shift to wetter areas performed by the chicks could be one reason why availability of wetlands positively influences the occurrence of adult Golden Plover in late July.

However, increasing availability of fen habitat did not lead to an increasing number of Golden Plovers detected in that certain habitat type. In contrary, most observations were made in dry heath (n = 108), fresh heath (n = 31) and grass heath (n = 18) rather than in willow (n = 8) and fen habitat (n = 2). Adult Golden Plover avoid dense vegetation like willow as found out by Pearce-Higgins and Grant (2006). Also, some shorebirds like lapwings actively defend their chicks while smaller plovers such as Ringed Plover distract predators by pretending of being injured to lead them away from their nests and chicks (Lovette et al. 2016). In the study region, Golden Plover were observed to repeatedly appear close to intruders, calling and running away to distract a potential threat (pers. obs.). They did this preferably on lightly heightened and exposed spots, which in mountain tundra often are covered by dry, fresh and grass heath vegetation. Avoidance of enclosed habitats and defence behaviour against predators may explain to some extent why individuals were observed in open, short vegetated areas.

Ringed Plover

Ringed Plover form monogamous breeding pairs and inhabit open areas close to rivers, lakes and coasts dominated by mud, gravel, rocks and short vegetation (Gejl 2017; del Hoyo et al. 1996; Summers et al. 2002). Summers et al. (2002) also stated low steepness as an important factor for habitat selection in Ringed Plover. In Southern Norway the species is related to pioneer habitats with rocky soil and closeness to open water (Østbye et al. 2009). Former assumptions are in accordance with the results from this study, where low primary productivity, flat slope and open water availability increased species occurrence (Table 4). Primary productivity is relatively low in dry heath, grass heath and meadow vegetation. The number of individuals observed increased when availability of these vegetation types increased, even though no individuals could be observed in meadow habitat. During fieldwork several individuals were observed along the edges of snow patches and streams, looking for food and showing their typical vigilance behavior (acting hurt) as soon as an intruder came close (pers. obs.). Snow patches remain longer in depressions and areas with northern orientation, which could explain the positive trend of northern aspect on the abundance of the species. The predator distraction display of adult Ringed Plover suggests that habitat selection of chicks mainly influences habitat use of adults.

The results of this study indicate that breeding Ringed Plover are habitat-specific when breeding in the arctic mountain tundra. The species appears to be a specialist rather than a generalist when choosing suitable breeding habitats, since they prefer pioneer habitats with open grounds and sparse vegetation.

Temminck's Stint

Statistical analysis supports the assumption of the Temminck's Stint being a generalist in habitat selection. GLM results did not reveal any preferences or avoidances of vegetation types or environmental features (Table 4) and observations in the field reflect an equal distribution throughout different habitat types (Figure 4). It was noticeable though that more than half of the observations focused on only two transects, AC38B (n = 8) and AC40B (n = 9). This fact suggests the Temminck's Stint to be a specialist rather than a generalist.

While Golden Plover breed in monogamous pairs, Temminck's Stint appear to have a two-clutch breeding system (Hildén 1975) where they accumulate in smaller groups of breeding males and females (Bairlein 1996, Østbye et al. 2009). A female stint mates with a male and lays a clutch of four eggs within his territory which is incubated by the male. After that, the female pairs with another male and lays a second clutch within his territory which she incubates herself. Males also pair with two different females, whereby the second female is mostly one that seeks for a new mate for her second clutch. A territory then contains two nests where male and female are responsible for a single brood each. Nest locations of the Temminck's Stint vary from year to year

(Østbye et al. 2009). Females need to be in good condition to lay two to three clutches and proper food supply within the territory is therefore highly important, also for the survival of the chicks later on (Lovette et al. 2016). Females were observed changing their nesting site when feeding conditions were unfavourable or stint densities were high (Østbye et al. 2009). Regarding the fact of food importance and that no specific habitat preferences were found for any vegetational or environmental factor in this study, their breeding system and prey abundance are very likely to be driving factors of Temminck's Stint occurrence. Also, habitat preferences might not be discovered because of the relatively small sample size or because not enough transects surveyed contained the landscape features the species depends on. Further investigations would be necessary to understand habitat selection of the Temminck's Stint in the Swedish mountains.

Redshank

Redshank breed in monogamous pairs, prefer to nest solitarily and nest close to open water bodies and bogs, where they select sheltered areas covered with low vegetation (Summers et al. 2002, Østbye et al. 2009). They build their nests in marshes on tufts of grass covered by leaves and blades of grass (del Hoyo et al. 1996, Gejl 2017). Considering their morphological appearance where its long legs and beak are perfectly adapted to muddy grounds and shallow water (Lovette et al. 2016), Redshank would be expected to be a specialist which preferably selects these wet habitats. This study reports inconsistent results regarding habitat preferences of Redshank in the Swedish mountains. According to observations made in the field, more than 80% (n = 18) of all Redshank were detected in wet heath, willow, fen and grassland habitats (Figure 4). This is in accordance with statements in the literature. Still, no significant results were revealed by the GLM, neither for a specific habitat type nor for humid areas in general (Table 4). Reliability of statistical analysis strongly depends on the sample size. Redshank had the smallest number of observations (n = 22) within species analysed and therefore explanatory power of the GLM might be low. Repeated surveys would be necessary to increase sample size and to make statistical analysis more reliable.

CONCLUSION

Wetlands showed the highest species diversity while wader abundance was highest in dry heath. The Golden Plover was revealed to be the most common generalist which might affects species diversity and abundance in the area to quite some extent. The Ringed Plover in contrary was found to be a specialist, inhabiting pioneer grounds close to open water shores. Most inconsistent results were found for habitat selection in Temminck's Stint. The species could not be clearly defined as generalist or specialist. This study could not detect any habitat preferences for the Redshank, which stays in contrast to descriptions found in the literature and its morphological appearance. Further investigations would be necessary to increase available data on the less frequent species to make statistical analysis more reliable. More diverse triangles throughout the Nature Reserve should be surveyed to include a broader range of wader species. Also, quality of environmental information needs to be improved. In conclusion, some waders showed stronger habitat selection than others and species abundance and diversity differed broadly between different habitat types.

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