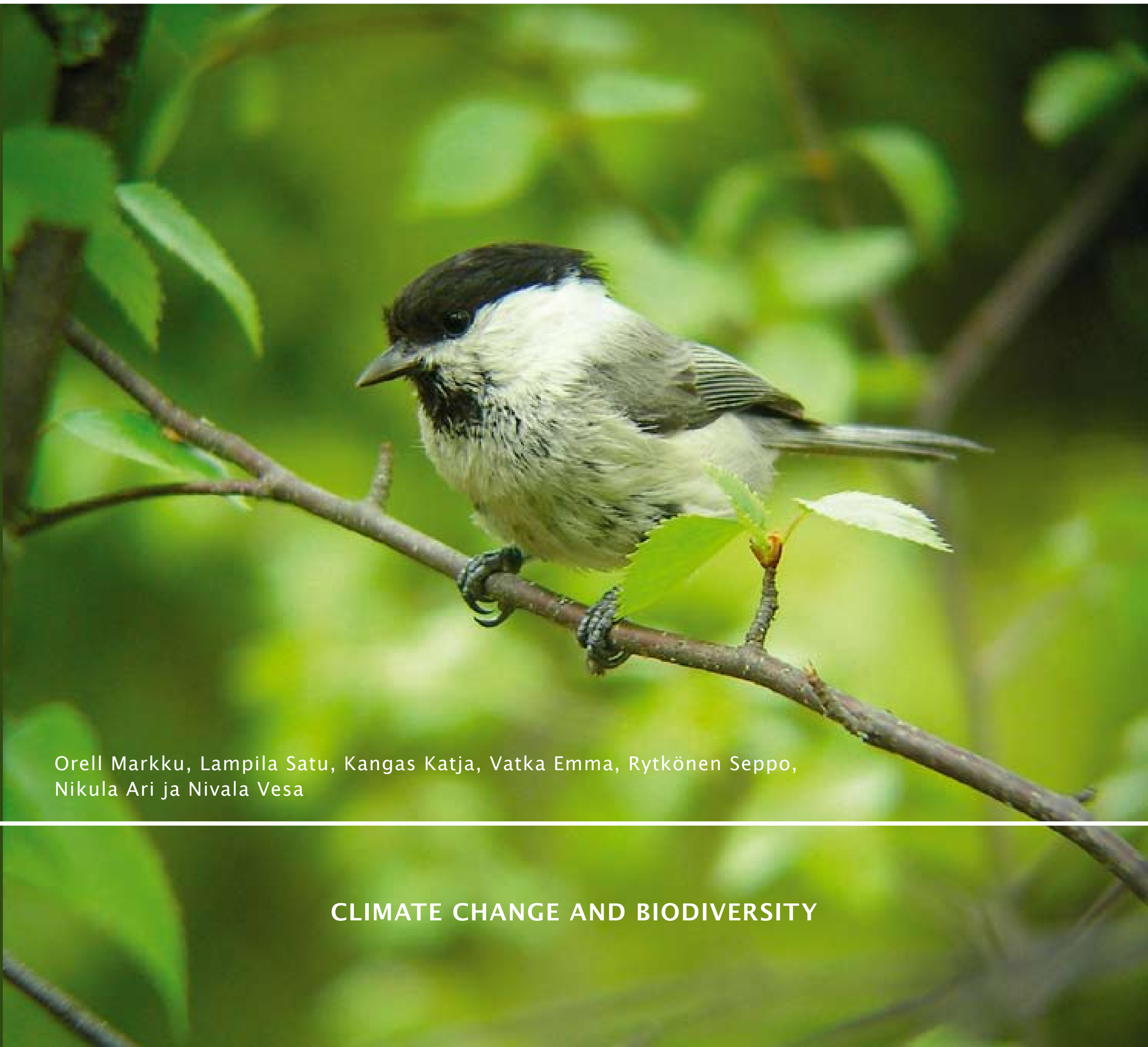
Climatic and Habitat Contributions to Populations of Managed Forest Landscapes



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CLIMATE CHANGE AND BIODIVERSITY

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Contents

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SUMMARY

Human-induced habitat destruction and climate change are two major deterministic threats to global biodiversity. Climate warming has caused changes in phenology e.g. in timing of birds' breeding season related to the food availability, which affects the breeding success. Modern forestry causes a threat to many forest-dwelling species, as it reduces and fragments habitats and declines their quality. We studied shifts in timing of reproduction in a boreal sedentary passerine, the willow tit (Poecile montanus), and the food availability in relation to the climate warming. To get better tools for conservation we studied the habitat characteristics determining nest site selection of the species in a managed forest landscape using generalized linear models. Willow tits' laying dates as well as the caterpillar food availability have advanced during the past decades, well explained by increased spring temperatures. Synchrony with the food availability has improved. The availability of nest-sites, i.e. standing rotten deciduous trees, is the most important factor affecting habitat selection. Our results indicate that the willow tit has a broad habitat preference, as it can establish breeding territories in fragmented forests and does not require mature or intact habitats for breeding. Today's forestry practices decrease the amount of dead wood and prevent the formation of new decaying trees and thus nest-sites for primary hole-nesting species. The benefits from improved sychrony will unlikely compensate the damages caused by forestry since the long term population trend has been declining. Forestry practices need to be amended to ensure the continuity in the availability of rotten wood.

Introduction 1

■ Human-induced fragmentation and destruction of habitats together with climate change are the major deterministic threats to global biodiversity. Recent climate change has caused changes in physiology, phenology and population dynamics of many species (Walther *et al.* 2002, Parmesan & Yohe 2003). At the local scale the effects of climate on populations may depend on habitat patterns. Interaction of climate change and habitat fragmentation may promote synchronous population changes and hence increase the risk of regional population declines (Travis 2002, Opdam & Wascher 2004). Taking into account the effects of climate change on (meta)populations, biodiversity research and conservation strategies are facing the challenge to integrate local scale population dynamics with land use changes and climatic fluctuations.

Modern forestry leads to the reduction of the total amount of suitable habitat resulting in heterogeneous landscapes with pure habitat loss and fragmentation effects (Andrén 1994). So far, avian studies have addressed to the effects of forest fragmentation or landscape on survivorship, distribution and movements of permanent-resident species in mid-latitudes (e.g. Doherty & Grubb 2002, Desrochers & Bélisle 2007, Olsson & Grubb 2007) or species richness in higher latitudes (e.g. Luoto *et al.* 2004) in fragmented agricultural mosaics. Thus there is a call for studies focusing on boreal managed forests (e.g. Pakkala *et al.* 2002, Brotons *et al.* 2003).

Populations of many boreal forest bird species have declined along with intensive forest harvesting (Helle & Järvinen 1986, Väisänen *et al.* 1986, Väisänen *et al.* 1998). Human-induced changes in landscape structure (habitat loss, fragmentation and decline in quality) threaten the viability of natural populations of boreal forest specialists. Deforestation can impair the winter survival of the forest associated sedentary species by reducing the carrying capacity of the habitat (e.g. Siffczyk *et al.* 2003). The forest cover may have remained the same but the composition and age structure of forests have dramatically changed from mature forests to young monoculture plantations (Kouki & Väänänen 2000). In addition, logging or thinning has decreased the amount of dead trees in forests destroying living conditions of many species depending on decaying wood. For cavity-nesting species, the availability of nest holes is essential and their deficiency can limit their population size (e.g. Stauffer & Best 1982, Raphael & White 1984, Li & Martin 1991). The presence of primary cavity-nesters, such as woodpeckers and some Parids, is beneficial to secondary hole-nesting species through the availability of old nest holes.

