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BOREAL POPULATIONS FACING CLIMATIC AND HABITAT CHANGES

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Abstract

Anthropogenic climate change and habitat loss and deterioration affect populations worldwide. Climate warming has changed phenologies of many species across trophic levels. Some predator populations now experience temporal mismatches with their prey, as timings of peak prey abundance and of the predator's highest food demands no longer meet. The temporal mismatch hypothesis suggests that the population's recruitment rate is related to its degree of synchrony with the food resources needed to feed offspring. However, species' and populations' responses to climate warming differ. Human land use alters and destroys habitats of countless species. For example, many boreal forest bird populations have declined, presumably due to intensive forestry. It has decreased the amount of dead wood, causing a threat to saproxylic species. Identification of the key characteristics of high-quality habitats is essential for conservation planning and for developing sustainable forestry. As individuals are suspected to settle in habitats that maximize their fitness, analysis of nest site selection can be used to identify the key habitats. My dissertation concerns the impacts of climate change and habitat deterioration on boreal populations. I use hole-nesting passerines as model species. By utilizing long-term data I show that breeding phenologies of *Parus major* and *Poecile montanus*, but not of *Cyanistes caeruleus*, have shifted earlier. Also, the timing of the food peak has advanced, improving the synchrony between *P. montanus* and caterpillars. In *P. major* and *C. caeruleus*, synchrony has remained good. However, the positive effect of good synchrony on breeding success seems to be conditional, arising only in certain circumstances, such as in years of high caterpillar abundance. I suggest that in boreal populations temperature affects timing of breeding mostly as a proximate factor. The availability of standing decaying trees used for nesting sites was the most important habitat characteristic determining the nest site selection of *P. montanus.* Remote sensing data alone was insufficient to produce reliable models, as the ecologically important small-scale factor can only be determined by direct field surveys. Omission of forest thinning in selected forest sites would ensure the continuous availability of decaying wood with positive influence on biodiversity in managed forests.

Keywords: climate warming, habitat loss, insect caterpillars, multi-model inference, nest site selection, Paridae, phenology, synchrony, the temporal mismatch hypothesis

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Tiivistelmä

Ihmisen aiheuttama habitaattien katoaminen ja huononeminen sekä ilmastonmuutos vaikuttavat populaatioihin kaikkialla maailmassa. Ilmaston lämpeneminen on muuttanut monien lajien fenologioita eri trofiatasoilla. Osalla saalistajalajien populaatioista suurin ravinnontarve ei enää ajoitu samaan aikaan saaliin runsaushuipun kanssa. Ajoituksen eriaikaisuus -hypoteesin mukaan todennäköisyys populaatioon rekrytoitumiselle riippuu synkronian asteesta saaliin kanssa. Ilmaston lämpenemisen vaikutuksissa lajeihin ja populaatioihin on kuitenkin vaihtelua. Ihmisen maankäyttö muuttaa ja tuhoaa lukuisien lajien elinympäristöjä. Esimerkiksi useiden boreaalisten metsien lintupopulaatioiden pienentymistä on selitetty intensiivisellä metsätaloudella. Lahopuun määrä metsissä on vähentynyt, mikä on uhka lahopuusta riippuvaisille lajeille. Korkealaatuisten habitaattien keskeisten piirteiden tunnistaminen on tärkeää luonnonsuojelun ja kestävän metsätalouden suunnittelulle. Koska yksilöiden oletetaan valitsevan niiden kelpoisuutta maksimoivia elinympäristöjä, pesäpaikanvalinta-analyysiä voidaan käyttää tärkeiden habitaattipiirteiden tunnistamiseen. Tarkastelen väitöskirjassani ilmastonmuutoksen ja habitaattien laadun vaikutuksia boreaalisiin populaatioihin. Mallilajeina käytän koloissa pesiviä varpuslintuja. Hyödyntämällä pitkäaikaisaineistoja osoitan, että lisääntymisen ajoittuminen on aikaistunut tali- ja hömötiaisella, mutta ei sinitiaisella. Myös ravintohuippu on aikaistunut, mikä on parantanut synkroniaa hömötiaisen ja sen pääasiallisen ravinnon eli toukkien välillä. Tali- ja sinitiaisella synkronia on pysynyt hyvänä. Hyvän synkronian myönteinen vaikutus lisääntymismenestykseen vaikuttaa kuitenkin ehdolliselta: se tulee esiin vain tietyissä olosuhteissa, kuten vuosina jolloin toukkia on runsaasti. Kevään lämpötilat näyttävät vaikuttavan pesinnän ajoittumiseen erityisesti proksimaattisena tekijänä. Pesäpaikkoina toimivien seisovien lahopuiden määrä on tärkein hömötiaisen pesäpaikanvalintaa määräävä tekijä. Kaukokartoitusaineisto yksinään ei riitä luotettavien mallien tuottamiseen, sillä ekologisesti tärkeät pienen skaalan tekijät voidaan kartoittaa vain suorin maastomittauksin. Metsien harventamatta jättäminen valituilla laikuilla turvaisi lahopuun jatkuvan saatavuuden, mikä vaikuttaisi myönteisesti talousmetsien biodiversiteettiin.

Asiasanat: ajoituksen eriaikaisuus -hypoteesi, fenologia, habitaattien katoaminen, hyönteiset, ilmaston lämpeneminen, Paridae, pesäpaikan valinta, synkronia, toukat, useiden mallien tulkinta

To my family.

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List of original publications

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I 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.

II Vatka E, Rytkönen S & Orell M (2013) Does the temporal mismatch hypothesis match in northern populations? (*Manuscript*)

III Vatka E, Kangas K, Lampila S, Orell M, Nikula A & Nivala V (2013) Nest site selection of a primary hole-nesting passerine reveals means to developing sustainable forestry. Journal of Avian Biology (*In press*)

The researcher has taken part in formulating the research problems and data collection (I, II), and has been mainly responsible for analyzing the data, drawing conclusions and being the primary author for all three articles.

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1 Introduction

Fast and geographically extensive environmental changes are major threats to biodiversity (Travis 2003, Opdam & Wascher 2004, Pereira *et al*. 2012). Humans have caused substantial changes in the living conditions of numerous species. Anthropogenic climate warming, habitat loss and deterioration affect populations worldwide. Their impacts on nature are studied by many scientists in order to find ways to escape from detrimental outcomes for biodiversity.

1.1 Climate warming and changes in synchrony

Climate change has affected phenology both in plant and animal kingdoms (e.g. Walther *et al*. 2002, Parmesan & Yohe 2003). As a consequence of warming springs, phenologies of several species in both aquatic and terrestrial ecosystems have shifted earlier (e.g. Parmesan 2006, Durant *et al*. 2007, Thackeray *et al*. 2010), changing the time window of food availability for higher trophic levels. Populations' responses to climate warming differ (Sanz 2002, Visser *et al*. 2003, Both *et al*. 2004). Some predator populations now experience temporal mismatches with their prey (e.g. Visser *et al*. 1998, Visser & Holleman 2001, Both *et al*. 2009, Donnelly *et al*. 2011), but the phenomenon is not universal (e.g. Cresswell & McCleery 2003, Charmantier *et al*. 2008, Bauer *et al*. 2010, Matthysen *et al*. 2011). Actually, in a few cases synchrony has improved (Costello *et al*. 2006, Both *et al*. 2009). Observed differences among populations in changes of synchrony are probably due to spatial variation in the intensity and detailed pattern of climate warming (Walther *et al*. 2002, Cresswell & McCleery 2003). Changes in synchrony between interdependent species can have far-reaching consequences throughout ecosystems, altering community structures and increasing the risk of population extinctions and biodiversity loss (Costello *et al*. 2006, Thackeray *et al*. 2010, Donnelly *et al*. 2011).

In seasonal environments, synchrony with the food peak is considered an important factor affecting breeding success and thus the evolution of timing of breeding (Lack 1950). For example, in Parids (*Parus* spp.) insect caterpillars living in the foliage of deciduous trees are the main food items used to feed the young (Perrins 1991, Rytkönen *et al*. 1996). Broods timed correctly with the caterpillar peak produce more and heavier fledglings (Nager & van Noordwijk 1995, Visser *et al*. 2006) which recruit to the breeding population more likely than young from ill-timed nests (e.g. Tinbergen & Boerlijst 1990, see also

Verboven & Visser 1998). For insectivores, timing of the food peak is highly affected by the spring temperatures, being earlier in warm springs than in cold ones (e.g. Visser *et al*. 1998, Eeva *et al*. 2000). Thus, climate warming can alter the environment of selection in timing of breeding by shifting the food peak earlier (Visser *et al*. 2004).

At high latitudes, however, food availability has generally peaked later than the offspring needs of local Parids, suggesting that other important ultimate factors are affecting the timing of breeding (Eeva *et al*. 2000, Rytkönen & Orell 2001). Early breeders are usually most productive with larger clutches and higher recruitment rate (e.g. Perrins 1965, Nager & van Noordwijk 1992, Reed *et al*. 2013b). They may gain from more time for moulting and hoarding (Orell & Ojanen 1980) and from prior residency of their offspring (Koivula *et al*. 1993). Net benefits of early "mismatched" breeding seem to outweigh the benefits of breeding later with the food peak. Yet, if the food peak shifts earlier due to the climate warming, the synchrony with the food peak may improve in such population. For example, Coal Tit's (*Periparus ater* L.) temporal match with the caterpillar peak improved during a study period of twenty years in the Netherlands (Both *et al*. 2009). Northern populations of temperate-origin Parids might benefit from such a change in synchrony. Albeit intensively studied in the mid-latitudes (e.g. Visser *et al*. 1998, Naef-Daenzer & Keller 1999, Cresswell & McCleery 2003, Charmantier *et al*. 2008, Both *et al*. 2009, Bauer *et al*. 2010, Matthysen *et al*. 2011), the changes in synchrony and its influences on breeding success in northern latitudes need further investigation. Previous studies cover only relatively short time periods (Eeva *et al*. 2000: six years, Rytkönen & Orell 2001: two years).

