Habitat selection in Paridae and possible impacts by forestry

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I want to dedicate this thesis to my fantastic mother who passed away far too early. I know you would have been really proud of me now!

"It could have been better"
Abstract

Parids are mostly sedentary birds and therefore habitat selection is important for both winter survival and reproduction in the breeding season. Because of their residency, parids are vulnerable to habitat fragmentation and loss of habitat. I reviewed habitat selection in parids in North-America and Europe and compared with a field study of populations of tits in an area of southeastern Norway with extensive forestry to discuss possible impact of forestry on parids.

North-American and European parids show similar patterns due to habitat selection. Almost all species forms stable flocks and are, to some extent, territorial during winter. The European species often form mixed-species flocks with other tits, golderest (*Regulus regulus*) and common treecreeper (*Certhia familiaris*). All species that form flocks also hoard food and are dependent on good hoarding sites. The great tit (*Parus major*) and the blue tit (*Cyanistes caerulus*) differ from the other species. They do not form stable flocks, are not territorial and do not hoard during winter. Together with coal tit (*Periparus ater*), they are also partly migratory.

Human land use, like modern forestry, is believed to have a great impact on the biodiversity. The consequences of modern forestry management have been habitat fragmentation and alteration, and loss of forest habitat has taken place. In my field study I looked at possible differences in population size and structure of winter flocking titmice communities in order to see if forestry may have an impact on the abundance of small sedentary passerines during winter. Point-transect with sound playback were used as method to collect data. The field work was done from 23rd January to 17th March 2015, in Varaldskogen State Forest, Norway. Abundant species in this forest area are willow tit (*Poecile montanus*), crested tit (*Lophophanes cristatus*), golderest, common treecreeper and great tit. The results did not show any major differences in abundances. Surprisingly, the willow tits turned out to be more abundant in plantation forest than in natural forest. Due to the relative small number of observations and only one year of collection of data (2015), further studies should aim at having more data from a longer period of time and to use improved methods.
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1 Introduction

In birds, habitat selection is one of the most studied areas of ecological research. Especially the breeding habitat has been focused on, with less attention on studies on habitat selection by resident birds in winter, when weather conditions and food limitation may result in more acute selection (Broughton et al., 2014). Research focusing on habitat alteration, fragmentation and loss caused by humans are important, since the changes may lead to a decline in bird populations (Siffczyk et al., 2003). This study focuses on how modern forestry and, through this, habitat fragmentation can affect populations of winter flocking titmice (Paridae spp). I present first a review of habitat selection by chickadees and titmice in North America and Europe, aiming to make an overview of the general trends. The motivation is to put this into the context of a field study focusing on winter flocking titmice communities in natural forests and plantation forests to compare possible effects caused by modern forestry. The second part is a presentation of this field study with a discussion where I try to link together the findings from my review with the result of the field work.

1.1 Habitat selection

A habitat can be defined as all biotic and abiotic resources and conditions (Mayor et al., 2009) that make occupancy in a given area possible for a species (Rueda et al., 2013). Habitat selection is a scale-sensitive process leading to a disproportionate use of available conditions and resources by individuals or populations to gain best possible fitness (Rueda et al., 2013). Obviously, immobile organisms such as plants or organisms with restricted mobility like plankton cannot choose their habitats once settled. Their success depends on external factors for effective dispersal (Bazzaz, 1991). Mobile animals can of course choose their habitat in a higher degree than plants. In its simplest form, habitat selection is to either accept or reject a habitat faced by an animal (Mayor et al., 2009).

The spatial and temporal scale of habitat selection depends on the mobility and behaviour of the organism (Mayor et al., 2009). Migratory birds may have different breeding and wintering habitat (Virkkala, 2004). In contrast, sedentary birds may occupy the same area both in the breeding and non-breeding season (Brown and Long, 2007). For sedentary birds, habitat qualities such as food availability and nesting/roosting sites are important both during winter and in the breeding season (Enoksson et al., 1995). These qualities will have an influence on
the birds’ fitness, both through survival during winter and breeding success during summer. In addition will competition, both inter- and intra-specific, and predation pressure affect the habitat choice (Cody, 1981). Only a few groups of forest bird species are sedentary in Norway; the grouses, a few raptors, the woodpeckers and the tit guild. The tit guild are cavity-nesting passerines which mainly use dead trees for nesting and consequently logging and forest management are important factors affecting the dynamics of the populations of these bird species (Virkkala, 2004).

1.2 Habitat fragmentation and forestry

Habitat fragmentation can be defined as the process where a larger area of a certain habitat is transformed into a number of smaller patches isolated from each other by a matrix of habitats unlike the original, i.e. breaking the habitat apart (Fahrig, 2003). This process will lead to a loss of the original habitat and a reduction of habitat patch size. The effect of habitat fragmentation per se is suggested to be generally much weaker than the effects of the habitat loss observed as a consequence of fragmentation (Fahrig, 2003). Habitat loss can have very harmful effects on biodiversity (Andren, 1994, Fahrig, 2003).

It has been recognized that habitat fragmentation and loss is a main threat for the species’ survival by transforming the landscape from being continuous and varying into a network of discrete habitat fragments (Ovaskainen and Hanski, 2003). To make it possible to predict the large-scale consequences, a general theoretical framework, "extinction threshold value" has been developed. This term refers to the percentage value of the focal habitat where a meta-population will go deterministically extinct and is used in model studies to predict the amount of habitat loss a population can tolerate (Ovaskainen and Hanski, 2003). Some theoretical studies suggest that the threshold-value for birds is 10-30% of suitable habitat remaining in the landscape (Andren, 1994, Fahrig, 2003). Various bird species have declined in European coniferous forests due to habitat alterations caused by forestry (Solonen and Jokimaki, 2011, Virkkala, 2016). Also in North America some species have experienced a population declined may because of loss of habitat (Hadley and Desrochers, 2008). Industrial forestry is known to have a great impact on species richness, and plays an important role in conservation of biodiversity (Chaudhary et al., 2016). Forestry leads to habitat fragmentation, alteration and loss e.g through clearcutting as management regime and has been criticized for having adverse ecological effects (Kuuluvainen et al., 2012).
1.3 Modern forestry in Norway

The majority of Norwegian boreal forests today are under active management as one of the largest renewable resources of the country (Bright et al., 2014). During the last 100 years the forestry has undergone shifts from less to more intensive management regimes (Ostlund et al., 1997, Okland et al., 2003). Before the mid-1900s, coniferous forests in Fennoscandia were harvested by high-grading selective cutting in various forms (Kuuluvainen et al., 2012). Both smaller and larger trees were logged, the first to fuelwood and the latter to commercial purposes mainly. Through this regime only tree density was reduced, the remaining trees had still various sizes (Wegge and Rolstad, 2011). After 1950, clearcutting became the main harvesting method and this rapidly led to fragmentation at the landscape scale and homogenization at the forest stand scale (Wegge and Rolstad, 2011). Even if the amount of forest cover has remained the same, the composition and age structure has changed dramatically from mixed mature forests to even aged coniferous stands through planting and subsequent thinning (Gustafsson et al., 2010, Vatka et al., 2014). After logging, replanting of spruce is done to rapidly initiate new production (Wegge and Rolstad, 2011, Tomter and Dalen, 2014). Pine is often naturally regenerated by leaving widely spaced seed trees (Wegge and Rolstad, 2011). In addition, drainage and ground preparation is undertaken (NOU, 2013). After a period of growth, understory thinning is performed to secure optimal development of the trees present (Kuuluvainen et al., 2012, Tomter and Dalen, 2014). Present-day forests are dominated by biologically young stands of coniferous trees of the same age or size, established on former clear-cuts (Nielsen and Totland, 2014).