The increase in ambient temperature has influenced a great variety of biological systems including the timing of reproduction (Walther *et al.* 2002, Parmesan & Yohe 2003), an important fitness-related life-history trait in birds (e.g. Perrins 1970, Dunn 2004). The increase in spring temperature can lead to the advancement of optimal breeding conditions by shifting the timing of food resources, essential for feeding the young. As a consequence birds are expected to advance their breeding accordingly if they behave in an adaptive way (Visser *et al.* 2004, Both *et al.* 2006). The nestling period is mainly determined by the onset of egg-laying (e.g. Cresswell & McCleery 2003), long before direct information is available about the food availability in the nestling period (Visser *et al.* 1998). Spring temperatures induce the emergence of invertebrates and may thus be used as a predictive factor, "a cue" of the future food availability (e.g. Visser *et al.* 1998). Spring temperatures also affect food availability (Perrins 1965, Bryant 1975) and thermoregulatory costs in the early stages of breeding (e.g. Stevenson & Bryant 2000). Perrins' (1965, 1970) energy limitation hypothesis suggests that this kind of constraining factors prevent birds from breeding earlier. For foliage-gleaning insectivores, such as Parids, caterpillars feeding on deciduous trees are the main food for nestling provisioning (Perrins 1991; Rytkönen *et al.* 1996). Well timed broods produce more and heavier fledglings, recruiting to the breeding population more likely than young from ill-timed nests (Tinbergen & Boerlijst 1990, Nager & van Noordwijk 1995, Visser *et al.* 2006).

For understanding the potential risks of climate change to biodiversity we need to know whether a species has potential to persist in a landscape that has suffered from a certain stage of habitat loss. Thus an important question can be raised: which species are able to keep pace with global climate change in a fragmented landscape? In iteroparous animals information about survival or population growth rate in fragmented landscapes is scarce thus far. We have investigated the population dynamics affected by the climate change and habitat fragmentation by studying a sedentary bird population in managed boreal forests. Our model species, the willow tit (*Poecile montanus*), has declined drastically in numbers in Finland and Fennoscandia since the 1940's (Väisänen *et al.* 1998), but the decline seems to have slowed down during the early 2000's. The research capitalizes on the unique combination of precise individual based demographic data as well as long-term time series, habitat quality measures derived from the Finnish multi-source forest inventory and climate data.

To gain more information on the effects of climate and environmental changes on the breeding performance in boreal forest habitats we focused on the following main questions. 1) With our long-term data we investigated, are there any shifts in timings of reproduction in the boreal sedentary passerine and the caterpillar abundance, the main food used for nestling provisioning, due to climate warming. To get better tools for conservation we studied, 2) what are the habitat characteristics determining nest site selection of the species in a forest landscape under continuous changes due to logging and thinning. Our ultimate goal is to elucidate the question, how species can cope with the global change.

The research is significant since we use a multidisciplinary approach by combining methodologies starting from remote sensing and analyses of life-history traits such as the timing of breeding. In addition to this general scientific interest, our project provides information which is directly applicable to the development of biodiversity assessment practises that better meet the requirements of the sustainable use of natural resources and land use planning.

This report is a compilation of a published paper (Vatka et al. 2011) and a manuscript (Kangas et al. 2011) that is due to submitted in September. The unpublished results will be given here only as a preliminary writing. Printing figures and tables in advance could hinder the paper be accepted to a high standard journal of ecology.

Methods 2

2.1. Study species and study area

■ The willow tit is a resident forest passerine and highly site tenacious after the juvenile establishment and first breeding (average breeding dispersal distance 244 m, Orell *et al.* 1999). The species is a primary hole nesting year round resident passerine (Orell & Ojanen 1983b). In most cases the pairs excavate the nesting holes in decaying stumps, mainly birch (*Betula* spp.), each breeding season (Orell & Koivula 1988) but can occasionally adopt already made holes or nest-boxes for breeding. During the nestling period, the parents feed the young with invertebrates, mostly caterpillars (e.g. *Epirrita autumnata*) if available but also with Diptera (Tipulidae, Culicidae), spiders Arachnoidea and aphids Aphidoidea. The proportion of caterpillars in the nestling diet can increase up to over 80 % when the caterpillar peak coincides with the nestling period (Rytkönen *et al.* 1996). Postnuptial moult takes place in summer shortly after breeding (Orell & Ojanen 1980). The early start of moult is an adaptation to the short summer, ensuring time for caching food for future use. During hoarding period in autumn and early winter, individuals build up external reserves of animal and plant food (Brodin *et al.* 1996), which later in winter can constitute up to two-thirds of the daily energy requirements (Haftorn 1959).

Willow tits spend winter in non-breeding, social, territorial flocks (Matthysen 1990), formed in late summer, when pair bonding also starts (Ekman 1979). Juveniles become settled within two months after independence (Ekman 1979). The core of the winter territory usually consists of a breeding territory of the adult pair from the previous season, and two to four non-kin juveniles (Ekman *et al.* 1981, Koivula & Orell 1988) or of three to five adult birds (Haftorn 1990, Lahti *et al.* 1996). The group members defend the territory against the intrusion of other conspecific groups. However, territoriality is not as strict as in the breeding season and territories may occasionally overlap (Haftorn 1999). Mixed species flocks (Haftorn 1990) seldom occurred in our study area (Koivula & Orell 1988, Lahti *et al.* 1996).

We collected the data in the Oulu area, northern Finland (65° N, 25° 30 E). The study area, currently 24.9 km^2 wide, consists of a mosaic forest landscape, clearly affected by forestry. The total area of clear-cuts has been on average 23 ha annually. Coniferous, deciduous and mixed coniferous forests are interspersed with saplings of different age, clear cuts, fields, and natural open areas such as treeless bogs, a small river and two small lakes. The dominating tree species consist of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) (Orell & Ojanen 1983b, Orell & Koivula 1988). Similar habitat types continue outside the study area.

2.2. Data collection

2.2.1. Breeding data

We used the long-term data on the reproductive biology and winter ecology of the model species, gathered since 1975 until present. By intensive monitoring of the population before and during the breeding season – from early April to late June – we were able to locate the territories and find all the nests and identify the non-breeding individuals (Orell *et al.* 1994). In monitoring the taped territorial song of the willow tit was played back in forest habitats of the study area which helped in locating the territory owners and unpaired individuals of both sexes. We determined the commencement of egg-laying, clutch size and time of hatching during routine inspections of the nests (Orell & Ojanen 1983a). For the analyses we used the annual median dates for the commencement of egg laying and hatching. We estimate that no more than 1–3 broods (out of 70–170 broods) annually escaped our attention (Orell *et al.* 1999).

2.2.2. Caterpillar abundance

The abundance of caterpillars foraging on birch was estimated for 1996 – 2009 using the frass-fall method (Zandt 1994) according to Rytkönen and Orell (2001). The caterpillar biomasses were estimated approximately weekly. We determined annual dates for caterpillar biomass peaks and initial and latter thresholds using a threshold limit of 0.1 g/m^2 to reflect the emergence and decline of the caterpillars. The peak date is the midday of the measurement period when the biomass is at its highest. The threshold date is the midday of a measurement period if the average biomass value of the period equals 0.10 g/m^2. In case the threshold limit is in between of the average biomasses of two consecutive periods, the threshold date is the first day of the latter measurement period.

2.2.3. Weather and habitat data

Our data of daily mean ambient temperatures come from Oulunsalo observatory (Finnish Meteorological Institute), situated ca. 20 km S of the study area.

For analysing nest site selection, we used willow tit nests site data from 1999 (163 nests, including 6 repeat nests) and 2004 (120 clutches including 3 replacement clutches). The breeding density was 6.1 and 4.5 pairs/ km^2 in 1999 and 2004, respectively. We compared the composition of these breeding territories with the overall habitat composition of the whole study area by selecting randomly the same number of points without willow tit nests (random points) as there were nests in the studied years. The random points could occur inside the study area in all habitat types except in water. The distance between a real nest and a random point was restricted to be at least 113 m to prevent overlap between the random points and nest points at the smallest studied scale. Around each nest and random point buffers of 1 ha, 4 ha and 34 ha were created. One ha buffer (radius 57 m) was selected to describe the territory core area and it is the smallest area from which the habitat variables (details below) could be calculated with reasonable accuracy. Four ha (radius 113 m) was chosen to roughly describe the surroundings of the nest hole where most of the foraging trips take place. For example, the great tits typically forage within 50 – 300 m from the nest (Rytkönen & Krams 2003). 34 ha (radius 329 m) buffer represents the observed maximum winter territory size and it is here referred to as the landscape scale (Siffczyk *et al.* 2003).