1.2 Changes in habitat quality and resulting effects on populations

Human land use causes habitat loss and fragmentation which affect populations worldwide (e.g. Robinson *et al*. 1995, Villard *et al*. 1999, Donovan & Flather 2002, Lampila *et al*. 2005). For example, many boreal forest bird populations have declined during the past decades, presumably due to forestry practices (Helle & Järvinen 1986, Väisänen *et al*. 1986, 1998). Forestry may cause population declines either by habitat loss per se or by reduced food availability (e.g. Lahti *et al*. 1998). In Finland, forestry practices have not substantially diminished the amount of forest cover, but the composition and age structure have changed dramatically from mature forests to coniferous dominated young forests (Kouki &

Väänänen 2000, Gustafsson *et al*. 2010). In addition, the amount of dead wood has decreased (Siitonen 2001, Ihalainen & Mäkelä 2009). Numerous dead wood dependent species are thus becoming increasingly threatened in managed forests (Dudley & Vallauri 2004).

For developing sustainable forestry and conservation planning of declining populations, new knowledge of the key characteristics of high quality habitats is essential. As individuals presumably settle in habitats that maximize their fitness (Fretwell & Lucas 1970), habitat selection analysis can be used to identify the ecologically important habitat characteristics. However, modeling habitat selection can be problematic since reliable data on presence and absence of the species, as well as on the important small-scale habitat elements is often lacking (e.g. Pakkala *et al*. 2002, Hurme *et al*. 2008).

1.3 Birds as model species

Birds have been used as model species in constructing theories on the development and maintenance of biodiversity. Their ecology and morphology are very well known and they are easy to mark individually, which allows e.g. detailed breeding success analysis, survival analyses (Doherty & Grubb 2002) and pedigree construction (Postma & Charmantier 2007). In hole-nesting species, such as Parids, it is relatively easy to record breeding variables (onset of egg-laying, hatching date, brood size, number of fledged chicks etc.). Parids are studied by a number of scientists across the Northern hemisphere, which enables comparisons between closely related species and populations in different environmental conditions.

1.4 Theoretical foundation

1.4.1 Timing of breeding (I, II)

Timing of breeding is a central life-history trait. It is associated with many features (e.g. body size, body condition, age) and has fitness consequences as it affects breeding success (Visser *et al*. 2006, Verhulst & Nilsson 2008). Thus, the evolution of timing of breeding can be affected by various selection pressures.

Temporal mismatch hypothesis

The temporal mismatch hypothesis proposes that population's recruitment rate depends on the degree of temporal synchrony between the phenology of a consumer and its food resources. The recruitment rate is the highest when the most energy-consuming part of the breeding cycle coincides with the peak availability of food (Durant *et al*. 2007). In birds, the availability of good-quality food during the nestling period is an important determinant of breeding success (Martin 1987, Naef-Daenzer & Keller 1999). For many species in seasonal environments, high-quality food is available only for a short period each year. Breeding season is considered to be adapted to coincide with this period (Lack 1950). Good synchrony improves the breeding success only with high food peaks (Durant *et al*. 2005), so in habitats where the food availability does not have substantial peaks, the timing of breeding may be more determined by other factors than the synchrony (Burger *et al*. 2012).

Proximate and ultimate factors in timing of breeding

Proximate factors are determinants with direct effects on the expression of a given trait. Ultimate factors, instead, are agents that affect fitness consequences of a trait and thus engage in the natural selection directing the evolution of the trait. In general, birds breed earlier in warmer springs (Dunn 2004). Spring temperature may affect timing of breeding via various mechanisms, which can be of proximate or ultimate nature.

Presumably, birds use cues in order to time their nestling period correctly with the food abundance peak (Visser *et al*. 2004, Lyon *et al*. 2008). Day length (photoperiod) affects timing of breeding as a triggering proximate factor for hormonal functions (e.g. Dawson 2002). This information can be supplemented by other cues, such as ambient temperature, rainfall, vegetation phenology or food availability (Hau *et al*. 2000, Dunn 2004, Dawson 2008, Bourgault *et al*. 2010, Thomas *et al*. 2010). Ambient temperature may have direct effects on gonadal development (Dunn 2004, Visser *et al*. 2009, but see Visser *et al*. 2011). The spring temperatures affect timing of breeding indirectly via food availability (Perrins 1965, Bryant 1975) and thermoregulatory costs during the early breeding stages (e.g. Stevenson & Bryant 2000). The energy limitation hypothesis of Perrins (1965, 1970) suggests that such proximate constraining factors prevent birds from breeding earlier than they do. Breeding too early could be adverse if

cold weather or lack of food impairs the breeding success or survival of the parent, i.e., weather and food availability can function as ultimate factors. On the other hand, at high latitudes short summers may act as time constraints because breeding late would mean less time for moulting and preparation for wintering or migration, decreasing survival (Eeva *et al*. 2000). Visser *et al*. (1998, 2006, 2009) suggest that birds use spring temperatures as a proximate predictive factor, a cue for the timing of future food availability. The idea is supported by similarity of phenological responses to the spring temperatures between the Great Tit (*Parus major* L.*)* and caterpillars and by the response of birds to temperatures even when food availability is not constraining the onset of breeding (but see Visser *et al*. 2011). The relative importance of different factors or cues can vary among species, populations and even among individuals in the same population (Lyon *et al*. 2008, Silverin *et al*. 2008). Timing of breeding can be considered as a result of an optimization process, affected by a variety of fitness costs and benefits from breeding at a given time (Verhulst & Nilsson 2008). The concept of adaptive mismatch has been suggested by e.g. Visser *et al*. (2012) and Lof *et al*. (2012) to describe a situation where a temporal mismatch with the food availability is the optimal situation in respect of total fitness (comprising present and future fecundity).

1.4.2 Nest site selection (III)

Habitat quality influences survival and breeding success. Consequently, successful habitat selection is a requisition for individuals' prosperity. Individuals should settle in habitats that maximize their fitness (Fretwell & Lucas 1970). Birds are suspected to select their habitats hierarchically from coarser spatial scales to foraging or nesting sites (Johnson 1980). Several biotic and abiotic factors, as well as their interactions, affect the selection process (Martin 2001). For example food availability (Alatalo *et al*. 1985, Li & Martin 1991), microclimate (Martin 2001), competition (Alatalo 1981, Nilsson 1984), nest predation (Nilsson 1984, Martin 1993, 2001) as well as inter- and intraspecific attraction (Ramsay *et al*. 1999, Forsman *et al*. 2009) can influence the selection process. Individuals may be forced to settle in low-quality sites if good habitats are no longer available, either because of competition for nest sites or habitat loss. The population growth rate will be affected if a large part of the population is living in suboptimal habitats.

Habitat selection modeling may produce divergent results depending on the spatial scale (Wiens *et al*. 1987) and the population density used (e.g. Jones 2001). In high population densities the competition for good quality sites may be more severe and a larger proportion of pairs may have to settle in suboptimal sites. Suorsa *et al*. (2005) suggest that for sedentary species the habitat characteristics within the territory are the most important factors for nest site selection.

For cavity-nesting species, the availability of nest holes is essential and their deficiency can limit population size (e.g. Stauffer & Best 1982, Raphael & White 1984, Li & Martin 1991). Occupied nests of cavity-nesting birds are often located in places with high density of suitable nesting trees (Raphael & White 1984, Li & Martin 1991). Supplying of new nest sites can increase the number of breeding pairs up to a certain level where other density-dependent factors start to limit the population size (e.g. Newton 1994, 1998, Wang *et al*. 2009). Provisioning and maintenance of nest sites play essential roles in the conservation of many endangered species (Jones 2004, Catry *et al*. 2009, Brazill-Boast *et al*. 2013).

1.5 Aims of the study

The main motive for this research arises from the interest in understanding the effects of anthropogenic environmental changes on nature. The research takes a boreal perspective, with two aims: (1) to study how climate change affects phenologies and synchrony between the prey and the predator and consequently acts on the evolution of life-history traits and (2) to find methods for identifying high-quality habitats that should be preserved in order to maintain biodiversity.

The dissertation comprises three research articles/manuscripts. The first two concern the effects of climate warming on phenologies and synchrony between insect caterpillars and Parids, as well as the effects of caterpillar availability on breeding success. The third one deals with the theme of habitat loss and deterioration, and aspires to identify key habitat characteristics for the Willow Tit, *Poecile montanus* Conrad.

The study addresses four research questions that are answered in the sub-studies indicated in parenthesis:

1. How does climate warming affect phenologies and synchrony between timings of food availability and the nutritional needs of predators in a boreal ecosystem? (I, II)

2. Is the temporal mismatch hypothesis adequate in explaining evolutionary adaptation in timing of breeding in northern populations? (II)
3. Is remote sensing data sufficient for identifying high quality habitats? (III)
4. What are the key habitat characteristics for *P. montanus*? (III)

1.6 Research setting and research approach

The research is part of work done in the Population, Conservation and Evolutionary Ecology research group at the Department of Biology, University of Oulu. The research group has strong traditions in collecting and applying long-term datasets of population surveys in birds (the longest time-series spans from 1969 to present), with information of breeding parameters and morphological measures of individually marked birds. Also, data on the phenology of the insect caterpillars has been collected from 1996 onwards. This research is founded on those datasets.