Whereas plantation forests typically consist of artificially bred plants to promote high growth, natural forests is naturally rejuvenated forest areas which are residuals after selective logging carried out 70-150 years ago (Rolstad et al., 2002). As a result of modern forestry regime, the forests are fragmented into a checkerboard pattern of clear-cuts and dense homogenized sapling stands, each of different age classes (Suorsa et al., 2005). Today, only 25% of the Norwegian forest areas are in a natural condition (Storaunet and Rolstad, 2015). Plantation forest is much less variable in structure than natural forest, especially in the vertical plane (Wegge and Rolstad, 2011). In addition to the differences in age structure and spatial patterns, there is a lower amount of dead wood and less structural complexity in managed forests compared to natural forests (Okland et al., 2003). Natural forests have also a more open tree layer than managed forests that was timbered 60-70 years ago (Okland et al., 2003).
2 A review on habitat selection in chickadees and titmice

2.1 Methods

I used some central books about parids (Haftorn 1956 and Otter 2007) and a literature search in the Web of Science as basis for the review on habitat selection in the Paridae-family. The string "habitat and paridae and winter" was used as a topic search in all databases in all years. This gave a result of 245 hits. To limit the amount I chose to read the titles and abstract and kept hits that referred to habitat selection and parids living in Europe and North-America. In addition I decided to omit hits that were not accessible in full text directly from Web of science. I also omitted articles written in other languages than English and Nordic languages (i.e Norwegian, Danish and Swedish). After the exclusion of these articles I ended up with 58, the latest published in March 2016. These publications were used to make a brief summary regarding habitat selection in chickadees and titmice.

2.2 Habitat selection in the Paridae

The parid family is well-studied both in terms of behaviour and ecology (Otter, 2007, Broughton et al., 2014). Most species included in the review are mainly sedentary (Tables 1&2). The great tit (*Parus major*), the blue tit (*Cyanistes caerulus*) and the coal tit (*Periparus ater*) are partly migratory, which means that a fraction of a population is migrating individuals, while the rest of the population is resident (Nilsson et al., 2006). The species can mainly be divided into three groups; the ones which prefer deciduous forest, those which prefer coniferous forest, and the generalists. This applies for both North American and European species. The only species distributed on both continents is the Siberian tit/grey-headed chickadee (*Poecile cincta*), but for convenience I have regarded the species as European and hence call it Siberian tit.

Most species form flocks during the non-breeding season, either in basic flock or discrete flock system (Ekman, 1989, Broughton et al., 2015). Several species, especially the European ones, form mixed flocks with other ecological and morphological similar species i.e goldcrests (*Regulus regulus*), treecreepers (*Certhia spp*) and nuthatches (*Sitta spp*) (Alatalo et
The basic flocks are characterized by a changeable assemblage of individuals with non-exclusive home range. The species forming basic flocks generally do not hoard and may migrate due to harsh weather conditions (Ekman, 1989, Dhondt, 2007, Broughton et al., 2015). Contrary, species forming discrete flocks are territorial in the non-breeding season, do hoard food and remain sedentary throughout the year (Ekman, 1989, Dhondt, 2007, Broughton et al., 2015).

An alternative strategy to flock formation are performed by so-called winter floaters. Winter floaters are most often juveniles that are not connected to any flocks (Hogstad, 2003). Instead they switch between different flocks or just roam around singly (Hogstad, 2003). The floater strategy is considered to be a way to improve chances to acquire a future territory and to obtain better knowledge of local food supplies (Hogstad, 2014). It is assumed that floaters are more expose to predation because they are less familiar with their surroundings due to the lack of an own territory. In addition they are supposed to have higher levels of competition than flock-members (Brown and Long, 2007). These factors may lead to lower fitness, higher mortality, and more stress compared to birds that are members of a stable flock (Hogstad, 2003, Brown and Long, 2007).

Independent of distribution, preferred habitat, social structure and hoarding behaviour, all the species have the same preferences of food types. Spiders and other arthropods are important during winter together with seeds (Nilsson, 1979, Suhonen et al., 1993, Barnea and Nottebohm, 1995, Cooper and Gessaman, 2004, Broughton et al., 2014). The hoarding species use autumn to cache food, storing it in the trees. The way of storing is species-specific, but common is the use of lichens and needles to do this (Haftorn, 1956, Petit et al., 1989).

### 2.2.1 Chickadees and titmice in North America

There are twelve species of parids living in North America, seven chickadees (*Poecile spp*) and five titmice (*Baeolophus spp*). The Mexican chickadee (*Poecile sclateri*) is poorly studied and omitted from my study due to lack of data. The Siberian tit is discussed under European tits. Because of lack of data, the only *Baeolophus* species considered in this study is the tufted titmouse (*B. bicolor*) (table 1).
Titmice in the North America are not as sympatric as the European species which is sympatric over much of their range. Only the black-capped (*Poecile atricapillus*) and boreal chickadees (*P. hudsonica*) have a broad overlap in their distribution, with a continent-wide range (Smith, 1967). The black-capped chickadee has the largest range, distributed from Alaska to Pennsylvania, and therefore lives in sympatry with several of the others parid species present in North America. The species uses a wide range of habitats and lives in both forests and suburban areas (Egan and Brittingham, 1994). The black-capped chickadee is also the most studied species of the parids in North America. Therefore the part of this review, concerning North American species, will primarily focus on this species and how it interacts with the other species.

Black-capped chickadees may form mixed-species flocks with boreal chickadees during winter in areas where the species co-occur. In areas of overlap the black-capped chickadee is more abundant than the rarer boreal chickadee. The boreal chickadee is a food specialist using only a few of the tree species available to foraging but during winter niche overlap is higher because of similar diets. This only occurs in the three coniferous tree species (Black spruce (*Picea mariana*), white spruce (*P. glauca*) and tamarack (*Larix laricina*) both chickadees use to forage. Niche-partitioning between the species may prevent competition. Black-capped chickadee is believed to be the dominant species (Gayk and Lindsay, 2012).