Variables describing the forest and other land use characteristics of the study area were derived from digital output maps of Finnish Multi-Source National Forest Inventory (MS-NFI) database (Tomppo et al. 2008). MS-NFI produces estimates for tree volume, age and other parameters for each tree species for every 25 m × 25 m land area. Digital maps of inhabited areas, agricultural fields, roads and other non-forest areas are used during the operation to separate forests from other land use areas. For the year 1999 breeding data we used MS-NFI data from 1992 and for 2004 from the year 2002. Due to time difference between breeding data and MS-NFI data younger forest classes are somewhat overrated especially for 1999 breeding data. Clear cuts that were more recent than the satellite images were digitized by hand from aerial photographs and our own field observations. For the analysis MS-NFI data was further classified to eight different forest and other land use classes.

For each radius, we calculated altogether 12 explanatory variables. For each habitat type we calculated proportion of the type (%LAND, %), mean patch size (PATCH, ha), and edge density (EDGE, m/100 ha) using FRAGSTATS (McGarigal & Marks 1995). However, in modelling PATCH and EDGE were only used for the buffer sizes of 4 ha and 34 ha. The other variables considered were the distance from the nest to the nearest ditch (DITCH, measured from base maps and calculated regardless of the buffer size, i.e. the value is the same for all the scales) and the amount of dead standing birches for excavating the nest hole (SNAG) within each buffer size.

Eight of the explanatory variables (Table 1) were percentages of different habitat types: coniferous forests (timber volume ≥ 40 m^3/ha) on mineral soil (CONF) and on peatland (CONPF), deciduous forests on mineral soil (DECF) and on peatland (DECPF), and mixed forest on mineral soil (CONDECF). Additionally, we included peatlands with thin or young deciduous (DECP) or coniferous (CONP, including pine sapling stands) forest (5 – 40 m^3/ha). Lakes and rivers, roads, power lines, clear cuts, open bogs, settlement areas and fields were considered open areas (OPEN), mean patch size of DECF, CONDECF, DECPF and CONPF combined (PATCH ha) and the amount of egde (m) of an open habitat (EDGE). The PATCH and EDGE variables were used for the 4 ha and 34 ha buffers.

2.3. Effects of climate change

2.3.1. Temporal trends and correlations

To illustrate the climate warming, we counted average mean daily temperatures for each date of the first half of the year for a reference period 1961 – 1990 and compared it with the average temperatures of a later period 2001 – 2010. We studied temporal changes in the timing of willow tit median laying dates and caterpillar peak dates by regressing them on calendar year.

We applied correlation analysis to look for the association between annual breeding time, ambient temperature and food availability (see e.g. Orell & Ojanen 1983a). We averaged daily mean temperatures for all time periods with lengths varying from 7 to 181 days, by altering the beginning and end dates of the periods in one-day intervals between 26 December (previous year) and 24 June (current

Table 1. Description of the habitat variables used and the buffer areas (ha) around the nest and random sites tested.

Variable name	Description	Buffer (ha)
CONF	% of coniferous forest (40 m^3/ha, conifers ≥ 60 % of total timber volume)	1, 4, 34
DECF	% of deciduous forest (40 m^3/ha, deciduous trees ≥ 60 % of total timber volume)	1, 4, 34
CONDECF	% of mixed forest (> 40 m^3/ha, conifers < 60 % and deciduous trees 1–59 % of total timber volume)	1, 4, 34
DECPF	% of deciduous peatland forest (> 40 m^3/ha, deciduous trees ≥ 60% of total timber volume)	1, 4, 34
CONPF	% of coniferous peatland forest (> 40 m^3/ha, conifers ≥ 60% of total timber volume)	1, 4, 34
DECP	% of deciduous peatland (5 – 40 m^3/ha, deciduous trees ≥ 60 % of total timber volume)	1, 4, 34
CONP	% of coniferous peatland (5 – 40 m^3/ha, conifers ≥ 60 % of total timber volume)	1, 4, 34
OPEN	% of open (0 – 4 m^3/ha, water, settlement areas, clear cuts, open bogs, fields)	1, 4, 34
DITCH	distance from the nest to the nearest ditch	1, 4, 34
SNAG	number of dead standing birch trees	1, 4, 34
PATCH	mean patch size of DECF, CONDECF, DECPF and CONPF combined (ha)	4, 34
EDGE	amount of edge (m) of an open habitat	4, 34

year). We computed Pearson's correlation coefficients between all of these temperature periods and the median laying dates and caterpillar peak dates. The temperature periods with the strongest correlations were chosen. For the caterpillar peak dates we used temperature data from the years 1996 – 2009. We searched the best correlating temperature period for the median laying dates from the entire study period 1975 – 2009 and the years 1996 – 2009, from which caterpillar biomass data are available. We explored climatic warming also by calculating the linear regressions of the temperature periods found on calendar years.

2.3.2. Synchrony of the food peak and timing of breeding

To study the synchrony of the food peak and timing of breeding we calculated the differences between the annual median hatching dates and initial and latter caterpillar threshold dates and the caterpillar peak dates. The food requirements of the willow tit nestlings are the highest at 8 – 13 days after hatching (Rytkönen et al. 1996), so the food peak should coincide with this time for breeding to be the most successful. The synchrony is interpreted in two ways. First, we consider the peak dates only – for the timing of breeding to be advantageous, the caterpillar peak date should co-occur with the period of the highest food demand. In another way of thinking, the caterpillar food should be abundant during this period, regardless of the peak date itself. Here we define "abundant" to be over the threshold value of 0.1 g/m2 of caterpillars. Parids use caterpillars as the main food source already at this level of caterpillar biomass (our unpublished data).

2.4. Habitat selection

2.4.1. Preliminary analysis

The relationship of calculated habitat variables was investigated with Spearman´s correlation. Most of the correlations were moderate ($r_s < 0.5$). On 4 ha and 34 ha scale the correlations between DECF and CONDECF ($r_s = 0.61$ and $r_s = 0.84$) and OPEN and EDGE ($r_s = 0.67$ and $r_s = 0.57$) were relatively high. To get an overall impression of the habitat preference or avoidance of the willow tit we compared the mean amount of each habitat type (%) between the nest and random point buffers with Wilcoxon rank sum test for both years and each buffer size.

2.4.2. Spatial autocorrelation

Autocorrelation is a common property of spatially sampled ecological variables and it violates the assumption of independent observations in statistical tests. To investigate spatial autocorrelation in the data we calculated Moran's I with function "Moran.I" in package ape in program R. The value of Moran's I indicated autocorrelation in 1999 (Moran's I = 0.014, P = 0.001), but not in 2004 (Moran's I = 0.004, P = 0.247). To examine the spatial pattern in more detail we plotted the spline correlograms ("spline.correlog" in R library ncf) with the maximum lag distance of 6800 m, which was the largest distance between nests in the area (Rhodes *et al.* 2009). The correlograms did not reveal strong autocorrelation except possibly at the short distances of 200 – 250 m. Therefore, we used autocovariate regression to account for the spatial correlation in the response variable and created a new explanatory variable, autocovariate (AC), with function "autocov_dist" in package spdep in R. (Dormann *et al.* 2007).

2.4.3. Modelling habitat selection

The response variable for the analyses was the presence or absence of a willow tit nest in a given location (PA). We used generalized linear models (GLM) to investigate the relative importance of different habitat variables in explaining the nest site selection. Because the response variable was binary, a binomial probability distribution and logit link function were used in analyses. We used the information-theoretic approach in model building and selection (Burnham & Anderson 2010). We created a set of 35 (for 1 ha buffer) and 49 (for both 4 ha and 34 ha buffers) competing models. AICc (AIC corrected for small sample size) differences (ΔAICc = model AICc – minAICc, which is the lowest AICc value in the model set) and AICc weights (AICc w) were used to rank the fit of each model to the data (Burnham & Anderson 2010). The best model is the one with the lowest

AICc value. The models were built to permit calculating Akaike weights for each variable separately to assess their relative importance for the willow tit, i.e. each variable was included in equal numbers (12 models) in the model sets. Because we assumed that willow tits prefer habitats with high density of deciduous trees and high soil water content, we grouped habitat variables to represent forests in general (CONF, DECF and CONDECF), conifer-dominated habitats (CONF, CONPF), deciduous tree-dominated habitats (DECF, CONDECF, DECPF, and DECP) and peatland habitats (DECPF, CONPF and DECP). The model fit with and without the autocovariate variable were compared to assess whether the inclusion of AC resulted in lower AICc values indicating improved model fit. The uncertainty in model selection was taken into account by averaging the parameter estimates and their standard errors over all the modes within $0 < \Delta\text{AICc} < 4$.