The research employs empirical data for testing theoretical hypotheses. The analysis of nest site selection (III) is mainly explorative, with a view to indicate the most important habitat characteristics. Most of the analyses are based on correlative statistical models [i.e., (generalized) linear (mixed effect) regression models]. When studying the effects of climate change on phenologies and synchrony (I, II), the approach is retrospective. However, the general goal is to gain understanding about the present and future effects of environmental changes and to find ways to avoid detrimental outcomes, such as the loss of biodiversity. Thus, the research includes a normative approach, giving recommendations for developing forestry practices (III).

2 Material and methods

2.1 Study species

The Great Tit *Parus major*, the Blue Tit *Cyanistes caeruleus* L. and the Willow Tit *Poecile montanus* are sedentary insectivorous hole-nesting passerines with broad distributions in temperate and subarctic areas of Europe, Asia and North Africa. *Poecile montanus* is indigenous in the boreal zone, whereas *C. caeruleus* and *P. major* populations in northern Finland are close to the northern edges of their distributions. *Poecile montanus* pairs excavate nesting cavities in standing decayed deciduous trees, i.e., snags (Orell & Koivula 1988, Orell *et al*. 1999), whereas *P. major* and *C. caeruleus* prefer man-made nest boxes. In Oulu (ca. 65°N, 25°30'E) the mean number of eggs in first clutches is 10 for *P. major* and *C. caeruleus*, and 7.6 for *P. montanus* (Orell & Ojanen 1983a, b, own observations). Incubation takes ca. 14 days and the nestling period ca. 18 days (Orell & Ojanen 1983b, c, del Hoyo *et al*. 2007). During the nestling season, parents feed their young with invertebrates, mostly insect caterpillars (e.g. *Epirrita autumnata*, Borkhausen) if available (van Balen 1973, Perrins 1991, Rytkönen *et al*. 1996, del Hoyo *et al*. 2007). Secondary prey items are also used, especially by *P. montanus* (e.g. diptera Tipulidae, Culicidae, spiders Arachnoidea and aphids Aphidoidea). Despite their relatively low abundance, caterpillars are the main food for nestling provisioning in Oulu populations (Rytkönen & Orell 2001). For example, the proportion of caterpillars in the nestling diet of *P. montanus* can be over 80% when the caterpillar peak coincides with the nestling period (Rytkönen *et al*. 1996). The food demand of the nestlings is estimated to be the highest at the age of 8–13 days (0 = the hatching day, van Balen 1973, Rytkönen *et al*. 1996).

Moulting takes place in late summer (Orell & Ojanen 1980). *Poecile montanus* hoards intensively animal and plant food, which plays an important role in the winter diet, in autumn (September – October) until the snow comes (Brodin *et al*. 1996). *Poecile montanus* spend the winter in small territorial flocks with a social hierarchy (e.g. Koivula & Orell 1988). Breeding territories are usually established within the winter territory (Ekman 1979). *Poecile montanus* has a broad habitat preference. It breeds in coniferous, mixed and deciduous forests, copses and scrubs (Cramp *et al*. 1993). Damp habitats are thought to be important for the species (e.g. Lewis *et al*. 2007). *Poecile montanus* usually avoid open

areas without cover from predators (Siffczyk *et al*. 2003). The populations have declined substantially across Europe (PECBMS 2012) and in Finland, presumably due to intensive forestry (Järvinen *et al*. 1977, Lampila *et al*. 2006). In Finland, the decline has leveled off and *P. montanus* is still considered a common species. On the contrary, *P. major* and *C. caeruleus* populations are growing and expanding their ranges (Väisänen *et al*. 1998, Kvist *et al*. 1999, PECBMS 2012).

2.2 Study area

The data were collected in the Oulu area, northern Finland (ca. 65°N, 25°30'E), in a habitat of coniferous, deciduous and mixed forests of varying ages, including young stands, swamps and clear cuttings (e.g. Orell & Ojanen 1983a, c, Orell & Koivula 1988, Lahti 1997, Rytkönen & Orell 2001, Siffczyk *et al*. 2003). The dominating tree species are the Scots pine (*Pinus sylvestris* L.), the Norway spruce (*Picea abies* (L.) Karst.) and birches (*Betula* spp.). Similar habitat types continue outside the study area. From 1969 onwards, wooden nestboxes (with entrance hole diameter of 3.2–3.4 cm and 121–156 cm^2 in area, Lambrechts *et al*. 2010) were provided for *P. major* in several separate sub-areas of 2–4 km^2 total (Orell & Ojanen 1983a, b, c). Since 1998, the nestbox area (ca. 8 km^2) has been more continuous, consisting of four neighboring sub-areas (Rytkönen & Orell 2001, Karvonen *et al*. 2012). The number of nestboxes has varied between ca. 100–400. Since 1998, ca. 75–100 wooden nestboxes (Ø 2.8 cm and 100 cm^2, Lambrechts *et al*. 2010) have been available for *C. caeruleus* in the southern parts of the current nestbox area. *Poecile montanus* nests were located each spring from a study area partly overlapping the nestbox area (Orell & Ojanen 1983a, Lahti 1997). The study area has expanded in size, starting from 0.57 km^2 in 1975 (Orell & Ojanen 1983a) and gradually increasing to 24 km^2 in 1991 and later (Orell *et al*. 1994).

2.3 Data

2.3.1 Data of breeding parameters (I, II)

Long-term breeding data on *P. major* (1969–2011, excluding 1994), *C. caeruleus* (1998–2011) and *P. montanus* (1975–2011) were used. During the breeding seasons (end of April – July), nests were routinely visited on a weekly basis, more

frequently close the time of estimated hatching. Onset of egg laying, time of hatching (both at accuracy of one day), clutch size, numbers of hatched and fledged young were determined (Orell & Ojanen 1983a, b, c, Orell *et al*. 1999). Only first nesting attempts per female in each season were considered. Parents were identified on the basis of unique combinations of aluminum and plastic color rings. Non-marked parents were captured, marked and measured as described by Orell and Koivula (1988) when the nestlings were 9–16 days old. Parents were sexed by the presence of a brood patch and plumage coloration, and aged as yearlings or older, on the basis of the coloration of primary coverts and alula (for *P. major* and *C. caeruleus*) or the tail feathers' shape (for *P. montanus*, Svensson 1997). Nestlings were weighed to the nearest 0.1 g when ringed at the age of 13–15 days.

2.3.2 Data of caterpillar food availability (I, II)

Caterpillar availability during breeding seasons was quantified with the frass-fall method (Zandt 1994) according to Rytkönen & Orell (2001) for 1996–2011. The frass-fall method bases on the quantity of caterpillar droppings that fall down on a certain area per unit of time. Biomasses of caterpillars foraging on birch (*Betula* spp.) were estimated in weekly periods. Annual caterpillar peak dates were determined as the middle day of a measurement period when the biomass was at its highest. Dates of the emergence and the decline of caterpillars were determined as the middle day of measurement period if the average biomass value of the period equals 0.10 g m^{-2}. In case the threshold limit was in between the average biomasses of two consecutive periods, the threshold date was the first day of the latter measurement period.

2.3.3 Temperature data (I, II)

The data of daily mean ambient temperatures was obtained from the Finnish Meteorological Institute, Oulunsalo observatory, ca. 20 km S of the study area.

2.3.4 Data of habitat variables (III)

Poecile montanus nests were located by intensive monitoring of the population during breeding seasons (from early April until late June). The study area was searched thoroughly and locations of all nest sites were thus known with

considerable accuracy. Data from two years was used (1999 with 162 nest sites and 2004 with 118 nest sites). The unoccupied sites were described by selecting the same numbers of randomly situated points inside the study area (162 and 118 for 1999 and 2004, respectively).

Habitat compositions (i.e. percentages of different habitat types) around each data point (occupied or unoccupied) were determined from the Finnish Multi-Source National Forest Inventory database (MS-NFI, Tomppo *et al*. 2008) on three spatial scales. The smallest scale with coverage of 1 ha (radius 57 m) describes the territory core area. It is the smallest area from which the habitat variables can be calculated with reasonable accuracy. The 4 ha buffer (radius 113 m) roughly describes the area where most of the foraging trips take place. The largest scale used (34 ha coverage with a radius of 329 m) represents the maximum winter territory size and it is referred to as the landscape scale (Siffczyk *et al*. 2003). MS-NFI produces e.g. estimates of volume for pine, spruce, birch and other deciduous trees for every 25 m × 25 m land area and includes information of man-made environments (inhabited areas, agricultural fields and roads). In addition to the variables derived from remote sensing data (MS-NFI and digital maps), estimates of the amount of decaying standing deciduous trees considered suitable for *P. montanus'* nesting sites were quantified by direct field surveys.

2.4 Statistical methods

2.4.1 Temporal trends in phenologies and a method to find the best correlative temperature periods (I, II)

Temporal trends in the onset of breeding in *C. caeruleus*, *P. montanus* and timing of caterpillar availability were examined by regressing annual median first-egg dates and caterpillar peak dates against the year. For *P. major*, the possible artifact from the changing habitat composition of the study area, as its extent has changed during the study, was considered. Sub-area specific annual median first-egg dates were regressed against the year while allowing for different intercepts for sub-areas.

A correlation analysis was used to investigate the association between phenologies and spring temperatures, following e.g. Orell and Ojanen (1983a) and Visser *et al*. (2006). Average temperatures (from daily mean temperatures)

were calculated for time periods of varying lengths, and Pearson's correlation coefficients were computed between all of these temperature periods and the median laying dates and caterpillar peak dates. The temperature periods with the strongest correlations were chosen.