Along the pacific coast the ranges of the black-capped chickadee and chestnut-backed chickadee (*P. rufescens*) overlap. The chestnut-back chickadee seems to have the second largest range overlap with black-capped chickadee. Habitat descriptions of the species indicate a general difference between the species, but during winter they are known to forage in mixed flocks. Even if they occur in mixed flocks the species use different feeding sites (Smith, 1967). The black-capped chickadee prefers deciduous trees, while the chestnut-back chickadee prefers coniferous trees. Their feeding sites in the trees also differ due to height above the ground (Smith, 1967). The black-capped chickadees forage mostly nearer the ground, while the chestnut-back chickadees seem to prefer to forage nearer the top. This is similar to the interaction patterns found by black-capped and boreal chickadees (Smith, 1967).

In eastern North America, populations of tufted titmice form mixed-species flocks either with Carolina (*P. carolensis*) or black-capped chickadees during the non-breeding season. The parids in these areas are nuclear species in foraging groups that also have several satellite species from other families such as nuthatches and treecreepers (Dolby and Grubb, 1999).
Black-capped and Carolina chickadees do not have overlapping distribution ranges (Merritt, 1981).

Black-capped chickadees have been shown to be both territorial and non-territorial. A population near Athabasca, Alberta, Canada seemed not to be territorial, here there was a broad overlap between flock ranges during winter, and different flocks shared the same resources (Desrochers and Hannon, 1989). This is in contrast to several other population studies done on North-American parids and also black-capped chickadee populations. The non-territorial populations had site-related dominance behaviour (Desrochers and Hannon, 1989).

During winter black-capped chickadees, Carolina chickadees, mountain chickadees (*P. gambelli*) and tufted titmice are known to select specific microhabitats as a response to shifting thermal conditions caused by wind. In harsh weather conditions these species select sheltered areas even if this is not the best foraging site. It is believed that the reason is to reduce energy loss (Wachob, 1996). Carolina Chickadees and tufted titmice were found to reduce their heights of feeding in the canopy and they shifted to leeward side of foraging substrate with increasing wind (Dolby and Grubb, 1999).

### 2.2.2 Tits in Northern Europe

There are more species of tits in Eurasia than in North America. Many of the species are abundant only in Asia, some endemic to minor areas. In Western Europe only seven species are distributed (table 2). Among these the Siberian tit is abundant in both Northern Fennoscandia and Alaska and Yukon, Canada. All of the seven species in Western Europe are well studies and included in this study.

Contrary to the chickadees and titmice in North-America, European tits are highly sympatric (Smith, 1967, Suhonen et al., 1994). Only two species, the marsh tit (*Poecile palustris*) and the blue tit, are abundant in deciduous forest only, the others prefer coniferous forests or are generalist with regard to macro-habitat. Only two species have a more limited distribution. These are the Siberian tit which lives only in the northernmost parts of Fennoscandia and in Alaska and the Yukon, and the crested tit (*Lophophanes cristatus*) which is most abundant to coniferous forests in Fennoscandia. The other species are distributed in more or less in whole Europe.
The Siberian tit co-occur with the willow tit (*P. montana*) farthest north, while all the other six species (except the Siberian tit) co-occur in more southern areas (Suhonen et al., 1994). The tits in Fennoscandia are mainly resident, but some species are partly migrants namely the blue tit, great tit and coal tit. The main pattern regardless of these species is that natal dispersal is longer than adult’s migrations (Bakken et al., 2006).

All tits in Fennoscandia form mixed species flocks during the non-breeding season (i.e autumn and winter). Most species form discrete social units with high coherence. These flocks are dominance structured often consisting of an adult pair with some non-kin juveniles (Ekman, 1989, Haftorn, 1999).

The blue tit and the great tit differ from the other European species. In addition to being partly migratory, they do not hoard and have a looser social structure with no territoriality during the non-breeding season. Because of the harsh winter environment in north Europe, their survival depends on human feeders and access to enough available food during winter. These species do not form winter flocks with a stable composition. They join flocks in what Ekman (1989) defined as basic flock structure. It is suggested that flocking behavior, territoriality, and hoarding behaviour are linked together. It is more important with a discrete and stable flock structure when food is hoarded and the birds are depending on finding food caches later on (Orell, 1989).
Table 1: A brief summary of habitat choice among the parids in North America. Chickadees and titmice are known to be generally sedentary birds being in the same macro-habitat through the year. Even sedentary birds can change micro-habitat between seasons. In this table the micro-habitat refers to the preferred habitat during the winter, i.e. the non-breeding season. All species that I found data on are hoarders and also territorial to some extent. This probably applies to all North American species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Macro-habitat</th>
<th>Micro-habitat</th>
<th>Hoarding</th>
<th>Territorial(w)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poecile atricapillus</td>
<td></td>
<td>Respond to thermal conditions.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poecile carolensis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountain chickadee</td>
<td>C</td>
<td>Prefer pine (Pinus spp) and incense-cedar (Calocedrus decurrens). Bark foraging.</td>
<td>ND</td>
<td>ND</td>
<td>(Morrison et al., 1985, Petit et al., 1989, Wachob, 1996, Cooper and Gessaman, 2004)</td>
</tr>
<tr>
<td>Poecile gambeli</td>
<td></td>
<td>Respond to thermal conditions.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poecile hudsonica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chestnut-backed chickadee</td>
<td>C/D</td>
<td>Incense-cedar. Bark foraging. Moist, shaded coniferous forest.</td>
<td>ND</td>
<td>ND</td>
<td>(Smith, 1967, Morrison et al., 1985)</td>
</tr>
<tr>
<td>Poecile rufuscens</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baeolophus bicolor</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

C: Coniferous forest +: Known to hoard/are territorial
D: Deciduous forest -: Do not hoard/are not territorial
ND: No data
Table 2: An overview of habitat choice of the seven species of tits living in Western Europe. All are distributed in Norway. Among the species of tits in Europe, great tit, blue tit and coal tit are known to be partly migratory, the rest are sedentary. Great tit and blue tit also differ from the others regarding hoarding behaviour and sociality. They do not hoard, do not form stable flocks during winter and are not territorial. Only the blue tit and marsh tit are solely deciduous forest species. Siberian tit is assumed to be hoarding and territorial, but there is not enough data to draw any conclusions.