2.4.4. Variation partitioning

We used the partial regression analyses (Borcard *et al.* 1992) to determine the relative effects of habitat variables at different spatial scales. The variance of nest site occurrences in both study years was partitioned into eight components: pure effects of a) territory core (1 ha), b) foraging area (4 ha) and c) landscape (34 ha), the joint effects of d) territory core and foraging area, e) territory core and landscape, f) foraging area and landscape, g) variables at all the three investigated spatial scales, and h) unexplained (residual) variation. As predictor variables at three spatial scales, we used the variables that were included in the GLM models with $\Delta\text{AICc} < 2$. Partial regression analyses with redundancy analysis (RDA) were done using the vegan package in R (Oksanen *et al.* 2008).

Results

3

3.1. Climate change

3.1.1. Temporal trends in temperature, timing of breeding and food abundance

■ The daily mean temperatures show uneven increase in the first half of the year in the 2000's compared with the reference period of 1961-1990 (Fig. 1). The relationship is not straightforward since the most pronounced warming has taken place in the two winter months, prior to and partly during the laying period (late April – early May). In the second half of May and in June temperatures have remained unchanged.

According to the whole data set (1975 – 2009), the average yearly median onset of egg-laying was on 13 May (SD = 3.88), in 1996 – 2009 two days earlier (SD = 2.86). The caterpillar peak date occurred on average 40 days after the median egg-lay-

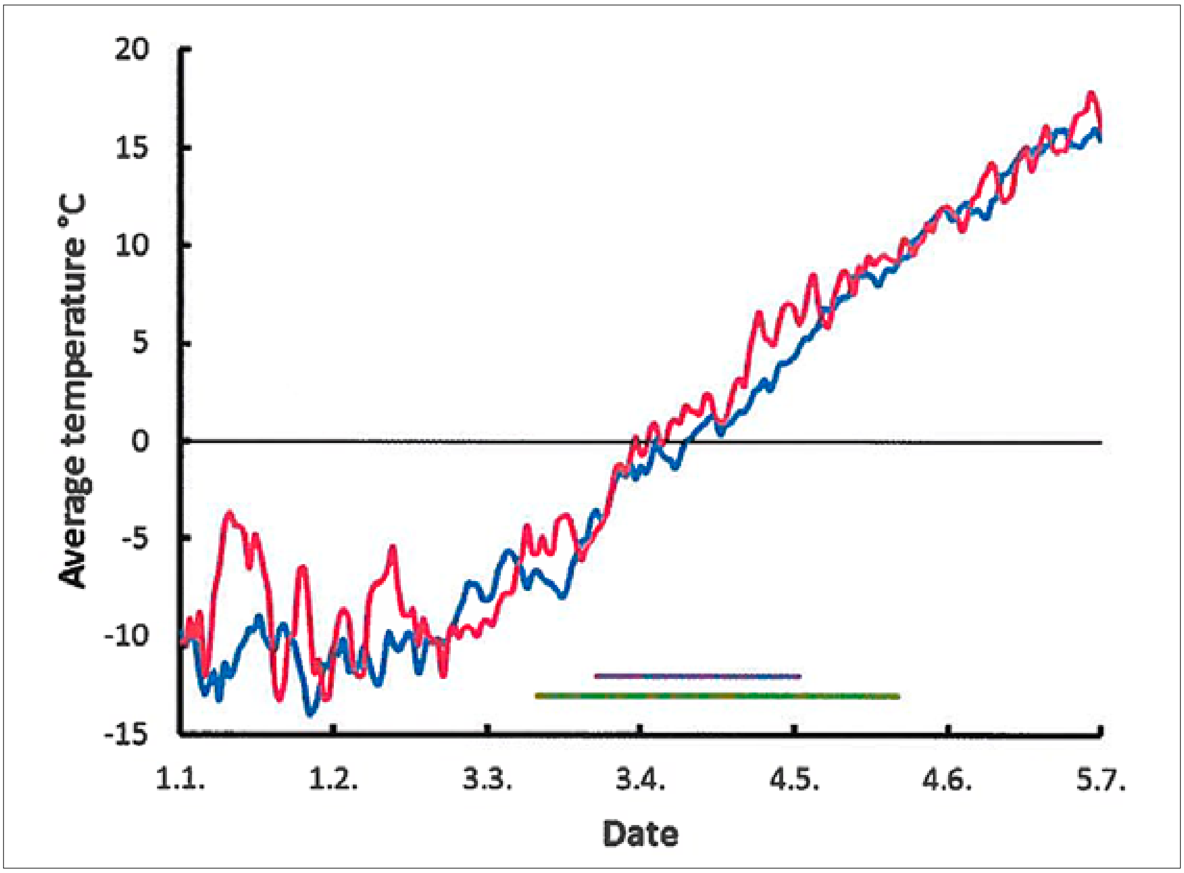

Fig. 1. Daily variation in ambient temperature (average of daily mean values) during January – June at the Oulunsalo observatory in two periods 1961–1990 (reference period, blue line) and 2001–2010 (red line). Horizontal lines depict the temperature periods showing the strongest correlation with the median laying date of the willow tit (violet) and with the caterpillar peak date (green).

ing date. Thus, willow tits generally bred too early to match the period of the highest food demand with the caterpillar peak – for a perfect match the time gap between the first egg day and the caterpillar peak date should have been 32 days (8 days of egg-laying + 14 days of incubation + 10 days = 32 days, Orell & Ojanen 1983a, b).

The median egg-laying date of willow tits advanced 0.16 days a year (S.E. = 0.060, p = 0.012) during the 35-year study period (1975 – 2009, Fig. 2). When considering years 1996 – 2009, the trend was more pronounced, although not significant (b = -0.24, S.E. = 0.185, p = 0.217). The caterpillar peak dates advanced by 1.02 days a year (S.E. = 0.470, p = 0.050) in 1996 – 2009. The regression coefficient of the median egg-laying date does not differ significantly from the regression coefficient of the caterpillar peak date (t = -1.552, S.E. = 0.505, p = 0.134). An exceptionally cold spring in 1997 may result in an overestimation of caterpillar advancement rates on a longer time scale. When 1997 was excluded from the analysis, the slope of the caterpillar peak date was less pronounced (b = -0.609, S.E. = 0.414, p = 0.169).

3.1.2. Pre-breeding temperatures related to timing of breeding and food abundance

The temperature period resulting in the highest correlation with the median laying date of willow tits was 27 March – 6 May when using data from the years 1975 – 2009. For the years 1996 – 2009 it was practically the same, 25 March – 5 May (Table 2). For the caterpillar peak date the best correlative temperature period was 13 March – 25 May (Table 2). According to a linear regression model (Fig.3) the median laying date advanced 1.77 days when the mean temperature of the period 25 March – 5 May rose by one centigrade (S.E. = 0.264, $p < 0.001$, $r^2 = 0.788$). The caterpillar peak date advanced 4.34 days (S.E. = 1.018, p = 0.001, $r^2 = 0.602$) per one centigrade increase in mean temperature. There were no significant year factors for the median egg-laying date or the caterpillar peak date. The regression coefficient for the median laying date differed from the regression coefficient for the caterpillar peak date (t = -2.446, SE = 1.0519, p = 0.022). Willow tits and caterpillars respond with different rates to the warming of the spring period.