To inspect climatic warming, linear regressions for the temperature periods found were computed with year as an explanatory variable.

2.4.2 Synchrony of the food peak and breeding phenologies (I, II)

To study the synchrony of the food peak and timing of breeding, the differences between the annual median hatching dates and timing of the caterpillar peaks were calculated. The food requirements of nestlings are the highest at 8–13 days after hatching (van Balen 1973, Rytkönen *et al*. 1996), so the food peak should coincide with this time for breeding to be the most successful. Synchrony was considered 'good' if the caterpillar peak date co-occurred with the period of the highest food demand for nestlings, defined according to annual median hatching dates. In addition, caterpillars were considered available during this period if the caterpillar biomass was over the threshold value of 0.1 g m^{-2}, regardless of the peak date itself.

2.4.3 Model selection and multi-model inference (II, III)

Similar model selection and multi-model inference principles were used in analyses of breeding success (II) and nest site selection (III). (Generalized) linear mixed effect models with different combinations of carefully selected explanatory variables were built and fitted to the data. The aim was to identify the variables that have influence on the response variables (i.e., measures of breeding success or site occupancy), and to determine the direction and size of the effects.

All continuous explanatory variables were centered to $\bar{x} = 0$ and scaled to SD = 0.5 to enable averaging of models with interaction terms and comparison of effect sizes of the factors (Schielzeth 2010, Grueber *et al*. 2011). The model sets contained all statistically and biologically relevant combinations of explanatory variables. The models were ranked with information-theoretic inference, the Akaike's information criterion (AIC or AICc) values. The models with ΔAIC(c) $\leq$2 were considered as the top models. As the model structure affects parameter estimates of a variable, a consensus was determined by averaging the

parameter estimates and their standard errors over the top models (Burnham & Anderson 2002, Grueber *et al*. 2011).

2.4.4 Synchrony with the caterpillars, timing of breeding and breeding success (II)

The effects of synchrony with caterpillar availability and timing of breeding on breeding success was analyzed in all three tit species using mean nestling mass per brood and number of fledged young, given that at least one young fledged, as response variables. The mean nestling mass is the average mass of nestlings in a brood at the age of two weeks. Data from the years 1996–2011 for *P. major* and *P. montanus* and from 1998–2011 for *C.caeruleus* was used (for which information of both breeding parameters and caterpillar food availability was available).

The analysis aimed at separating the effects of synchrony with the caterpillars and timing of breeding *per se*, such as the effect of high-quality individuals breeding earlier, or the adverse effect of cold weather for early broods. Thus, competing linear mixed-effect models with either synchrony or timing as explanatory variables were created. 'Synchrony' was defined for each nest as the difference between the day when the nestlings were 10 days old and the caterpillar peak date (synchrony = hatching date + 10 – caterpillar peak date). Synchrony values 0 indicate a perfect match, and the more the value departures from zero, the greater is the mismatch. 'Timing' was defined as the relative timing of breeding within the study population (timing = hatching date – annual median of hatching dates). Both linear and quadratic terms of 'synchrony' and 'timing' were tested. 'Synchrony' and 'timing' were highly correlated (r_s >0.6) in *P. major* and *C. caeruleus* and therefore they were not allowed to enter the same model in any of the species for comparison's sake.

Additional explanatory variables were included in the analysis to control for effects of caterpillar peak height, female age, breeding density and clutch size. All two-way interaction terms between 'synchrony', 'synchrony^2', 'timing', 'timing^2' and peak height and other variables were allowed for. Female identity was considered as a block random factor in all tested models. Models were ranked according to AIC values.

2.4.5 Nest site selection analysis (III)

To study the nest site selection of *P. montanus*, the habitat composition of the breeding territories was compared with the composition of randomly selected unoccupied sites. As preliminary analysis, the average values of habitat variables were compared between the occupied and unoccupied sites with two-sided Mann-Whitney U test. In addition, the availability of snags (i.e., standing decaying deciduous trees) in each habitat class was studied. Generalized linear mixed-effect models were used to investigate the importance of different habitat variables for the nest site selection. The response variable was the presence or absence of a *P. montanus* nest in a given location.

The analysis was conducted in two stages. First, only the effects of the habitat variables that could be determined by remote sensing methods were considered. At the second stage, also the availability of nesting sites, snags, determined by direct field surveys (variable snag and its two-way interactions with the habitat type variables), was taken into consideration. *Poecile montanus*' favor to habitat types is expected to be conditional on the availability of snags. Year was treated as a block random factor. The models were ranked according to AICc.

To roughly describe the model performance, the model accuracy (*A*) was determined for the averaged models. First, the expected nesting probabilities for each data point were calculated. Nesting probabilities <0.5 were determined as "expected absence" and ≥ 0.5 as "expected presence". The observed and expected values were then compared and accuracies (*A*) were calculated as the proportion of successful predictions. Accuracy larger than 0.5 indicates that the model predicts the presence or absence of a nest better than at random.

3 Results

3.1 The effects of warming climate on phenologies, synchrony and breeding success

3.1.1 Temporal trends and changes in synchrony (I, II)

The median egg-laying date of *P. montanus* advanced 0.16 days a year in 1975–2009 (Fig. 1). When considering the years 1996–2009, the trend was more pronounced although not significant, ca. 0.24 days a year. For *P. major*, corresponding advancement rates were ca. 0.15 days per year in 1969–2011 and ca. 0.34 a year in 1996–2011. For *C. caeruleus*, no temporal trend in the onset of egg laying was detected for 1998–2011. Caterpillar peak date had an advancing trend, ca. 0.86 days per year in 1996–2011. However, the trend was overemphasized by an extraordinary late year in the beginning of the time series (1997). When caterpillar peak dates were estimated for 1969–2011 by using the mean temperatures of the best correlative temperature period (see below), the trend was more gradual, ca. 0.24 days per year. The observed trend of caterpillars did not significantly differ from the trends of *P. montanus* or *P. major*.

Synchrony with the caterpillar peak was fairly good during the study period in *P. major* and *C. caeruleus* (Fig. 2). In *P. montanus*, breeding has generally taken place early in respect to timing of the caterpillar peak. With advancing caterpillar peaks (Fig. 1), the synchrony between the caterpillar peak and food demands of *P. montanus* improved (Fig. 2), although the trend is not statistically significant (b=0.752, SE=0.399, t=1.883, p=0.084). The timing of breeding matched better with the caterpillar availability (i.e., the period when the caterpillar biomass was over the threshold value of 0.1 g m^{-2}) in the second half of the study period (2003–2009) than in the first half (1996–2002) in *P. montanus*. No signs of increasing asynchrony can be seen in any of the species studied over the study years.

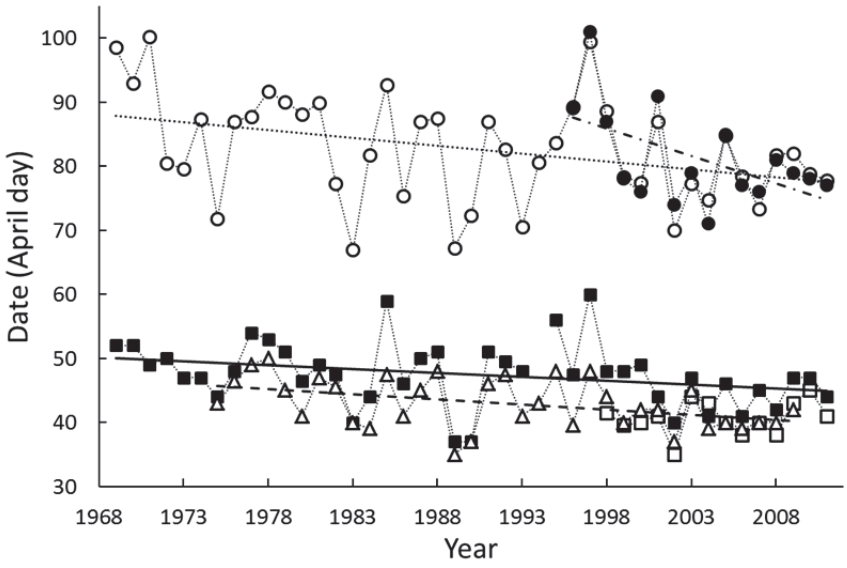

Fig. 1. Timing of the median onset of egg-laying of *Parus major* (sub-areas pooled, closed squares), *Cyanistes caeruleus* (open squares), *Poecile montanus* (open triangles), and the caterpillar peak dates (closed circles) in the Oulu area. Temporal trend is statistically significant for *P. montanus* (broken line), nearly significant for *P. major* (solid line), and for the caterpillar peak dates (dash dot line) and non-significant for *C. caeruleus*. Open circles represent caterpillar peak dates estimated by the mean temperatures of 13 March–25 May and the dotted line the corresponding temporal trend.