<table>
<thead>
<tr>
<th>Species</th>
<th>Macro-habitat</th>
<th>Micro-habitat (winter)</th>
<th>Hoarding</th>
<th>Territorial (w)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marsh tit <em>Poecile palustris</em></td>
<td>D</td>
<td>Prefer English oak (<em>Quercus robur</em>) if available. Forage on branches in the mid-layer.</td>
<td>+</td>
<td>-</td>
<td>(Suhonen et al., 1994, Hinsley et al., 2007, Broughton et al., 2014, Broughton et al., 2015)</td>
</tr>
<tr>
<td>Siberian tit <em>Poecile cincta</em></td>
<td>C/M</td>
<td>Conifers. Trunk and branches. Old forest.</td>
<td>ND</td>
<td>ND</td>
<td>(Virkkala, 1990, Suhonen et al., 1994)</td>
</tr>
<tr>
<td>Great tit <em>Parus major</em></td>
<td>C/D</td>
<td>Nestboxes as roosting site. Use feeders. Suburban areas.</td>
<td>-</td>
<td>-</td>
<td>(Dhondt and Eyckerman, 1980, Suhonen et al., 1994, Broughton et al., 2015)</td>
</tr>
<tr>
<td>Blue tit <em>Cyanistes caeruleus</em></td>
<td>D</td>
<td>Nestboxes as roosting site. Suburban areas. Twigs. Feeders.</td>
<td>-</td>
<td>-</td>
<td>(Dhondt and Eyckerman, 1980, Suhonen et al., 1994, Broughton et al., 2015)</td>
</tr>
</tbody>
</table>

C: Coniferous forest  +: Known to hoard/are territorial
D: Deciduous forest  -: Do not hoard/are not territorial
M: Mixed forest
ND: No data
2.3 Ecology of Norwegian titmice in winter

In Norway the tits follow a relatively clear distribution pattern. The marsh tit and the blue tit have the most southerly distribution, preferring deciduous woodland in Southern Norway. In winter the blue tit also lives in mixed forests. The willow tit, coal tit and crested tit are coniferous tits, which are abundant in the whole of Norway apart from the northernmost part. The Siberian tit is found in Finnmark and mountain areas in Southern Norway. The great tit is the generalist amongst the tits in Norway. It is the most numerous one, living in all habitats, but prefers deciduous woodlands and mixed forests. It is also abundant in suburban areas, and has a strong association to humans, being one of the most common birds at feeders (Bakken et al., 2006).

2.3.1 Social structure

The coniferous tits in Norway are known to form mixed-species flocks during winter together with goldcrest (Regulus regulus) and common treecreeper (Certhia familiaris). In deciduous forest the nuthatches (Sitta europea) can follow flocks of marsh tits. Contrary to the breeding territories, the winter territories of the flocks are believed to be overlapping (Haftorn, 1999), but still defended to some extent (Ekman, 1979). Resource dispersion hypothesis (RDH) suggests that territory size depends on distribution of patches of resources. The flock size is believed to vary with the quality of resource patches (Carr and Macdonald, 1986, Siffczyk et al., 2003). The size of the territory is affected by the landscape composition; the birds increase their territories to compensate for loss of optimal habitat for instance caused by forestry. The optimal and preferred habitat for small wintering birds is mature forests. An extended use of suboptimal habitat such as bogs and saplings may also compensate for habitat loss and fragmentation (Siffczyk et al., 2003). Because of territorial defence, only a limited number of flocks can live within a forest area (Hogstad, 2003). In addition, a bigger home range area leads to higher rate of locomotion and defence cost and thus a need for more food. A result may be higher mortality and hence a decrease in the population (Siffczyk et al., 2003).

2.3.2 Foraging, competition and predation

Trade-offs between food availability, predation risk, and social dominance may affect how the tit guild is structured (Suhonen, 1993). It is assumed that formation of mixed-flock has some
adaptive advantages as improved feeding efficiency and defense against predators (Ekman, 1979). Both sociality and hoarding food are important factors for the parids due to increased survival (Siffczysk 2003). Storing tits can retrieve food from edges and store them in the forest interior and in this way they avoid predation pressure and harsher weather conditions found at the edges during winter (Siffczysk et al., 2003). Lack of possible hoarding sites can be a limiting factor (Suhonen and Alatalo, 1991).

The main factors causing mortality for tits in the winter season are probably predation and starvation (Krams, 2001), and can in general be related to food availability (Jansson et al., 1981). A selection of foraging site is assumed to be a trade-off between getting enough food and avoiding predation. The dominant species is assumed to choose the best site due to both requirements. Especially, the dominance hierarchy which applies to these communities of tits has been well studied (Krams, 2001). Studies agree on the crested tit as the dominant species and the willow tit and the goldcrest as subordinate (Haftorn, 1956) following a weight-related pattern (Suhonen et al., 1992). This leads to a separation of foraging sites in the trees and a restricted site selection in the presences of different tit species (Alatalo et al., 1987). The differentiation seen in choice of foraging place in trees correlates strongly with the storing patterns (Haftorn 1956). Typically, the treecreeper forage at the trunk, the willow tit at the innermost part of branches, the crested tit in the middle and coal tit and goldcrest at the outermost part of the branches (Haftorn, 1956). The spacing-patterns are also clearly linked to where food resources can be found (Jansson et al., 1981). Observational studies suggest an interspecific exploitation competition between the species (Alatalo et al., 1986). The common tree creeper differs to such an extent from the others by being specialized to feed on the trunk and do not have competition with the others species due to food resources (Alatalo et al., 1987). To survive the harshest winter days it is likely that the tits require some threshold density of food items all over their territories. Days with ice and snow covered branches can be critical due to high search cost.

In addition to hoarding behaviour, the formation of flocks can be an anti-predator behaviour (Solheim, 1984). The food availability influences the predation risk directly (Jansson 1981). Food resources are limited and this is another part of the selection and segregation of foraging sites (Suhonen et al., 1992). Potential predators on tits and other small birds are small mustelids, squirrels, woodpeckers, and raptors like Eurasian sparrowhawk (*Accipiter nisus*) and pygmy owl (*Glaucidium passerinum*) (Hogstad, 2015). During the winter the pygmy owl
is the main predator on passerines (Suhonen, 1993). Especially subordinate and younger individuals are vulnerable to predation (Jansson et al., 1981, Suhonen, 1993). The main reason for winter mortality has previously been claimed to be food competition verified through higher survival rate in populations with low density (Ekman et al., 1981). In recent year it has been more common to claim that predation has a greater impact on community structures than competition (Suhonen et al., 1993). Due to their segregation at different foraging sites the species undergoes different predation risk (Suhonen, 1993). The pygmy owl preys mostly on species foraging in the outer part of the trees, i.e. the goldcrest (Suhonen, 1993). On the other hand, the crested tit and the willow tit exploit sites less exposed to predation (Suhonen et al., 1993). There is no doubt that just a little predation from pygmy owl can devastate a flock (Solheim 1984)
3  A field study of winter flocking tits in natural forests and plantation forest

3.1  Aim of the study

The aim of the field study was to compare the populations of small wintering birds i.e. tits, goldcrest and common treecreeper, in natural forests and managed forests to investigate if there is any differences due to forest management. Both population size and community composition were looked into. Based on my review and knowledge about habitat selection and social structure among Norwegian parids I expect that modern forestry will affect the population sizes. The conifer titmice are known to prefer mature forests and to avoid open areas (Siffczyk et al., 2003). When forestry leads to an increase of suboptimal habitat for the focal species, the population size of wintering birds may decrease. I predicted that the overall population size of small wintering birds in my study area is quite small. In addition, I predicted that the dominant species, crested tit, will be more numerous than the subordinate species. I also predicted that the common treecreeper should be more numerous in natural forest since this species is known to be an old forest specialist.