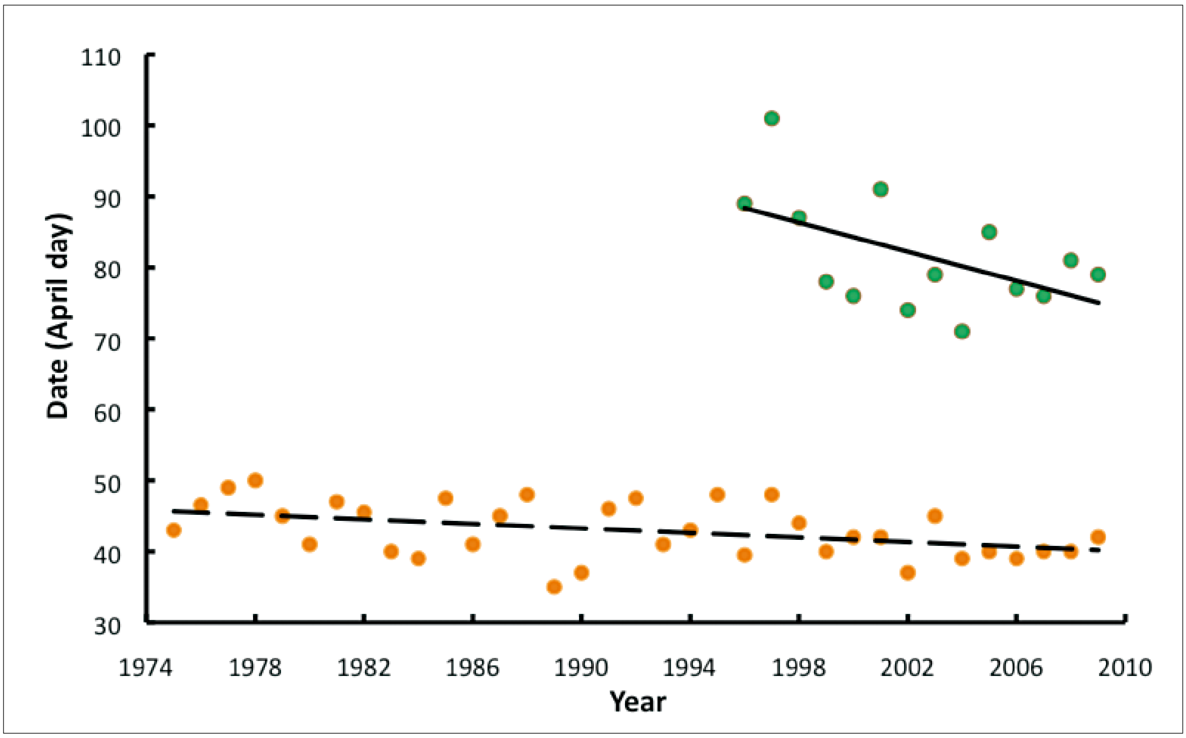

Fig 2. Advancement of median egg laying date (orange circle) and caterpillar biomass peak date (green circle) during the study period. The dashed line is the linear regression line for the laying date (b = -0.160, SE = 0.060, P = 0.012) and the solid line for the caterpillar peak date (b = -1.024, SE = 0.470, P = 0.050). Modified from Vatka et al. (2011).

The best correlative periods (in the willow tit and the caterpillars) coincide partly with the time of increased spring temperatures (Fig 1). The mean temperatures of these spring periods had rising non-significant trends (Table 2).

3.1.3. Synchrony between timing of breeding and food abundance

The timing of the caterpillar food peak in relation to median hatching dates fluctuated in 1996 – 2009 (Fig. 4). The caterpillar peak date coincided with

Table 2. a) The best correlative temperature periods with timing of breeding and food abundance, and b) the rise (b ± SE) of the mean temperatures of these periods (°C/year). Modified from Table 1 in Vatka et al. (2011).

		a) Best correlative period			b) Rise of temperature	
Variable	Years	Temperature period	r	df	b (SE)	p
Median laying date	1975–2009	27 March – 6 May	−0.847***	34	0.042 (0.023)	0.074
	1996–2009	25 March – 5 May	−0.888***	13	0.140 (0.091)	0.147
Caterpillar peak date	1996–2009	13 March – 25 May	−0.954***	13	0.145 (0.073)	0.070

*** $p < 0.001$

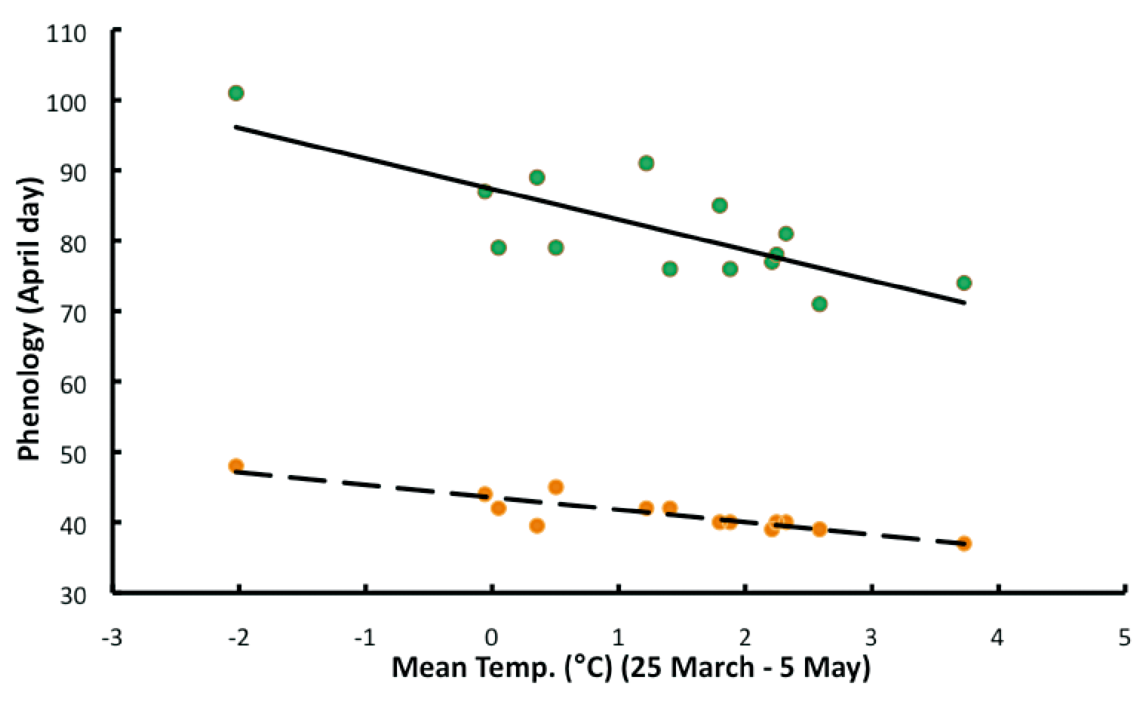

Fig 3. Laying date (orange circles) and caterpillar biomass peak dates (green circles) against the mean temperature of March 25–May 5. The dashed line is the linear regression line for the laying date and the solid line for the caterpillar peak date on temperature. Modified from Vatka et al. (2011).

the period of the highest food demand in two years (2000 and 2004, Fig. 4). Caterpillars were abundant (i.e. caterpillar biomass was over the threshold limit of 0.1 g/m^2) during the period of the highest food demand in seven years (1999, 2002, 2003, 2004, 2005, 2006 and 2007). By this contemplation, no signs of increasing asynchrony can be seen (Fig. 4). Actually, the timing of breeding has matched better with the food peak in the second half of the study period (2003 – 2009) than in the first half (1996 – 2002).

years. At the territory and foraging area scales the coniferous forest habitat in the occupied sites was as common as in the non-occupied sites in 1999. In 2004 the respective habitat was underrepresented around the nests. Coniferous peatland forests are found more often in willow tit nesting habitats than in random sites, the difference being pronounced in 2004. Open areas were avoided. Patches were of similar sizes whereas edges were more pronounced in the random site buffers than around nest sites. The difference was significant for the 4 ha buffer for