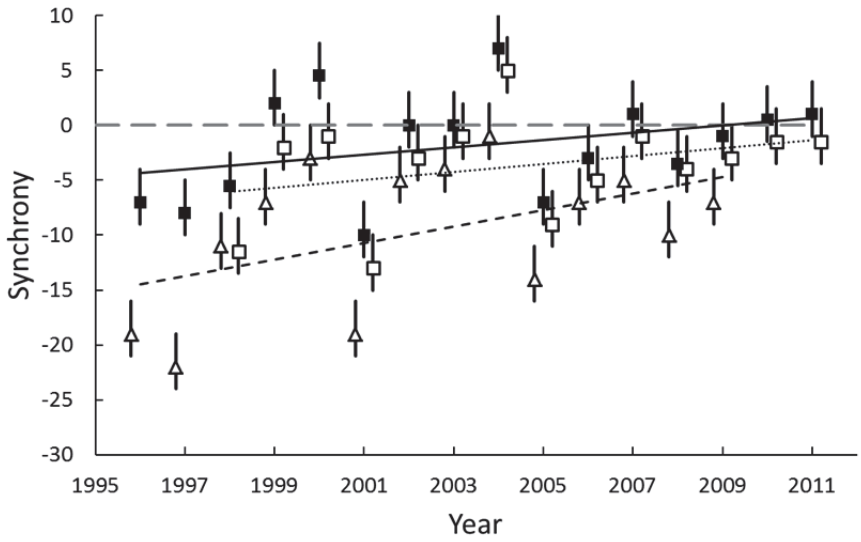

Fig. 2. The changes in synchrony with the caterpillar peak in *Parus major* (closed squares, solid line), *Cyanistes caeruleus* (open squares, dotted line) and *Poecile montanus* (open triangles, broken line). The grey broken line indicates the timing of the caterpillar peak date (synchrony = 0). Vertical bars represent the period of the highest food demand in average timed nests (nestlings are 8–13 days old). Synchrony is considered to be "good" if the period of the highest food demand co-occurs with the caterpillar peak date. The trends are statistically non-significant (for *P. major* b=0.334, p=0.205; for *C. caeruleus* b=0.362, p=0.263; for *P. montanus* b=0.752, p=0.084).

3.1.2 The relationship between temperature and phenologies (I, II)

Phenologies were highly correlated with spring temperatures (Table 1). Both the caterpillar peaks and the onset of egg laying occurred earlier in warm springs than in cool ones (Table 1, Fig. 3). Caterpillar peaks advance at the same rate with *P. major*'s laying date when the mean temperature of the spring period 29 March–15 May increases. Similarly, phenologies of *C. caeruleus* and caterpillars advance in parallel with increasing mean temperatures of the period 24 March–10 May.

However, caterpillars respond with different rates than *P. montanus* to the temperature changes of the spring period best correlating with their laying dates (Fig. 3). If birds used the temperature of the spring period as a predictive cue for the timing of caterpillars as suggested by Visser *et al*. (2006) and acted

accordingly, the responses should be alike. When the synchrony values at the population level (synchrony = median hatching date + 10 – caterpillar peak date) in *P. montanus* were regressed against mean temperatures of 25 March–5 May, the trend was positive (b=2.709, SE=1.065, t=2.544, p=0.026), indicating that rising spring temperatures lead to improving synchrony.

The mean temperature of the caterpillar peak's impact period rose nearly significantly, 0.12°C per year, during 1996–2011. The mean temperature of *P. major*'s impact period increased 0.05°C per year during 1969–2011. For the *C. caeruleus*' temperature period, no change was detected in 1998–2011 and for the *P. montanus*' period, the rising trend of 0.04°C per year was non-significant in 1975–2009.

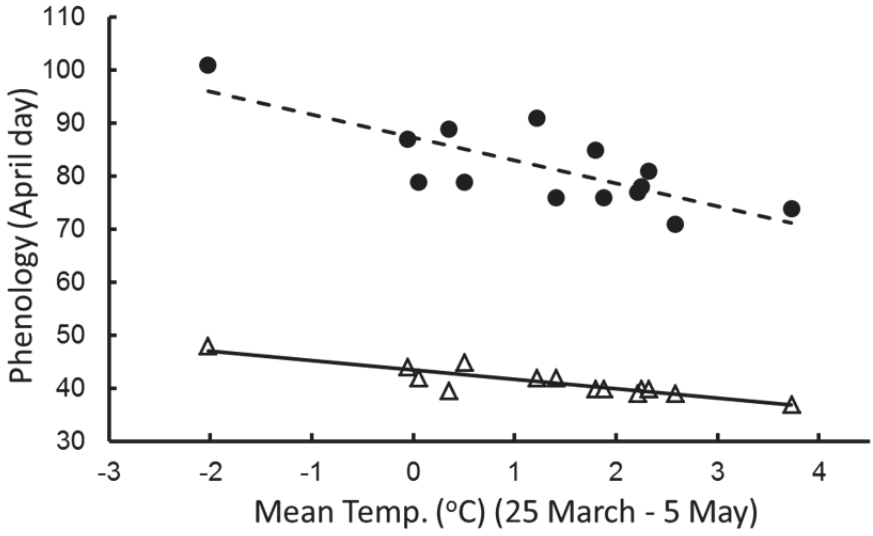

Fig. 3. *Poecile montanus* laying dates (open triangles) and caterpillar biomass peak dates (closed circles) in 1996–2009 against the mean temperature of March 25–May 5. The solid line is the linear regression line for the laying date and the dashed line for the caterpillar peak date on temperature. (Modified from Fig. 2 in I, published by permission of Wiley-Blackwell.)

Table 1. Best correlative temperature periods for the caterpillar peak date and median egg-laying dates (LD) of *Parus major*, *Cyanistes caeruleus* and *Poecile montanus*.

Phenology	Years	Temperature period	r	df
Caterpillar peak date	1996–2011	13 March–25 May	-0.955***	15
Parus major LD	1969–2011	29 March–15 May	-0.849***	41
Cyanistes caeruleus LD	1998–2011	24 March–10 May	-0.866**	13
Poecile montanus LD	1975–2009	27 March–6 May	-0.847***	34

*** $p < 0.001$; ** $p < 0.01$

3.1.3 The effects of synchrony and timing on breeding success (II)

Synchrony with the caterpillar peak affected quality and number of fledged young in all studied species and it seems to have more explanatory power than timing of breeding *per se*. 'Synchrony' models outcompeted 'timing' models in explaining breeding success in all three species, expect for the mean nestling mass in *C. caeruleus* where the top model set comprised both 'synchrony' and 'timing' models. However, the synchrony effect appears to be conditional, as different levels of caterpillar abundance (measured as caterpillar peak height), female age or breeding density resulted in differing responses.

Good synchrony improves nestling quality measured as mean nestling mass in *P. major* only if the caterpillar peak is high. The nestlings grow slightly heavier if the caterpillar peak occurs some days later than the expected timing of the highest food demand. In *C. caeruleus*, well-synchronized breeders had heavier nestlings than both very early and very late ones, and older females seemed to benefit from breeding later (in respect to timing of the caterpillars or timing of the population average) than the yearlings. Also for *P. montanus*, birds in good synchrony have heavier nestlings than birds breeding before the caterpillar peak. The effect is more pronounced in high breeding densities and in large clutches. In all three species, nestlings grew on average heavier in years of high caterpillar peaks or when raised by older females. Nestlings in large broods were lighter than in small ones. Negative density effect was found in *P. major* and *P. montanus*, but not in *C. caeruleus*.

For all three species, the number of fledged young was on average highest in broods that were timed some days before the caterpillar peak. Yet, the difference in fledgling production is irrelevantly small between the synchrony values with the highest score and synchrony value 0. For *P. major* and *P. montanus*, the effect of synchrony was more intense with high caterpillar peaks. In addition, for *P.*

montanus the highest number of fledged young was attained in different phases of synchrony in different breeding densities and age groups: young females performed better when breeding a little later than older females. The number of fledglings was typically larger in years of high caterpillar abundance and in large broods in all studied species. Older females usually produced more fledglings than young females in *P. major* and *C. caeruleus*. A negative effect of breeding density could be found only in *P. montanus*.

3.2 Identification of the key habitat characteristics (III)

Remote sensing data alone turned out to be insufficient for identification of the key habitat characteristics for *P. montanus*, indicated by low model accuracies. Allowing for an ecologically important small-scale habitat element that could be determined only by direct field surveys, the availability of nesting sites greatly improved model performance. The availability of snags was by far the most important habitat characteristic determining nest site selection in *P. montanus*. It seemed to prefer moist habitats with high densities of deciduous trees and to avoid open areas, but did not require mature or intact habitats for breeding. Most of the habitat selection seemed to occur at a small scale.

4 Discussion

The research has both theoretical and practical implications. Theoretical offerings contribute to the knowledge of the effects of climate change on synchrony and proximate and ultimate factors affecting an important life-history trait, timing of breeding. Meanwhile, practical recommendations propose changes in forestry practices for sustainable development. I discuss the reliability of the analysis and give suggestions for further research.

4.1 Theoretical implications

4.1.1 Generality of climate change-driven temporal mismatches in birds (I, II)

Warming spring temperatures seem to affect the level of synchrony between the highest energy demands of nestling and the availability of food (insect caterpillars) in a boreal population of *P. montanus*, but not in *P. major* or *C. caeruleus*. In the Netherlands, climate change has led to asynchrony between the timing of breeding of *P. major* and *C. caeruleus* and the abundance of caterpillars feeding on oak leaves (Visser *et al*. 1998, 2006, Both *et al*. 2009). However, most studies in *P. major* have not found signs of climate change-driven temporal mismatches: in Wytham Wood, UK (Cresswell & McCleery 2003, Charmantier *et al*. 2008), in the Czech Republic (Bauer *et al*. 2010) or in Belgium (Matthysen *et al*. 2011). In fact, the observed change in synchrony in *P. montanus* is one of the few verified cases of improving temporal match between food availability and food needs (see also Both *et al*. 2009 for the Coal Tit *Parus ater*). Temporal mismatches may be more common and irremediable in long-distance migrants (e.g. Both *et al*. 2010, Saino *et al*. 2011), but exceptions to this rule exist (Bauer *et al*. 2010, Townsend *et al*. 2013).