In addition to human caused habitat transformation it may be important to consider possible additional effects of climate changes. The global warming may lead to changes in the species’ distribution patterns. Species like blue tit and great tit that depend on feeding from humans and having a more southern ecology may benefit from the human-induced climate changes. Species preferring more cold weather and harsher condition, like willow tit and Siberian tit, may suffer from the climate changes and be displaced from their current habitats.

Linking together the human-induced changes of habitat by forestry and climate change, I predicted that willow tit especially will have low population size in my study area.
3.2 Methods

3.2.1 Study area

The field work was performed at Varalскogen, a state-owned forest (60°10'N, 12°30'E) located in Kongsvinger municipality, Hedmark County, in Norway adjacent to the Swedish border (figure 1). The study area covers around 100 km² with a gently undulating terrain between 200 and 400 m.a.s.l. Climate is continental, with cold winters (average -7.2°C in January), warmer summers (average 15.3°C in July), and low to moderate amount of precipitation (700-1000 mm). During the study period, snow covered the ground during December-April. The forest is dominated by two conifers, Norway spruce *Picea abies* (40% of standing volume) and Scots pine *Pinus silvestris* (58%), interspersed with birch *Betula ssp* and aspen *Populus tremula*. Generally, spruce is found in more fertile sites and pine is dominant on dryer and poorer sites as well as around bogs and mires. The field layer is dominated by blueberry (*Vaccinium myrtillus*) in the spruce-dominated forest, while the less productive pine forest is dominated by cowberry (*V. vitis-idaea*), ericaceous shrubs and heather (*Calluna vulgaris*).

Forest characteristics

Natural forests were 150-200 years old with no major human interventions the last 70 years. Plantations were 55-70 years old and a result of replanting and one or more understory thinnings afterwards. In cultivated parts of the area (i.e logged and replanted) the field layer consists more or less of a mixture of forbs and graminoids instead of the native blueberry cover. In older plantation forest blueberry has re-established as the field layer. Heather and cowberry usually manage to be maintained as cover in areas with pine logging (Wegge and Rolstad, 2011). The tree density was higher in plantation forest than in areas with natural forest (table 3). Natural forest area was more vertical heterogeneous with stands of different age classes scattered randomly around, whereas plantation forest was characterized by more even-aged stands.

To find a measurement for the forest quality and habitat quality I used site index which is a measure of the production capacity of a forest area (table 3). Site index is divided into four classes; high, medium, low or no production capacity. In addition areas with water, roads etc. are classified separately. To find the site index of my sample areas, I used NIBIO map.
resources "Kilden" and the function "Skogportal" to draw polygons, defining my sample areas and asked for a report on the site quality of the chosen area. The term AR5 which specifies 13 different classes was used. Finally I found the percentage portion of each site index class within each sample area (appendix 1).

Table 3: The table shows the differences between the forest types due to overstory tree density per hectare, the stand age and the distance to settlements.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Tree density (ha)</th>
<th>Stand age (yr)</th>
<th>Distance to settlements (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silkisberget (P)</td>
<td>700</td>
<td>59-67</td>
<td>900</td>
</tr>
<tr>
<td>Snustjern (P)</td>
<td>1000</td>
<td>62</td>
<td>3400</td>
</tr>
<tr>
<td>Ratikken (P)</td>
<td>850</td>
<td>56-61</td>
<td>900</td>
</tr>
<tr>
<td>Lebiko (P)</td>
<td>770</td>
<td>55-64</td>
<td>1000</td>
</tr>
<tr>
<td>Larbekken (P)</td>
<td>840</td>
<td>56-66</td>
<td>3000</td>
</tr>
<tr>
<td>Emtberget (N)</td>
<td>570</td>
<td>150-207</td>
<td>1800</td>
</tr>
<tr>
<td>Taroberget (N)</td>
<td>665</td>
<td>172-196</td>
<td>2900</td>
</tr>
<tr>
<td>Saerkilamp (N)</td>
<td>680</td>
<td>172-207</td>
<td>3900</td>
</tr>
<tr>
<td>Lodinberget (N)</td>
<td>670</td>
<td>196-214</td>
<td>1300</td>
</tr>
<tr>
<td>Torvhuk (N)</td>
<td>530</td>
<td>172-192</td>
<td>2000</td>
</tr>
</tbody>
</table>

P: Plantation forest  N: Natural forest

3.2.2 Sampling design

Sample areas

Within the study area I selected five sample areas in natural forests and five in plantation forests. Each area was spaced apart with two to three km (figure 1). In natural forest the areas was on average 22 ha with a range from 11 ha to 44 ha. The plantation forest areas were on average 20 ha with a range from 11 to 31 ha. The forests composition in the sample areas are believed to be as equal as possible within each forest type. In each sample area a predefined route with five counting stations were followed. One area, Snustjern, had four counting stations due to the smaller size of the area and proximity to clearcuts.
Figure 1: At the right map the study area is marked in green on the map, situated east of Kongsvinger, south-east in Norway. The study area is adjacent to Sweden; the border is the lilac line. The left map shows how the sample areas were located in the study area. Red dots correspond to areas with natural forests and red circles correspond to plantation forest areas. The settlement in the area is scarce and is mainly located at north-east of Varaldsøen.

**Bird census**

Birds were counted using a point transect method, as described by Gregory et al. (2004). Following a predefined route, birds were counted at regularly spaced counting stations. The counting stations were spaced apart with 200-300 m to avoid counting the same bird twice during the same survey (figure 2). The first censuses was done in March and April 2014 in four study areas, Taroberget, Emtberget, Silkisberget and Snustjern as a pilot study. Due to a winter characterized by relative high temperature and little snow, the snow cover was almost gone already early in March. The results of the pilot study are excluded from the analysis due to a major expansion of the censuses following year. In addition the birds may had started to prepare for the breeding season due to the early spring in 2014. The part of bird censuses used in the analysis was done from 23\textsuperscript{rd} January to 17\textsuperscript{th} Marsh in 2015. The number of sample areas was expanded to 10 areas in 2015, and all areas were visited at three times during this season.
The censuses were performed from late of January to the middle of March. In other words, earlier than the pilot study to avoid that the flocks started to split up for the breeding season.

Figure 2: The figure is a simplified sketch over a sample area. The dots represent the counting stations, and the dashed circles shows the area the counting station covers. The counting stations were spaced apart with 200-300 metres which correlates with the assumed size of a winter territory.

Birds were censused using playback. A mix of the different songs and calls to crested tit, willow tit, coal tit, great tit, goldcrest and common tree creeper were used as playback. The mix was played for around 10 minutes. After playing the sound mix once, around 5 minutes of silence followed to listen for and observe birds. This sequence of playing sounds and silence to listen and observe were done twice at every counting points. Mostly the birds responded quickly to the sound. To hold the risk of counting the same birds at a neighbouring counting station to a minimum, the volume of the playback was kept low. The equipment used for playback was a Philips Raga 4 G mp3-player and a Senz SS014 pocket speaker.