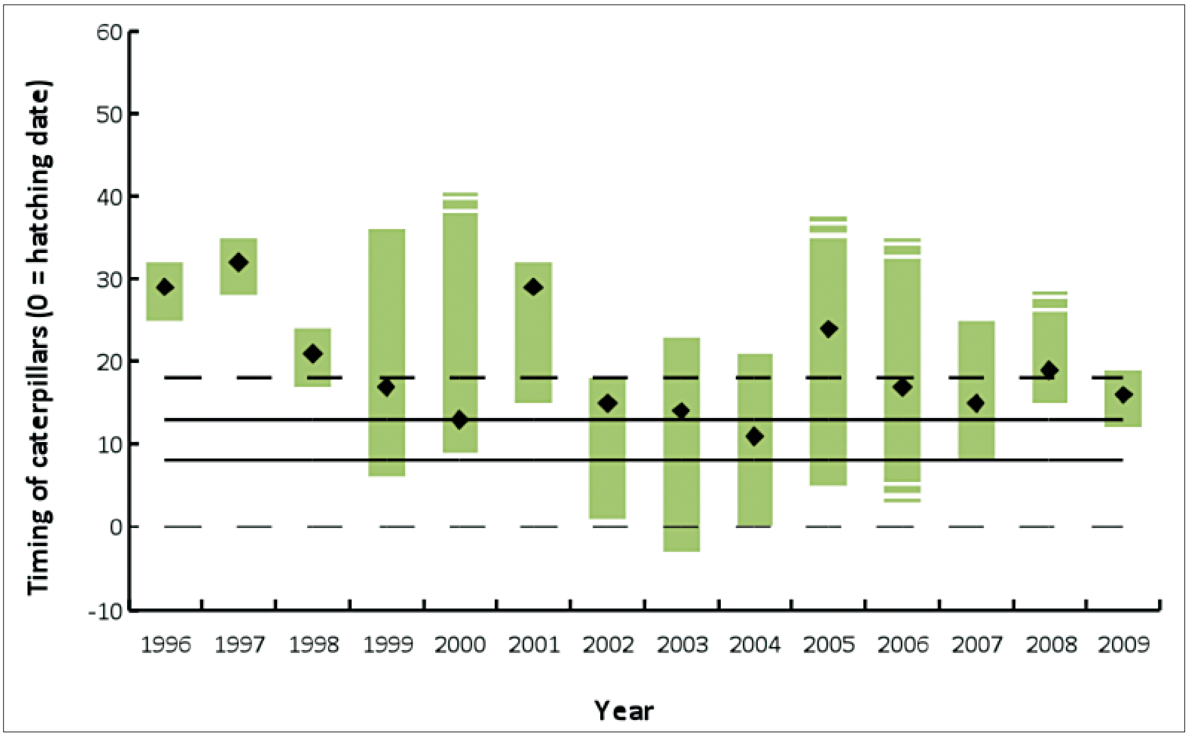

Fig. 4. Timing of the caterpillar abundance in relation to the median hatching date of willow tits (0 = the hatching date) in 1996–2009. Green bars present the period when the caterpillar biomass tops the threshold level of 0.1g/m^2. For some years, the threshold dates were not met during the frass-fall measurements – absent data is indicated with broken bars. The caterpillar biomass peak dates are indicated with dots. Average nestling period (from hatching to 18 days old) is marked with broken lines. The greatest demand for food takes place when the nestlings are approximately 8–13 days old (marked with solid lines). Modified from Vatka et al. (2011).

3.2. Habitat selection

3.2.1. Results from the preliminary analysis

Habitat structures around nest and random sites differed from each other at all buffer levels. The direction of the difference was consistent across both years ($P < 0.01$, $\bar{x} = 111$ m) and for the 34 ha buffer in 1999 ($P < 0.05$, $\bar{x} = 298$ m). Distance to the nearest ditch was significantly shorter from a nest (67 m) than from a randomly selected point (110 m, $P < 0.005$). The number of birch snags within the buffer was always significantly larger ($P < 0.01$ for all tests) for the nest sites than for the random points. On average, there were 1.8 snags around the nest site and 0.3 snags around the random point within the 1 ha buffer (4 ha: 3.5 *vs*. 1.0, 34 ha: 14.6 *vs*. 11.2).

3.2.2. Models to describe the habitat selection

There was considerable uncertainty in model selection and no single model could be regarded as the unanimously best model. Therefore, we used model averaging and multimodel inference (Burnham & Anderson 2010). The autocovariate variable did not improve the fit of the models and was discarded (results not shown). We treated all the models within $0 < \Delta AICc < 4$ as competing models.

Five and seven of the 35 models got reasonable support in 1999 and 2004, respectively, when considering the buffer size of 1 ha . In the buffer size of 4 ha six models of 49 were regarded as top models in both years. At the winter territory scale (34 ha) the model selection uncertainty was somewhat lower compared with the smaller scales of 1 and 4 ha, since four and five models out of 49 got reasonable support.

The most important variable for the nest site selection of the willow tit was the number of suitable snags within the buffers in both years. SNAG was the only variable included in all the best competing models with the highest relative importance (AICc w = 0.96 – 1.00). The factors OPEN and DITCH were quite often included in the best models and the relative importance of DITCH increased along with increasing buffer size. The factor coniferous peatland forest proved rather important predictor of the territory core area especially in 2004. EDGE and PATCH entered the best models only once with low relative importance in 1999. The support for the rest of the variables was practically nonexistent (DECF AICc w = 0.070, CONDECF AICc w = 0.070).

3.2.3. Variation partitioning

The three spatial scales together explained 44.2 % and 42.6 % of the variance of the nest site selection in 1999 and 2004, respectively. In both years the joint effect of territory core and foraging area variables were considerably high, 25 % in 1999 and 28 % in 2004, explaining larger proportion of the variance than any of the studied scales alone. The other joint effects were generally low. The variance explained by the landscape scale alone was negligible.

Discussion 4

4.1. Timing of reproduction

■ In our study we confirmed that the caterpillar abundance and the commencement of willow tit egg-laying have advanced in the Oulu area along with spring warming. Both variables showed high correlation with spring temperatures, which is in line with previous studies (e.g. Dunn 2004, Visser *et al*. 2006). However, caterpillars and willow tis respond at different rates to spring warming. We found no signs of emerging asynchrony. On the contrary, synchrony improved with moderate positive effects on breeding success (see also Vatka *et al*. 2011). The onset of egg-laying in the willow tit advanced at about the same rate (b = -0.160 in 1975 – 2009) as found by Gienapp *et al*. (2006) for the great tit in the Netherlands (b = -0.182). The observed change in better synchrony reflects results from the coal tit (*Parus ater*) in the Netherlands (Both *et al*. 2009). Adaptation to exploiting alternative food resources (Rytkönen *et al*. 1996) makes willow tits less dependent on caterpillars compared with the southern newcomer species, the great and the blue tit (Rytkönen & Krams 2003). This may be reason for the small effect of the synchrony upon the breeding success in the willow tit. Still, synchrony had larger impact on the nestling survival rate of broods attended by young females, probably due to increasing foraging ability with age (e.g. Desrochers 1992).

Spring temperatures inducing the emergence of invertebrates may be used as a predictive factor, "a cue", of the future food peak (Visser *et al*. 2006). If this is true we should find similar responses of phenologies in insectivorous birds and caterpillars to the warming spring. Our results with different responses for the willow tits and caterpillars suggest a contrasting pattern. Spring temperatures do not seem to act as a cue for the willow tit in timing of the caterpillar peak, or alternatively the willow tits act inconsistently. Spring temperatures do have a role in the timing of breeding also as a constraining, proximate factor (Perrins 1965, Bryant 1975, Stevenson & Bryant 2000). To fully understand the evolution of reproductive traits under the climate change, we should discern between proximate and ultimate causes – ambient temperature can affect in both ways. Thus, there is a call for further research to be carried out in different trophic levels, habitats, climatic zones and species.

4.2. Habitat selection

The most important factor for willow tit nest site selection in all studied scales was the presence of standing decaying birch trees (seldom alders, *Alnus sp.*, Orell & Ojanen 1983b). Other variables played a minor role. The results were rather congruent in both years. Variation partition shows that the territory core scale and the foraging area scale explained most of the total variation. However, proportion of unexplained variance was pronounced.