4.1.2 Reliability of temporal trends in phenology

Observed temporal trends in variables of a cyclic nature, such as in climate-related phenologies, can be largely affected by the cycle phases at the start and end of the data series. For example, according to the observed trend, the timing of the caterpillar peak seems to advance at a considerably fast rate (I, II). However,

the true trend is likely somewhat gentler, as the beginning of the caterpillar time series happened to take place at a period of years with cool springs (I, II). The longer the time series, the more reliable the observed overall trend behind the cycles. But then again, it would be irrational to expect that true changes would happen linearly over long time periods.

4.1.3 Temperature as a proximate factor in phenologies (I, II)

Visser *et al*. (2006, 2009) suggest that birds use spring temperature as a cue for the timing of the food peak, as temperature seems to affect predator and prey phenologies similarly. In the current study, similar responses to spring temperatures among phenologies of *P. major*, *C. caeruleus* and caterpillars were found. However, the temperature period defined for *P. montanus* did not seem to function as a cue about timing of the caterpillars. The temperature cue to reproductive endocrinology and gonadal growth in male *P. major* becomes decreasingly less important with increasing latitudes (Silverin *et al*. 2008). However, in the north the indirect effects of spring temperatures on bird phenologies, e.g. via thermoregulation and food availability in the early breeding stages, may have more weight compared to southern latitudes (Bourgaut *et al*. 2010).

4.1.4 Temperature as an ultimate factor in phenologies (II)

Synchrony seems to explain variation in quality and number of fledglings better than timing of breeding *per se* in all three species. However, the positive effect of good synchrony on breeding success seems to arise only in certain conditions, such as with high caterpillar abundances, or high breeding densities. Thus, the temporal mismatch hypothesis alone may be insufficient in explaining the evolution of timing of breeding in boreal populations. Dunn *et al*. (2011) note that the mismatch hypothesis may not apply in environments with constant or high food abundance. This idea could be generalized to state that the temporal mismatch hypothesis may not apply in environments where the food availability does not have pronounced peaks, either because of constantly high or relatively low food availability (see also Burger *et al*. 2012). Caterpillar availability is substantially lower in boreal forests than in temperate broad-leaved forests (Rytkönen & Krams 2003). In Oulu, the caterpillar biomass has always been less

than 1 g m^{-2}, whereas for example in the Netherlands, the caterpillar biomasses in oak woods can be more than 60 g m^{-2} (van Balen 1973).

The models describing breeding success explained only part of the variation in response variables (7–57%, II). This suggests that some important factors are not taken into account. The aim of the analysis was not to describe in detail all factors that affect breeding success but to test if synchrony with the food peak matters. Nevertheless, I acknowledge that changing the model structure (i.e., including other variables) might affect the parameter estimates of the variables of interest as well as their standard errors, and thus influence the interpretation. For example, parents' individual properties, infections and other diseases, weather conditions during the nestling period or habitat composition of the breeding territories might be worth considering. However, reliable data on many of these variables is lacking. In addition, further research is needed to identify the habitat and weather characteristics that matter.

If changing spring temperatures do not affect the level of synchrony between two trophic levels (as seems to be the case in *P. major* and *C. caeruleus*), temperature will have little effect as an ultimate factor in phenologies via this mechanism. Even in a Dutch *P. major* population where climate change has induced a phenological mismatch, although synchrony with the food availability does influence the nestling production (e.g. Visser *et al*. 2006), it may have only weak effect on the population growth rate if recruitment is density-dependent (Reed *et al*. 2013a). Also other timing- and temperature-related factors contribute to the adaptation of timing of breeding in birds (Eeva *et al*. 2000, Rytkönen & Orell 2001), the strength of which can be altered by the climate change. As springs and autumns become warmer, the growing period becomes longer and snow fall will be delayed (Jylhä *et al*. 2007, Ruosteenoja *et al*. 2011). This would affect the food availability and thermoregulatory costs during the egg laying and incubation periods (Perrins 1965, Bryant 1975, Stevenson & Bryant 2000, Dunn *et al*. 2011) and give more time for birds to moult and hoard in the autumn (Eeva *et al*. 2000). Thus, they may be the key mechanisms through which the climate change affects timing of breeding.

The results of the effects of synchrony on breeding success in this study imply that boreal Parid populations might experience a situation of adaptive mismatch: reproductive outcome seems to be the highest when breeding some days before the caterpillar peak. However, the interpretation is not unambiguous. Such a pattern may arise because of some timing-related factor that was not taken into account in the analysis causes true adaptive mismatch, or just because the

definition of the period of the highest energy demands in nestlings, and therefore the definition of "good synchrony", may be incorrect.

4.1.5 Nest site selection analysis

Remote sensing data alone appears insufficient for identifying the high-quality habitats. This is the case for species that require some small-scale elements, such as specific type of nesting sites that cannot be located with remote sensing methods. This is unfortunate, as proper models built with pure remote sensing data could be used to pinpoint high-quality habitats over vast areas, and this information could be further used for conservation planning. Nevertheless, Luoto *et al*. (2002) were successful in modeling the distribution of the threatened Clouded Apollo butterfly (*Parnassius mnemosyne* L.) with pure remote sensing data. They managed to define remote sensing variables that could replace the ecologically important factor, the distribution of the larval host plant *Corydalis solida* L. (Luoto *et al*. 2001), but unfortunately their model seems to function only in a restricted geographical area.

Nest site selection analysis in this study is limited to within territory inspection. Habitat selection that may occur in larger scales during natal dispersal of *P. montanus* is thus overlooked. In a more or less continuous forest landscape, an approach describing selection of forest patches (Newton 1998) seems inappropriate. It would be possible to describe habitat compositions of nest sites over larger scales (i.e., to use larger buffers), but the geographical extent of the study area may be too small for having enough variation in the data. Searching for nests and snags over larger areas would again be very laborious. In addition, one cannot tell apart the effects of nesting site availability alone and other possible correlative factors linked to the same habitats (e.g. food availability).

4.1.6 Validity of multi-model inference

Interpretation of averaged parameter estimates instead of point estimates derived from averaged models may not be a fully appropriate statistical approach. The key issue is the way model averaging uses model weights (w_i) to weight parameter estimates from different models. Model weights describe the performance of the model as a whole, but it may not reflect the parameter estimate's accuracy of a single variable. Such use of weights is justified only if the goodness of the model (here measured with information criterion) is

determined by the accuracy of the parameter estimates. This is at least partly true. The idea of averaging the parameter estimates arises from the need to take the insecurity of the model selection into account. However, I am rather confident about the analysis ability to identify the most important factors and to give them parameter estimates of right sign.

4.2 Practical implications for developing forestry practices

The results from the nest site selection analysis in *P. montanus* give rise to practical implications for sustainable forestry planning. The availability of nesting sites, standing decaying deciduous trees, is the key habitat characteristic for *P. montanus*. Decreased nesting site availability is one of the plausible causes for the descending trend in the population size. For the conservation and maintenance of dead wood-dependent species, changes in forestry practices are necessary to maintain the habitat quality. Most importantly, continuous availability of standing decaying wood should be guaranteed (Siitonen 2001, Tikkanen *et al*. 2012). Repeated thinning and removal of deciduous trees, bushes and dead trees prevents the formation of new decaying trees. Omission of such actions in selected forest sites would contribute to the emergence of decaying wood also in younger forest stages. This would be a cost-effective means to maintain biodiversity in managed forests (Tikkanen *et al*. 2012).

4.3 Recommendations for further research

In this study, the fitness effects of temporal synchrony with the food availability were studied only in respect of the breeding success during the nestling period. It would be very interesting to investigate synchrony's fitness consequences in regard to the recruiting ability of the nestlings, as well as to the survival and future breeding success of the parents. This would promote our understanding of the effects of climate change on population demographical processes.

Studying climate change-driven temporal mismatches has been a hot topic in recent years. I would like to remind that climate change may affect phenologies via various other mechanisms, some of which may be more relevant than synchrony, especially in high latitudes. Proximate and ultimate factors affecting timing of breeding vary between populations and species (Ludwig *et al*. 2006, Waite & Strickland 2006, Lehikoinen *et al*. 2011). Further research is needed in different trophic levels in many climatic zones, habitats and species to pinpoint

the mechanisms through which climate change affects phenologies and population demographics in different geographical areas and ecosystems.

Species' ability to endure in changing environments depends on their adaptation capability. Wild populations can adapt to changing environments by phenotypic plasticity or microevolution. Methods of quantitative genetics (e.g. Postma & Charmantier 2007) are used to obtain measures of existing genetic variation behind traits of interest. Long-term datasets with pedigree information are pivotal for this type of analysis. Again, populations and species may differ in their potential for adaptation and thus wide-ranging research is needed to accomplish a general view of the evolutionary potential and possible consequences to biodiversity.

For identifying high-quality habitats over large geographical areas, the challenge is to find ways to code the ecologically important small-scale habitat elements with remote sensing data. In some cases that might be an impossible task. Also, habitat quality cannot always be described by interpreting habitat selection only, as the ultimate definition of habitat quality is determined by breeding success and survival in a given habitat. Thus, the fitness consequences of selecting a habitat should be studied as well (Jones 2001).

5 Conclusions

Climate warming affects phenologies in both invertebrates and insectivorous birds: timing of the caterpillar peak has advanced and so has timing of breeding in northern populations of *P. montanus* and *P. major*. These phenological changes have not, however, led to temporal mismatches between the food availability and food demands in *P. montanus*, *P. major* or *C. caeruleus*. In fact, this study presents one of the few documented cases of improving synchrony, in *P. montanus*. The positive effect of good synchrony on breeding success seems to be conditional, arising in years with high insect caterpillar abundances or high breeding densities. Some implications of adaptive mismatch or possibly incorrect definition of "good synchrony" were found. Spring temperatures seem to function mainly as a proximate factor in timing of breeding.