During the period of field work the snow depth varied between 70 cm to 40 cm, and in some places the snow had disappeared before late visits. All these censuses are included in the statistical analysis. During the field work done in 2015 snow depth varied between around 70 cm in the beginning to a mix of patches with and without snow at the end of the period. The field work was exclusively done in fairly good weather with little or no wind and no snowfall due to the fact that birds are less active in bad weather. The work was done mainly between 09.00 in the morning and 15.00 in the afternoon. The different sample areas were visited at different times of day in a way that every area was visited both early and late in the day.
3.2.3 Statistical methods

The counts had many zeroes and the distribution of observations was therefore highly skewed. This precluded standard parametric statistical tests. Therefore ranking tests for non-parametric data were used. To check for differences between population sizes the Mann-Whitney U-test was performed. I used Fisher exact test to check if individuals from different species occurred together more often than assumed by chance. The species were tested pairwise.

Generalized Linear Mixed Models (GLMM) was used for regression analysis to look at significant differences between groups. Species was used as response variable, whereas forest type and day of survey were used as fixed variables. Sample area, survey number and counting stations were considered as random effects. I used occurrence instead of abundance and a binomial modeling. In the analysis the occurrence of species was compared relative to forest type. All statistical analyses were conducted in R version 3.0.1 for windows (R Core Team, 2013). The R package "lme4" was used to conduct the GLMMs (Bates et al., 2015). The graphs are made mainly in excel.

The observation data for 2014 are included in the analysis of community structure and the graph showing the distribution of flock size.

3.3 Results of the field study

3.3.1 Population size

Summarized, 147 countings were done at 49 different counting stations and 87 (59%) of these had no observations of birds. The counting stations were visited three times. Overall there were rather small differences in number of observed birds between the forest types (figure 3). Only willow tit had a significant difference in numbers between observations in the two forest types, being more abundant in plantation forests.
The GLMM-analysis did not show any significant differences between the forest types for other species than the willow tit, which was five times more common in plantations than natural forests (table 4). The analysis showed that the day of census had a significant negative effect on the number of observation of crested tit. The observations of crested tit decreased closer to spring. The effect may be considered as weak due to p-value close to 0.005 (0.0483). An INLA (integrated nested Laplace approximations) analysis showed that observations of great tit significantly increased with day. In other words, great tits were more often observed in the forest nearer spring than in midwinter. This analysis was run by E. Heegård at NIBIO.

The results from the ranking test support the findings from the GLMM (table 5). The only species that had a significant difference in observed number of individuals between the forest types was the willow tit.

Figure 3: The bar graphs show the average number of individuals of each species observed in natural forest and plantation forest. All sample areas are added together. Overall the abundance of birds was about the same in both forest types. Only willow tit was observed significantly more in plantation forest than in natural forest. Over half the time of counting no birds were observed.
Table 4: Model output of a model with forest type and day survey were used as fixed variables. The only significant findings were that willow tit is significantly more abundant in plantation forest and that crested tit had a negative effect of time.

| Species        | Parameter      | Estimate | Std. Error | z-value | Pr (>|z|) |
|----------------|----------------|----------|------------|---------|-----------|
| Crested tit    | Intercept      | -0.1589  | 0.8339     | -0.191  | 0.8488    |
|                | TypePlantation | 0.1199   | 0.5172     | 0.231   | 0.8171    |
|                | Day            | -0.0307  | 0.0156     | -1.975  | 0.0483*   |
| Willow tit     | Intercept      | -3.9899  | 1.5397     | -2.591  | 0.00956   |
|                | TypePlantation | 2.3628   | 1.1054     | 2.138   | 0.03256*  |
|                | Day            | -0.0078  | 0.0219     | -0.356  | 0.72153   |
| Goldcrest      | Intercept      | -1.2063  | 0.8160     | -1.478  | 0.138     |
|                | TypePlantation | 0.6031   | 0.4537     | 1.329   | 0.184     |
|                | Day            | -0.0134  | 0.0144     | -0.931  | 0.352     |
| Treecreeper    | Intercept      | -2.2456  | 1.0249     | -2.191  | 0.0284    |
|                | TypePlantation | -0.2414  | 0.6155     | 0.0392  | 0.6949    |
|                | Day            | 0.0061   | 0.0164     | 0.374   | 0.7082    |
| Great tit      | Intercept      | -50.7532 | 19.6615    | -2.581  | 0.00984   |
|                | TypePlantation | -0.7643  | 11.9685    | 0.064   | 0.94908   |
|                | Day            | 0.2270   | 0.2576     | 0.881   | 0.37831   |

Table 5: The Mann-Whitney U-test performed on the different species based on forest type supported the findings of GLMM. Only the willow tit had a significant difference in abundance between the two forest types (p<0.05).

<table>
<thead>
<tr>
<th>Mann-Whitney U-test, n1= n2=20</th>
<th>W-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crested tit</td>
<td>124.5</td>
<td>0.622</td>
</tr>
<tr>
<td>Willow tit</td>
<td>59</td>
<td>0.006*</td>
</tr>
<tr>
<td>Goldcrest</td>
<td>99.5</td>
<td>0.589</td>
</tr>
<tr>
<td>Common treecreeper</td>
<td>127</td>
<td>0.542</td>
</tr>
<tr>
<td>Great tit</td>
<td>134</td>
<td>0.239</td>
</tr>
</tbody>
</table>

3.3.2 Community structure

I did not observer bigger mixed flocks. Mostly I observed only one or two birds at the same time. Figure 4 shows the distribution of flock size separated by forest. Counting with zero observation is included and accounts for around 50% of the counting in each forest type species added together.
The result of Fisher exact test showed that mostly birds of different species occurred together more often than expected by chance (table 6). The treecreeper was most likely to occur independently from the tits.

Table 6: The table shows the results of Fisher exact test, p-values. Almost all species occurred significantly more often together than expected by chance. Only the treecreeper occurred apparently with others just by chance.

<table>
<thead>
<tr>
<th></th>
<th>Crested tit</th>
<th>Willow tit</th>
<th>Goldcrest</th>
<th>Treecreeper</th>
<th>Great tit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crested tit</td>
<td>0.005*</td>
<td>&lt;0.001*</td>
<td>0.12</td>
<td>0.01*</td>
<td></td>
</tr>
<tr>
<td>Willow tit</td>
<td>0.04*</td>
<td></td>
<td>0.31</td>
<td></td>
<td>0.03*</td>
</tr>
<tr>
<td>Goldcrest</td>
<td></td>
<td></td>
<td>&lt;0.001*</td>
<td>0.004*</td>
<td></td>
</tr>
<tr>
<td>Treecreeper</td>
<td></td>
<td></td>
<td></td>
<td>&lt;0.001*</td>
<td>0.008*</td>
</tr>
<tr>
<td>Great tit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 4: As the bar chart shows, mostly I observed zero birds. There were rarely observed flocks with more than two members. In this graph type of species is not taken into account. Some of the observations of two birds may have been pairs of the same species.
4 Discussion

4.1 Comparing species

The human impact by forestry on forest ecosystems has been the focal point of several studies and discussion the last decades (Fahrig, 2003). In this study I have focused on habitat selection among parids in North-America and Europe and how modern forestry can affect the populations through habitat transformations and loss of optimal habitat. I found some general patterns due to habitat selection in the non-breeding season among seven North-American and six European species of parids. Almost all species are sedentary, forms flocks and hoard food during winter. The great tit and blue tit differ from the other species in the way that they are partly migratory, have a looser social structure and do not hoard food. Coal tit is also known to be partly migratory, but coal tit do not migrates in a seasonally pattern (Bakken et al., 2006). The coal tit is a hoarder as the other species.