Our results highlight the importance of the presence of decaying trees in the selection of breeding habitats of a primary hole-nesting species. Increasing the proportion habitat occupancy with increasing number of decaying wood is understandable considering the species' breeding habits. In spring when establishing breeding territories willow tits make trials to dig holes in many decaying snags before the final nesting hole is completed. Places with many possible snags are therefore favoured. Also other studies have found the density of suitable nesting trees to be higher near occupied nests of cavity-nesters (Raphael & White 1984, Li

& Martin 1991). In commercial forestry dead trees are usually removed, creating a shortage of suitable nest sites. Therefore, the competition over snags can be pronounced in intensively managed landscapes, such as our study area, and individuals with lower social rank may be forced to settle in lower quality sites.

The factor (DITCH), describing the distance of the nest site and the random site to the nearest ditch, entered some of the top ranking models. Based on the Akaike weights the relatively high importance of this factor increased substantially at the winter territory scale. Drainage is very common in the study area, where almost all the peatlands have been managed in such a way for silvicultural purposes. The willow tit seems to favour especially coniferous peatland forests as breeding habitat, which was apparent in both years. This and other possible habitat preferences diminished at the largest scale. We think this is the main reason why more variance remains explainable by the distance to the nearest ditch at the largest scale since the factor DITCH has the same value independent of the scale. The presence of dead trees lost its power slightly at the largest scale, since all except one random site included at least one standing decaying snag.

In general there were more deciduous and mixed forests as well as deciduous and coniferous peatland forests within the nest site buffers than within the random point buffers. However, there is a tendency that coniferous forests are less favoured in lower density population than in high density population. It may be that when the breeding density increases part of the pairs are outcompeted from the best habitats (forested peatlands) probably to less favoured habitats.

None of the willow tit nests were situated in open habitats in the study years and this factor entered some of the best models in nearly all cases, the foraging scale being an exception in 2004. Open habitat was more important in high density (1999) than in lower density year (2004), possibly because the avoidance of open areas becomes more apparent with larger sample size. This result also suggests that willow tit territories and foraging areas around them may consist of a variety of habitats, including even plots of open sites.

The result that the density of edges and patch size entered the best models only once and with low relative importance confirms the above reasoning that willow tits' habitat requirements are rather broad. This suggests that forest fragmentation would not play a noticeable role in the habitat selection of the species. The result is in agreement with our observation that willow tit nests can sometimes be found just on the edge of the forest and the clear-cut area if suitable decaying snags are available. The availability of suitable snags may also override the negative effects of forest fragmentation highlighting the overall importance of nest-sites over the other variables in habitat selection. The edges to open habitats or saplings did not affect to the winter territory size of the willow tit (Siffczyk *et al.* 2003). Probably willow tits can benefit to some extent from the higher invertebrate density on edges (Helle & Muona 1985).

In both years a large fraction of the explained variance was shared between the territory and foraging area scales whereas and the variance explained by the landscape scale was negligible. This result indicates that most of the habitat selection occurs within the small scale. Similar results have been found e. g. for the Eurasian treecreeper (*Certhia familiaris,* Suorsa *et al.* 2005). They suggested that it might be because for a sedentary species habitat characteristics within the territory are probably the most important factors for nest site selection.

The considerably high unexplained variance in both years suggests that there are important unmeasured biotic and abiotic variables. We did not consider for example habitat characteristics in the immediate vicinity of the nest. Our habitat data were based on remote sensing and it is known that the accuracy of the data in terms of detailed forest characteristics is not very good at small scales (Tokola & Heikkilä 1997). Assessing the importance of habitat characteristics e.g. canopy cover at nest-site scale calls for further investigation. Biotic interactions (such as predation or interspecific competition and facilitation) can also influence the habitat selection of the birds (Martin 2001). For example, the nest location can be affected by conspecific attraction, which was the case in the black-capped chickadee (*Poecile atricapillus*), where females tend to nest near territory boundaries especially if a neighbouring male is of high rank (Ramsay *et al.* 1999). The presence of avian predators does not seem to affect nest site selection of the willow tit in our study area. They may not be able to avoid breeding in the proximity of predators, because they start excavating their nest holes before the predators arrive (Thomson *et al.* 2006).

4.3. Conclusions

Our results show that along with increasing spring temperature, our model species, the willow tit, has significantly advanced its breeding schedule in northern Finland during the past 35 years. This has improved the synchrony of the time of the highest food demand – provisioning of nestling – with the food availability, which amends the nourishment supply of the young. This has modest positive effects on the breeding success especially in yearling parents.

Habitat changes due to commercial forestry have negative impacts on the species during the breeding time. Willow tits cannot breed in open areas, such as clear-cuts. In forested areas they accept a variety of habitats, coniferous peatland forest belonging to the most favoured environments. Landscape level conditions do not seem to be as important as the local habitat characteristics for the territory occupancy in forested habitats. At the local scale the persistence of the species is limited by the availability of standing decaying wood for nesting holes. Repeated thinning and removal of deciduous trees, bushes and dead trees is a common forestry policy. Commercial forestry targeting the efficient production of coniferous timber prevents the formation of new decaying trees and thus nest-sites for primary hole-nesting species. The possible benefits achieved from the climate warming will unlikely compensate the damages caused by habitat loss and quality deterioration. For conservation and maintenance of populations of the hole-nesting birds changes in forest planning is necessary to keep up the key characteristics of the habitat. Most importantly, this entails more careful thinning of forests to ascertain continuous availability of decaying wood for nesting sites.

References

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

Borcard, C., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**: 1045–1055.

Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81–83.

Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. 2009. Climate change and unequal phonological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* **78**: 73–83.

Brodin, A., Lahti, K., Lens, L. & Suhonen, J. 1996. A northern population of Willow Tits *Parus montanus* did not store more food than southern ones. *Ornis Fennica* **73:** 114–118.

Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A. & Rajasärkkä, A. 2003. Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. *Landscape Ecology* **18**: 377–393.

Bryant, D. M. 1975. Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* **117**: 180–216.

Burnham, K. P. & Anderson, D. R. 2010. Model selection and multimodel inference. A practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, USA.

Chevan, A., & Sutherland, M. 1991. Hierarchical partitioning. *American statistics* **45**: 90–96.

Cresswell, W. & McCleery, R. 2003. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology* **72**: 356–366.

Desrochers, A. & Bélisle, M. 2007. Edge, patch, and landscape effects on Parids distribution and movements. In. Otter, K.A. (ed.) Ecology and behaviour of chickadees and titmice. An integrated approach, Oxford Univ. Press, New York, pp. 243-261.

Desrochers, A. 1992. Age-related differences in reproduction by European Blackbirds: restraint or constraint. *Ecology* **73**: 1128–1131.

Doherty, P. F. Jr. & Grubb, T. C. Jr. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. *Ecology* **83**: 844–857.

Dormann, C. F., McPherson, J. M., Arau´jo, M. B., Bivand, R., Bolliger, J., Carl, G. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**: 609–628.

Dunn, P. 2004. Breeding dates and reproductive performance. *Advances Ecol. Res.* **35**: 69–87.

Ekman, J., Cederholm, G. & Askenmo, C. 1981. Spacing and survival in winter groups of willow tit *Parus montanus* and the crested tit *P. cristatus*. *Ornis Scand.* **10**: 56–68.

Ekman, J. 1979. Coherence, composition and territories of winter social groups of the willow tit *Parus montanus* and the crested tit *P. cristatus*. *Ornis Scand.* **10**: 56–68.

Gienapp, P., Postma, E. & Visser, M. E. 2006. Why breeding time has not responded to selection for earlier breeding in a songbird population. *Evolution* **60**: 2381–2388.

Haftorn, S. 1959. The proportion of spruce seeds removed by the tits in a Norwegian spruce forest in 1954–1955. *Kgl Nor Vidensk Selsk Forh* **32**: 121–125.

Haftorn, S. 1990. Social organization of winter flocks of willow tit in a Norwegian subalpine birch forest. In: Blondel J, Gosler A, Lebreton J-D, McCleery R (eds). Population biology of passerine birds. NATO ASI Ser, vol G24, Springer, Berlin Heidelberg New York, pp. 401–413.