Human land use causes habitat loss and degradation. For instance, many boreal forest bird populations have declined during recent decades, likely due to intensive forestry. In this study, I searched for habitat elements that should be maintained in order to preserve biodiversity in managed boreal forests. As a case example, I studied the nest site selection of *P. montanus*. Remote sensing data alone seems insufficient for identifying ecologically important habitat features. The study shows that the availability of standing decaying trees, used for nesting sites, is the key habitat feature for *P. montanus*. Securing continuity in the availability of decaying wood is important for the biodiversity in managed forests. Changes in forestry practices are needed to develop sustainable forestry.

References

Alatalo RV (1981) Habitat selection of forest birds in the seasonal environment of Finland. Ann Zool Fenn 18: 103–114.

Alatalo RV, Lundberg A & Ulfstrand S (1985) Habitat selection in the Pied Flycatcher *Ficedula hypoleuca*. In: Cody ML (ed.) Habitat selection in birds. Orlando, Academic Press: 59–83.

Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. J Wildl Man 74: 1175–1178.

Balen JH van (1973) A comparative study of the breeding ecology of the great tit *Parus major* in different habitats. Ardea 61: 1–93.

Bauer Z, Trnka M, Bauerová J, Možný M, Štěpánek P, Bartošova L & Žalud Z (2010) Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. Int J Biom 54: 99–111.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH. & White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24: 127–135.

Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, Eeva T, Enemar A, Gustafsson L, Ivankina EV, Järvinen A, Metcalfe NB, Nyholm NEI, Potti J, Ravussin P-A, Sanz JJ, Silverin B, Slater FM, Sokolow LV, Török J, Winkel W, Wright J, Zang H & Visser ME (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proc R Soc Lond B 271: 1657–1662.

Both C, Asch M van, Bijlsma RG, Burg AB van den & Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? J Anim Ecol 78: 73–83.

Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ & Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc R Soc Lond B 277: 1259–1266.

Bourgault P, Thomas D, Perret P & Blondel J (2010) Spring vegetation phenology is a robust predictor of breeding date across broad landscapes: a multi-site approach using the Corsican blue tit (*Cyanistes caeruleus*). Oecologia 162: 885–892.

Brazill-Boast J, Pryke SR & Griffith SC (In press) Provisioning habitat with custom-designed nest-boxes increases reproductive success in an endangered finch. Austral Ecol.

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 Fenn 73: 114–118.

Bryant DM (1975) Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. Ibis 117: 180–216.

Burger C, Belskii E, Eeva T, Laaksonen T, Mägi M, Mänd R, Qvarnström A, Slagsvold T, Veen T, Visser ME, Wiebe KL, Wiley C, Wright J & Both C (2012) Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. J Anim Ecol 81: 926–936.

Burnham KP & Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach, 2nd edn. Springer.

Catry I, Alcazar R, Franco AMA & Sutherland WJ (2009) Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. Biol Cons 142: 2782–2791.

Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB & Sheldon BC (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320: 800–803.

Costello JH, Sullivan BK & Gifford DJ (2006) A physical-biological interaction underlying variable phenological responses to climate change by coastal zooplankton. J Plank Res 28: 1099–1105.

Cramp S, Perrins CM, Brooks DJ, Dunn E, Gillmor R, Hall-Craggs J, Hillcoat B, Hollom PAD, Nicholson EM, Roselaar CS, Seale WTC, Sellar PJ, Simmons KEL, Snow DW, Wincent D, Voous KH, Wallace DIM & Wilson MG (1993) Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Volume VII Flycatchers to Shrikes. Oxford University Press.

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. J Anim Ecol 72: 356–366.

Dawson A (2002) Photoperiodic control of the annual cycle in birds and comparison with mammals. Ardea 90: 355–367.

Dawson A (2008) Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. Philosophical Transactions B 363: 1621–1633.

Doherty PF & Grubb TC (2002) Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83: 844–857.

Donnelly A, Caffarra A & O'Neill BF (2011) A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. Int J Biom 55: 805–817.

Donovan TM & Flather CH (2002) Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecol Appl 12: 364–374.

Dudley N & Vallauri D (2004) Deadwood – living forests. URI: http://assets.panda.org/downloads/deadwoodwithnotes.pdf. Cited 2010/6.

Dunn P (2004) Breeding dates and reproductive performance. Adv Ecol Res 35: 69–87.

Dunn PO, Winkler DW, Whittingham LA, Hannon SJ & Robertson RJ (2011) A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? Ecology 92: 450–461.

Durant JM, Hjerman DØ, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N & Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecol Lett 8: 952–958.

Durant JM, Hjermann DØ, Ottersen G & Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33: 271–283.

Eeva T, Veistola S & Lehikoinen E (2000) Timing of breeding in subarctic passerines in relation to food availability. Can J Zool 78: 67–78.

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.

Forsman JT, Hjernquist MB, Gustafsson L (2009) Experimental evidence for the use of density based interspecific social information in forest birds. Ecography 32: 539–545.

Fretwell SD & Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor XIX: 16–36.

Grueber CE, Nakagawa S, Laws RJ & Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24: 699–711.

Gustafsson L, Kouki J & Svedrup-Thygeson A (2010) Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. Scand J For Res 25: 295–308.

Hau M, Wikelski M & Wingfield JC (2000) Visual and nutritional food cues fine-tune timing of reproduction in a Neotropical rainforest bird. J Exp Zool 286: 494–504.

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.

Hoyo J del, Elliott A & Christie D (2007) Handbook of the birds of the world, Vol. 12. Picathartes to tits and chickadees. Lynx Edicions.

Hurme E, Mönkkönen M, Reunanen P, Nikula A & Nivala V (2008) Temporal patch occupancy dynamics of the Siberian flying squirrel in a boreal forest landscape. Ecography 31: 469–476.

Ihalainen A & Mäkelä H (2009) Kuolleen puuston määrä Etelä- ja Pohjois-Suomessa 2004-2007. Folia Forestalia 1/2009: 35–56.

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 6: 65–71.

Jones CG (2004) Conservation management of endangered birds. In: Sutherland WJ, Newton I & Green RE (eds) Bird Ecology and Conservation. A Handbook of Techniques. Oxford University Press: 269–302.

Jones J (2001) Habitat selection studies in avian ecology: a critical review. Auk 118: 557–562.

Jylhä K, Ruosteenoja K, Räisänen P & Järvenoja S (2007) Projected changes in heavy precipitation and snow cover in Finland. Proc Climate change impacts and adaptation in the hydrology of urban areas. Third International Conference on Climate and Water. Helsinki, Finland: 227-232.

Järvinen O, Kuusela K & Väisänen RA (1977) Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. Silva Fenn 11: 284–294.

Karvonen J, Orell M, Rytkönen S, Broggi J & Belda E (2012) Population dynamics of an expanding passerine at the distribution margin. J Avian Biol 43: 102–108.

Koivula K & Orell M (1988) Social rank and winter survival in the willow tit *Parus montanus*. Ornis Fenn 65: 114–120.

Koivula K, Lahti K, Orell M & Rytkönen S (1993) Prior residency as a key determinant of social dominance in the willow tit (*Parus montanus*). Behav Ecol Sociobiol 33: 283–287.

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

Kvist L, Ruokonen M, Lumme J & Orell M (1999) Different population structures in northern and southern populations of the European blue tit (*Parus caeruleus*). J Evol Biol 12: 798–805.

Lack D (1950) The breeding seasons of European birds. Ibis 92: 288–316.

Lahti K (1997) Social status and survival strategies in the willow tit *Parus montanus*. Acta Univ Oul A 292.

Lahti K, Orell M, Rytkönen S & Koivula K (1998) Time and food dependence in willow tit winter survival. Ecology 79: 2904–2916.

Lambrechts MM, Adriaensen F, Ardia DR, Artemyev AV, Atiénzar F, Bańbura J, Barba, E, Bouvier J-C, Camprodon J, Cooper CB, Dawson RD, Eens M, Eeva T, Faivre B, Garamszegi LZ, Goodenough AE, Gosler AG, Grégoire A, Griffith SC, Gustafsson L, Johnson LS, Kania W, Keišs O, Llambias PE, Mainwaring MC, Mänd R, Massa B, Mazgajski TD, Møller AP, Moreno J, Naef-Daenzer B, Nilsson J-Å, Norte AC, Orell M, Otter KA, Park CR, Perrins CM, Pinowski J, Porkert J, Potti J, Remes V, Richner H, Rytkönen S, Shiao M-T, Silverin B, Slagsvold T, Smith HG, Sorace A, Stenning MJ, Stewart I, Thompson CF, Tryjanowski P, Török J, Noordwijk AJ van, Winkler DW & Ziane N (2010) The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithol 45: 1–26.

Lampila P, Mönkkönen M & Desrochers A (2005) Demographic responses by birds to forest fragmentation. Conserv Biol 19: 1537–1546.

Lampila S, Orell M, Belda E & Koivula K. (2006) Importance of adult survival, local recruitment and immigration in a declining boreal forest passerine, the willow tit *Parus montanus*. Oecologia 148: 405–413.

Lehikoinen A, Ranta E, Pietiläinen H, Byholm P, Saurola P, Valkama J, Huitu O, Henttonen H & Korpimäki E (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. Oecologia 165: 349–355.