Considering micro-habitat selection, the species differ more. They have different foraging niches both vertically and horizontally in the tree (see for example Haftorn 1956, Smith 1967 and Wachob 1996). In addition they prefer to some extent different species of trees to forage (Morrison et al., 1985). Although the different preferences of foraging sites, all chickadees and titmice in this study are omnivorous. During winter spiders and other arthropods together with seeds are the main diet (Haftorn, 1956, Gayk and Lindsay, 2012).

4.2 Field Study

4.2.1 Effects of forestry

In my study there were few differences in small wintering bird populations between natural forests and plantation forests in Varaldskogen State Forest. On the species level I found that the willow tit was more abundant in plantation forest than in natural forest, but all other species were more or less equally distributed in both forest types. During the field work I did not observe larger flocks, more common was to observe one or two birds. The coal tit was not observed during the field work.
Except for the willow tit there was no significant difference in abundance of birds in natural forest compared to plantation forest. Therefore I suggest that both types represent an equally habitat for tits. Notably, the plantation forests surveyed in this study were 55-70 years old and therefore consisted of relatively mature trees. Also my observation of approximately the same number of treecreepers in both forest types supports my assumption that the differences between natural forest and mature plantation forest are small, with similar habitat quality. A study done by Le Tortorec (2013) also found that habitat loss did not have the expected negative influence on the treecreeper, but this study focused on the reproductive success not on winter survival. He stated that the predation risk increased with increasing amount of preferred habitat which meant that both habitat were equally good (Le Tortorec et al., 2013).

The willow tit was seen five times more in plantation forest than in natural forest although natural forest is assumed to be the preferred habitat also for willow tit (Siffczyk et al., 2003). Willow tit may benefit more from higher tree density in plantation forest than the others in the way of hoarding, foraging and protection against predation. It is also possible that willow tit can make more use of food from edges and clear cuts in greater extent than others. This is in contrast to Eggers (2014) findings due to negative effects by understory thinning. A possible explanation may be that reduction of optimal habitat reduces the carrying capacity in the area (Siffczyk et al., 2003), even if the remaining population can benefit from the habitat changes. These factors may have caused a possible long-term population decline in willow tits, induced by forestry, also in my study area.

The sample areas were as similar as possible due to forest composition within each type of forest. There were differences in composition of the natural forest and plantation forest due to tree density and heterogeneity. The natural forest had on average lower site quality due to productivity, and lower tree density than the plantation forest. Due to understory thinning the plantation forest had a relative dense canopy and open understory. Eggers and Low (2014) stated that this practice will affect the long-term population trends negatively, especially for willow tits. Contrary, the natural forest is characterized by an open canopy, with a more dense and scruffy understory. This is in accordance with characteristics on natural forest versus older plantation forest by two other studies (Okland et al., 2003, Kuuluvainen et al., 2012). In addition the amount of dead wood was relative low, especially in areas with plantation forest. The reduction in dead wood can be related to forestry (Kuuluvainen et al., 2012). Natural forests are maintained by partial disturbances which strongly differ from the disturbances.
caused by clear cutting practice. This may have severe ecological consequence such as less biodiversity (Kuuluvainen et al., 2012).

From an economical point of view it is most profitable to harvest timber in areas with highest productivity. Therefore it can be questioned if areas with present day natural forest initially had a larger portion of unsuitable habitat (e.g. more large bogs and mires) than the areas that have been logged. If that is the case, the two forest types may be more similar than expected, both lacking optimal quality of habitat for sedentary passerines. In this study this issue was not looked into, and further investigation must be done to quantify the percentage unsuitable habitat in the different forest types.

4.2.2 Population size

In this study, more than half of the time no birds were observed at the counting stations. When birds were observed usually just one or two were seen. The impression is that the population of small sedentary passerines at Varaldskogen was relative low, especially the population of willow tit. Several studies from both North-America and Europe have shown a decline in the population size for some chickadees and titmice due to habitat loss and climate change. For example the North-American boreal chickadee experienced a serious population decline from 1966 to 2004 (Hadley and Desrochers, 2008). Boreal chickadee is considered as vulnerable to habitat changes by modern forestry and Hadley and Desrochers (2008) suggested that the population declines were caused by loss of high-quality wintering habitat (Hadley and Desrochers, 2008). The Siberian tit is often considered as the ecological equivalent to the boreal chickadee and also this species has experienced a decline in Europe at the end of last century (Virkkala, 1990).

In Finland and Sweden the willow tit and Siberian tit, have experienced a serious decline during the last 40 years. The decline of the willow tit is reported to be more than 60%. At the same time the population of the crested tit has been stable (Väisänen, 2003; Lindström et al., 2009 in Eggers and Low, 2014). Forestry is also here suspected to cause this trend through the adverse effect by rapid landscape transformation (Jarvinen and Vaisanen, 1979, Siffczyk et al., 2003). In addition to habitat loss, climate change is assumed to have affected the negative population trend (Virkkala, 2016).
In Britain the marsh tit and the willow tit have suffered a serious decline from around 1970 to now. Both species are now on the national red list in UK (Baillie et al., 2014, Broughton et al., 2014). The marsh tit experienced a decline by 71% between 1967 and 2009. Habitat degradation and increasing competition from other tits, such as great tit and blue tit, has been suggested as causes to this decline (Broughton, 2012). It is reasonable to assume that great tit also can outcompete for example the willow tit and Siberian tit in Norway in terms of food and nesting sites. Feeding by humans allows the great tit to expand its distribution range.

During my field study I observed the great tit move from areas near human and into the forest late in the season. It is possible that great tit may outcompete the other tits due to nesting sites and foraging in the breeding season.

Presently natural forest remains less than 20% of the area at Varaldskogen, and thus over 80% is plantation forest. It is possible that the winter flocks need territories much larger than expected. This can explain the relative low frequency of observations. It is also in accordance with the resources dispersion hypothesis (RDH), which suggests that the territory size depends on the distribution of resource patches and thus the flock size should vary with the quality of the patches (Carr and Macdonald, 1986, Siffczyk et al., 2003). It is also worth noting that the remaining natural forest is at the suggested extinction threshold value for birds (Fahrig, 2003, Ovaskainen and Hanski, 2003). This alone can have had a negative impact on the small wintering passerines in the area.