Haftorn, S. 1999. Flock formation, flock size and flock persistence in the Willow Tit Parus montanus. *Ornis Fenn* **76**: 49–63.

Helle, P. & Järvinen, O. 1986. Population trends on North Finnish land birds in relation to their habitat selection and changes in forest structure. *Oikos* **46**: 107–115.

Helle, P. & Muona, J. 1985. Invertebrate numbers in edges between clear-fellings and mature forest in northern Finland. *Silva Fennica* **19**: 281–294.

Kangas, K., Lampila, S., Orell, M., Nikula, A. & Nivala, V. 2011. Nest site selection of a sedentary cavity nesting passerine bird in a fragmented landscape. (Manuscript).

Koivula, K. & Orell, M. 1988. Social rank and winter survival in the Willow Tit *Parus montanus*. *Ornis Fennica* **65**: 114–120.

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

Lahti, K., Koivula, K., Orell, M. & Rytkönen, S. 1996. Social dominance in free-living Willow Tits *Parus montanus*: determinants and some implications of hierarchy. *Ibis* **138**:539–544

Li, P. & T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *Auk* **108**: 405–418.

Luoto, M., Virkkala, R., Heikkinen, R.K. & Rainio, K. 2004. Predicting bird species richness using remote sensing in boreal agricultural-forest mosaics. *Ecol. Applicat.* **14**: 1946–1962.

Martin, T. E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology* **82:** 175–188.

Matthysen, E. 1990. Nonbreeding social organization in Parus. In: Power DM (ed) Current ornithology 7. Plenum Press, New York, pp. 209–249

McGarigal, K. & Marks, B.J. 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 122 p.

Nager, R. G. & van Noordwijk, A. J. 1995. Proximate and ultimate aspects of phenotypic plasticity in timing of Great Tit breeding in a heterogenous environment. *The American Naturalist* **146**: 454–474.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. & Stevens, M. 2008. Community ecology package. R package version 1.11-2. R Foundation for Statistical Computing, Vienna, Austria

Olsson, J.R. & Grubb, T.C., Jr. 2007. Winter adaptations in chickadees and titmice and the added effect of habitat fragmentation. In. Otter, K.A. (ed.) Ecology and behaviour of chickadees and titmice. An integrated approach, Oxford Univ. Press, New York, pp. 263–275.

Opdam, P. & Wascher, D. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* **117**: 285–297.

Orell, M. & Koivula, K. 1988. Cost of reproduction: parental survival and production of recruits in the willow tit *Parus montanus*. *Oecologia* 77: 423–432.

Orell, M. & Ojanen, M. 1980. Overlap between breeding and moulting in the Great Tit *Parus major* and Willow Tit *P. montanus* in northern Finland. *Ornis Scandinavica* **11**: 43–49.

Orell, M. & Ojanen, M. 1983a. Timing and length of the breeding season of the great tit *Parus major* and the willow tit *P. montanus* near Oulu, Northern Finland. *Ardea* **71**: 183–198.

Orell, M. & Ojanen, M. 1983b. Breeding biology and population dynamics of the willow tit *Parus montanus*. *Ann. Zool. Fennici* **20**: 99–114.

Orell, M., Koivula, K., Rytkönen, S. & Lahti, K. 1994. To breed or not to breed: causes and implications of non-breeding habit in the willow tit *Parus montanus*. *Oecologia*, **100**, 339–346.

Orell, M., Lahti, K., Koivula, K., Rytkönen, S. & Welling, P. 1999. Immigration and gene flow in a northern willow tit *(Parus montanus)* population. *J. Evol. Biol.* **12**: 283–295.

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

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

Perrins, C. M. 1965. Population Fluctuations and Clutch-Size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* **34**: 601–647.

Perrins, C. M. 1970. The timing of birds' breeding seasons. *Ibis* **112**: 242–255.

Perrins, C. M. 1991. Tits and their caterpillar food supply. *Ibis*, **133 suppl. 1**: 49–54.

Ramsay, S.M., Otter, K. and Ratcliffe, L.M. 1999. Nest-site selection by female black-capped chickadees: settlement based on conspesific attraction? *The Auk* **116**:604-617.

Raphael, M. G. & M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildl. Monogr.* No. 86.

Rhodes, J. R., McAlpine, C. A., Zuur, A. F., Smith, G. M. & Ieno, E. N. 2009. GLMM applied on the spatial distribution of koalas in a fragmented landscape. In. Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (eds). Mixed effect models and extensions in ecology with R. Springer Science+Business Media, New York, pp. 469–492.

Rytkönen, S. & Krams, I. 2003. Does foraging behaviour explain the poor breeding success of great tits *Parus major* in northern Europe? *J. Avian Biol.* **34**: 288–297.

Rytkönen, S. & Orell, M. 2001. Great tits, *Parus major*, lay too many eggs: experimental evidence in mid-boreal habitats. *Oikos* **93**: 439–450.

Rytkönen, S., Koivula, K. & Orell, M. 1996. Patterns of per-brood and per-offspring provisioning efforts in the Willow Tit *Parus montanus*. *Journal of Avian Biology* **27**: 21–30.

Siffczyk, C., Brotons, L., Kangas, K. & Orell, M. 2003. Home range size of willow tits: a response to winter habitat loss. *Oecologia* **136**: 635–642.

Stauffer, D. F. & L. B. Best. 1982. Nest site selection by cavity-nesting birds of riparian habitats in Iowa. *Wilson Bull.* **94**: 329–337.

Suorsa, P., Huhta, E., Jantti, A., Nikula, A., Helle, H., Kuitunen, M., Koivunen, V. & Hakkarainen, H. (2005) Thresholds in selection of breeding habitat by the Eurasian treecreeper (*Certhia familiaris*). *Biol. Conserv.* **121**: 443–452.

Stevenson, I. R. & Bryant, D. M. 2000. Climate change and constraints on breeding. *Nature* **406**: 366–367.

Thomson, R. L., Forsman, J. T., Mönkkönen, M., Hukkanen, M., Koivula, K., Rytkönen, S. and Orell, M. 2006. Predation risk effects on fitness related measures in a resident bird. *Oikos* **113**: 325–333.

Tinbergen, J. M. & Boerlijst, M. C. 1990. Nestling Weight and Survival in Individual Great Tits *(Parus major)*. *J. Anim. Ecol.* **59**: 1113–1127.

Tokola, T. & Heikkilä, J. 1997. Improving satellite image based forest inventory by using a priori site quality information. *Silva Fennica* **31**: 67–78.

Tomppo, E., Haakana, M., Katila, M. & Peräsaari, J. 2008. Multi-Source National Forest Inventory Methods and Applications Springer, Series: Managing Forest Ecosystems Vol. **18**, 374 p.

Travis, J. M. J. 2002. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. Lond. B.* **270**: 467–473.

Väisänen, R. A., Lammi, E. & Koskimies, P. 1998. Distribution, numbers and population changes of Finnish breeding birds. Finnish with English summary. Otava, Helsinki, Finland.

Väisänen, R. A., Järvinen, O. & Rauhala, P. 1986. How are extensive, human caused alterarions expressed on the scale of local bird populations in boreal forests? *Ornis Scandinavica* **17**: 282–292

Vatka, E., Orell, M. & Rytkönen, S. 2011. Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. *Global Change Biology* **17**: 3002–3009.

Visser, M. E., Both, C. & Lambrechts, M. M. 2004. Global climate change leads to mistimed avian reproduction. *Advances Ecol. Res.* **35**: 89–110.

Visser, M. E., Holleman, L. J. M. & Gienapp, P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**: 164–172.

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998. Warmer springs lead to mistimed reproduction in great tits *(Parus major). Proc. Royal Soc. Lond. Ser.B* **265**: 1867–1870.

Walther, G.-R., Post, E., Convey, P. *et al*. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.

Zandt, H. S. 1994. A comparison of three sampling techniques to estimate the population size of caterpillars in trees. *Oecologia* **97**: 399–406.

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