Lewis AJG, Amar A, Cordi-Piec D & Thewlis RM (2007) Factors influencing Willow Tit *Poecile montanus* site occupancy: a comparison of abandoned and occupied woods. Ibis 149: 205–213.

Li P & Martin TE (1991) Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108: 405–418.

Lof ME, Reed TE, McNamara JM & Visser ME (2012) Timing in a fluctuating environment: environmental variability and asymmetric fitness curves can lead to adaptively mismatched avian reproduction. Proc R Soc B 279: 3161–3169.

Ludwig GX, Alatalo RV, Helle P, Lindén H, Lindström J, Siitari H (2006) Short- and long-term population dynamical consequences of asymetric climate change in black grouse. Proc R Soc Lond B 273: 2009–2016.

Luoto M, Kuussaari M, Rita H, Salminen J & von Bonsdorff T (2001) Determinants of distribution and abundance in the clouded apollo butterfly: a landscape ecological approach. Ecography 24: 601–617.

Luoto M, Kuussaari M & Toivonen T (2002) Modelling butterfly distribution based on remote sensing data. J Biogeogr 29: 1027–1037.

Lyon BE, Chaine AS & Winkler DW (2008) A matter of timing. Science 321: 1051–1052.

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18: 453–487.

Martin T (1993) Nest Predation and Nest Sites. BioScience 43: 523–532.

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

Matthysen E, Adriaensen F & Dhondt AA (2011) Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus major*). Glob Change Biol 17: 1–16.

Naef-Daenzer B & Keller LF (1999) The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J Anim Ecol 68: 708–718.

Nager RG & Noordwijk AJ van (1992) Energetic limitation in the egg-laying period of great tits. Proc R Soc Lond B 249: 259–263.

Nager RG & Noordwijk AJ van (1995) Proximate and ultimate aspects of phenotypic plasticity in timing of Great Tit breeding in a heterogenous environment. Am Nat 146: 454–474.

Newton I (1994) The role of nest sites in limiting the number of hole-nesting birds: a review. Biol Cons 70: 265–276.

Newton I (1998) Population Limitations in Birds. Academic Press.

Nilsson SG (1984) The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand 15: 167–175.

Opdam P & Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol Cons 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, 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.

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 Scand 11: 43–49.

Orell M & Ojanen M (1983a) Effect of habitat, date of laying and density on clutch size of the Great Tit *Parus major* in northern Finland. Holarctic Ecol 6: 413–423.
Orell M & Ojanen M (1983b) Breeding biology and population dynamics of the willow tit *Parus montanus*. Ann Zool Fenn 20: 99–114.
Orell M & Ojanen M (1983c) 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.
Pakkala T, Hanski I & Tomppo E (2002) Spatial ecology of the three-toed woodpecker in managed forest landscapes. Silva Fenn 36: 279–288.
Parmesan C & Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.
Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37: 637–69.
PECBMS (Pan-European Common Bird Monitoring Scheme) (2012) Trends of common birds in Europe, 2012 update. URI: http://www.ebcc.info/index.php?ID=485 Cited 2012/11.
Pereira HM, Navarro LM & Martins IS (2012) Global biodiversity change: the bad, the good, and the unknown. Annu Rev Env Resour 37: 25–50.
Perrins CM (1965) Population Fluctuations and Clutch-Size in the Great Tit, *Parus major* L. J Anim Ecol 34: 601–647.
Perrins CM (1970) The timing of birds' breeding seasons. Ibis 112: 242–255.
Perrins CM (1991) Tits and their caterpillar food supply. Ibis 133 Suppl. 1: 49–54.
Postma E & Charmantier A 2007. What 'animal models' can and cannot tell ornithologists about the genetics of wild populations. J Ornithol 148 Suppl. 2: S633–S642.
Ramsay SM, Otter K & Ratcliffe LM (1999) Nest-site selection by female black-capped chickadees: settlement based on conspesific attraction? Auk 116: 604–617.
Raphael MG & White M (1984) Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl Monogr 86.
Reed TE, Grøtan V, Jenouvrier S, Sæther B-E & Visser ME (2013) Population growth in a wild bird is buffered against phenological mismatch. Science 340: 488–491.
Reed TE, Jenouvrier S & Visser ME (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. J Anim Ecol 82: 131–144.
Robinson SK, Thompson FR III, Donovan TM, Whitehead DR & Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987–1990.
Ruosteenoja K, Räisänen J & Pirinen P (2011) Projected changes in thermal seasons and the growing season in Finland. Int J Clim 31: 1473–1487.
Rytkönen S, Koivula K & Orell M (1996) Patterns of per-brood and per-offspring provisioning efforts in the Willow Tit *Parus montanus*. J Avian Biol 27: 21–30.
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.

Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Hüppop K, Hüppop O, Lehikoinen A, Lehikoinen E, Rainio K, Romano M & Sokolov L (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proc R Soc Lond B 278: 835–842.

Sanz JJ (2002) Climate change and breeding parameters of great and blue tits throughout the western Palearctic. Glob Change Biol 8: 409–422.

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1: 103–113.

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.

Siitonen J (2001) Forest mamagement, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49: 11–41.

Silverin B, Wingfield J, Stokkan K-A, Massa R, Järvinen A, Andersson N-Å, Lambrechts M, Sorace A & Blomqvist D (2008) Ambient temperature effects on photo induced gonadal cycles and hormonal secretion patterns in Great Tits from three different breeding latitudes. Horm Behav 54: 60–68.

Stauffer DF & Best LB (1982) Nest site selection by cavity-nesting birds of riparian habitats in Iowa. Wilson Bull 94: 329–337.

Stevenson IR & Bryant DM (2000) Climate change and constraints on breeding. Nature 406: 366–367.

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 Cons 121: 443–452.

Svensson L (1997) Euroopan varpuslinnut – sukupuolen ja iän määritys. Gummerus.

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ & Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Change Biol 16: 3304–3313.

Thomas DW, Bourgault P, Shipley B, Perret P & Blondel J (2010) Context-dependent changes in the weighting of environmental cues that initiate breeding in a temperate passerine, the Corsican blue tit (*Cyanistes caeruleus*). Auk 127: 129–139.

Tikkanen O-P, Matero J, Mönkkönen M, Juutinen A & Kouki J (2012) To thin or not to thin: bio-economic analysis of two alternative practices to increase amount of coarse woody debris in managed forests. Eur J Forest Res 131: 1411–1422.

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

Tomppo E, Haakana M, Katila M & Peräsaari J (2008) Multi-Source National Forest Inventory. Methods and Applications. Manag For Ecosyst 18.

Townsend AK, Sillett TS, Lany NK, Kaiser SA, Rodenhouse NL, Webster MS & Holmes RT (2013) Warm springs, early lay dates, and double brooding in a North American migratory songbird, the Black-Throated Blue Warbler. PLoS ONE 8: e59467.

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc R Soc Lond B 270: 467–473.Verboven N & Visser ME (1998) Seasonal variation in local recruitment of great tits: the importance of being early. Oikos 81: 511–524.

Verhulst S & Nilsson J-Å (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philos T Roy Soc B 363: 399–410.

Villard M-A, Trzcinski MK & Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Cons Biol 13: 774–83.

Visser ME, Adriaensen F, Balen JH van, Blondel J, Dhondt AA, Dongen S van, du Feu C, Ivankina EV, Kerimov AB, de Laet J, Matthysen E, McCleery R, Orell M & Thomson DL (2003) Variable responses to large-scale climate change in European *Parus* populations. Proc R Soc Lond B 270: 367–372.

Visser ME, Both C & Lambrechts MM (2004) Global climate change leads to mistimed avian reproduction. Adv Ecol Res 35: 89–110.

Visser ME & Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. Proc R Soc Lond B 268: 289–294.

Visser ME, Holleman LJM & Caro SP (2009) Temperature has a causal effect on avian timing of reproduction. Proc R Soc Lond B 276: 2323–2331.

Visser ME, Holleman LJM & 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 ME, te Marvelde L & Lof ME (2012) Adaptive phenological mismatches of birds and their food in a warming world. J Ornithol 153: S75–S84.

Visser ME, Schaper SV, Holleman LJM, Dawson A, Sharp P, Gienapp P & Caro SP (2011) Genetic variation in cue sensitivity involved in avian timing of reproduction. Funct Ecol 25: 868–877.

Visser ME, Noordwijk AJ van, Tinbergen JM & Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proc R Soc Lond B 265: 1867–1870.

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

Väisänen RA, Lammi E & Koskimies P (1998) Distribution, numbers and population changes of Finnish breeding birds. Otava.

Waite TA, Strickland D (2006) Climate change and the demographic demise of a hoarding bird living on the edge. Proc R Soc Lond B, 273: 2809–2813.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O & Bairlein F (2002) Ecological responses to recent climate change. Nature 416: 389–395.

Wang Y-P, Siefferman L, Wang Y-J, Ding T-S, Chiou C-R, Shieh B-S, Hsu F-S & Yuan H-W (2009) Nest site restoration increases the breeding density of blue-tailed bee-eaters. Biol Cons 142: 1748–175.

Wiens JA, Rotenberry JT & Van Horne B (1987) Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48: 132–147.

Zandt HS (1994) A comparison of three sampling techniques to estimate the population size of caterpillars in trees. Oecologia 97: 399–406.

Original publications

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II Vatka E, Rytkönen S & Orell M (2013) Does the temporal mismatch hypothesis match in northern populations? (*Manuscript*)

III Vatka E, Kangas K, Lampila S, Orell M, Nikula A & Nivala V (2013) Nest site selection of a primary hole-nesting passerine reveals means to developing sustainable forestry. Journal of Avian Biology (*In press*)

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