However, the natural forest areas at Varaldskogen are larger than the presumed winter territory size of 25 ha. Therefore, it is not likely that forestry is the only reason for a possible low population density of sedentary passerines. Food availability can be a constraint for higher density and explain a low population density. Anyhow all sampling areas were mature forest and should therefore have provided enough food. Hoarding tits obtain food items also outside the territory and store them in trees in the territory (Haftorn, 1956). The "winter food limitation" states that when large areas are of suboptimal habitat with lower amount of food, it may affect the population size even if the area of optimal habitat is bigger than assumed size acquired for winter territory (Haftorn, 1956). In this study the actual amount of available food was not investigated, and therefore it is impossible to conclude that food availability is scarce in the area.
4.2.3 Community structure

Several studies refer to average flock size of around four individuals for willow tit and two individuals for crested tit (Ekman, 1979, Eggers and Low, 2014). In mixed flocks there are usually around 6-7 individuals of different species. The North-American parids may form even larger mixed flocks (Ekman, 1989). I never observed such flocks during my field work. In other words the flock sizes in Varalسكogen were less than expected. It has been suggested that flock formation is an adaptation to improved antipredator effect (Ekman, 1979), but the structure of the community is affected by a trade-off between food availability, predation risk and social dominance (Suhonen, 1993). The pygmy owl, which is the main predator during winter, was not observed during my study, but it may have been overlooked. Occasionally I played the sound of pygmy owl, but no reaction was observed doing this. This suggests that the predation pressure was low in the study area. Given that the forestry may have led to less food it may be a better choice to live solitary or in smaller flocks. Considering an assumption that predation risk is negligible there is likely that formation of bigger groups would be a disadvantage for survival. Flocks of tits are known to split into subgroups to forage when the risk of predation is low (Suhonen, 1993). Splitting up may increase the foraging efficiency and can explain the many observation of one or two individuals compared to bigger flocks. Flocks also shrink during winter because of mortality. My survey was done in late winter and therefore it is likely that the populations were lower than when the flocks emerge in autumn.

The crested tit is known as the social dominant species. Therefore it is likely that the higher rates of willow tits seen in plantation forest were caused by repression from crested tits, which is also in majority according to the censuses. But the results revealed that willow tit and crested tit appeared together more often than expected by chance. The significant difference in abundance of willow tit may therefore have other reasons than the social hierarchy found in flocks of tits. As suggested above, one explanation can be that willow tit can exploit edges and clear cuts better than crested tit. It is also known from other areas that while willow tit have had a population decline, that the population of crested tit have been stable (Eggers and Low, 2014). It is not unlikely that this can be the case in my study area too.
4.3 Effects of climate change

Together with forestry, climate change are main drivers of change in biodiversity today, but the combined effect is poorly known (Virkkala, 2016). A recent study by Virkkala (2016), shows that the total population of birds in Finland has declined on average 0.89% per year the last 12 years. The largest decrease had willow tit, with a decline to less than one third of the initial population (Virkkala, 2016). Forestry practice has been stated to reduce suitable wintering habitat and carrying capacity for especially willow tit (Siffczyk et al., 2003). The Norwegian population may have had a similar decline which may explain the difference in population size between crested tit and willow tit.

As mention above, mean flock size of willow tit is assumed to be approximately four and for crested tit two individuals, which means that willow tit have been more abundant. In Finland the mean weighted density of willow tit populations has moved north during the last 40 years (Virkkala, 2016). Therefore it is most probably a combined effect of both forestry and climate warming explaining the serious population decline for the species. Although it seems that crested tit may have adapted better to habitat changes it is not unlikely that also crested tit will experience a negative trend due to the combined effect of climate change and forestry.

Contrary to the effects on Siberian tit and willow tit, the partly migratory great tit and blue tit may benefit from the climate changes. Higher winter temperature may lead to less migration and an increasing sedentary population of these tits (Nilsson et al., 2006) as well as increased human winter feeding. But studies done on this is not unambiguous, and more studies should be done. Anyhow, if the winter populations of great tit and blue tit increase, this will lead to higher inter-specific competition for resources which again can have a negative impact on the subordinate species (relative to great tit) like the willow tit, crested tit and Siberian tit.

4.4 Limitations and further studies

Studying how forestry and climate change may have an impact on population size and community structures in sedentary birds need observations over time to be able to detect any possible changes. Censuses from just one year will not catch up natural annual population fluctuations and it will neither show how populations develop over time.
The survival of sedentary birds depends on that their home range meets their requirements during the whole year, in other words shelter and enough food in winter and good nesting sites in summer. Parids are hoarders and need good caching sites. I did not look into the possibilities to hoard in the different forest types. Differences in understory and shrub layers, and the amount of food were not examined due to lack of time.

Further studies should aim to, in greater extent, quantify any possible differences between the forest types. Also nest site and breeding success should be investigated in larger scale. Bird ringing could be used to distinguish the different individuals and to get a better understanding of movements. I think it would be important to gain knowledge of the annual cycle, to get a better understanding of how forestry and climate changes may affect the populations of parids. Also the impact of bigger clear-cuts and saplings should be investigated. A space for time approach is a possible way to see how modern forestry may affect bird populations over time. In such approach areas with different successional stages can be used as substitute for studying one area over long time (i.e 60-70 years). Studying forest areas in different successional stages could give a picture on how impacts by forestry will affect the bird populations over long time.
5 Conclusion

The parids clearly have some general patterns of habitat preferences. It seems that the North-American species are ecological equivalents to the European ones. Studies on parids in North-America may therefore also apply for European species and vice versa.

A lot of studies have been performed on habitat selection in parids, and mostly they conclude that modern forestry has a negative impact. Natural forest is assumed to be the preferred habitat, but from my study I found that older plantation forest did not seem to differ much from natural forest as habitat for the winter flocking tit mice. In Norway forest management has changed from clear-cutting to retention systems the last decades. This is assumed to reduce the impact on biodiversity remarkably. Therefore present forestry may affect the bird populations less than old fashion clear cutting.

Other studies have showed that populations of willow tit have had a serious decline elsewhere in Europe. This may also be the case in Norway because in my study I observed few willow tits. Hence, for this species, it will be important to protect the habitat, i.e natural forest.
References


Appendix 1

Measurement of the site quality due to forestry in my sample areas. The data was extracted from forest reports requested from the map resource Kilden at NIBIO.

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<tr>
<th>Area</th>
<th>Size (daa)</th>
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<th>Low site quality</th>
<th>Unproductive forest</th>
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Appendix 2

List of the song and calls used in the field work. The sound mix was played shuffled.

1. Willow tit
2. Crested tit
3. Coal tit
4. Goldcrest
5. Treecreeper
6. Willow tit song and call
7. Coal tit
8. Crested tit
9. Goldcrest
10. Great tit