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VARIABLE EFFECTS OF CHANGING CLIMATE ON LIFE-HISTORY TRAITS OF TWO PASSERINE BIRDS

by

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For Tanja

Niilo, Aino *and* Eini

For the life work of

Lars von Haartman *(1919 – 1998)*

Photo: Johan von Numers

LIST OF ORIGINAL PAPERS

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

I. Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K. and Lehikoinen E. 2004 Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology* 10: 1610-1617.

II. Laaksonen, T., Ahola, M., Eeva, T., Väisänen, R.A. and Lehikoinen, E. 2006. Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos*, 114: 277-290.

III. Ahola, M., Laaksonen, T., Eeva, T. and Lehikoinen, E. Long-term changes and density-dependence in selection on timing of breeding and clutch size in the pied flycatcher. *Manuscript.*

IV. Ahola, M., Laaksonen, T., Eeva, T. and Lehikoinen, E. Great tits lay fewer eggs than they are selected for – a study of climate- and density-related changes in reproductive traits. *Manuscript.*

V. Ahola, M., Laaksonen, T., Eeva, T. and Lehikoinen, E. 2007. Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology* 76: 1045-1052.

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CONTENTS

1. INTRODUCTION

The effects of human-induced global climate change on our ecosystems have concerned scientists and environmentally conscious people already since the early 1970s (e.g. Sawyer 1972, Fong 1979). In the boreal countries, the predicted increasing greenhouse effect was then seen primarily as an opportunity for agriculture and forestry and as a promise of lower energy needs for heating (e.g. Kauppi & Posch 1985). More recently the concern has also been heard in political discourse. As in most things, change is the basic and only unchangeable circumstance in climate too. Weather conditions vary within and between days, seasons and years for various reasons, most of which are natural and part of the system. This time, however, a century of intensive exploitation (i.e. burning) of fossil fuels by human societies has markedly increased the carbon dioxide content of the troposphere. In combination with deforestation and certain other factors, this has led to the observed non-natural greenhouse effect and a surplus rise in global temperatures over and above natural variation. The extent of the increase in yearly global mean temperatures, the one to six degrees predicted for the 21st century (IPCC 2007), may seem like a minor change, as temperatures vary much more even within a single day. Such a change, however, may for example shift the limit of regular winter snow-cover markedly toward the poles and raise the mean sea surface level. Spatial changes in precipitation may also cause great harm; they would apparently increase drought most in areas with a considerable proportion of the entire human population (IPCC 2007).

1.1. Effects of climate change on bird populations

In addition to these threats to human society, climate change is also affecting nature in many ways. The annual solar cycle, and the consequent seasonality in climatic factors, determine annual cycles in nature. In the case of birds too, conditions during different life-history events are regulated by variation in climatic factors. The impact of climatic change can be positive or negative, depending on the direction and magnitude of the change as well as on the species and area in question. The effect can basically appear in any of the processes determining the success of a population. Circumstances during the breeding season affect reproductive success, while those outside the breeding season determine the survival and condition of individuals prior to the next breeding. The effects of climate change on nature have been closely studied for the last two decades in order to understand the possible threats and increasing conservation challenges (reviewed by e.g. McCarty 2001, Root & Schneider 2002, Walther *et al.* 2002, Parmesan 2006). For this purpose birds have been good study objects; their life-history parameters have been long and widely studied, and their reactions to climatic factors can thus be extrapolated.

1.2. Timing of migration and breeding

In temperate latitudes, the annual rhythm of living organisms is strongly determined by seasonal changes in the photoperiod. Birds need to time their breeding to the period of highest productivity of the environment in order to ensure a sufficiency of food for their offspring. Birds use different cues for the timing of their life-history events. For example such factors as photoperiodism (Lambrechts *et al.* 1997), phenological development of the environment (Slagsvold 1976, Blondel *et al.* 1993), ambient temperature (Wingfield *et al.* 2003) and the achievement of physical breeding condition as a result of enhanced food conditions (Martin 1987, Rowe *et al.* 1994, Brommer *et al.* 2002), can all induce birds to start their spring migration and breeding.

The impacts of climate change on migratory birds are of particular concern, since these species may be affected by changes anywhere along the migration route or at the breeding or wintering grounds (Bairlein & Winkel 2001). Recent studies have reported the advancement of spring migration times with rising local temperatures in the target area (Sparks *et al.* 1999, Tryjanowski *et al.* 2002, Lehikoinen *et al.* 2004), with warmer local climate along the migration route (Huin & Sparks 1998, Huin & Sparks 2000, Strode 2003), and with a large-scale climatic measure, the North Atlantic Oscillation - index (Forchhammer *et al.* 2002, Hüppop & Hüppop 2003).

Most birds in temperate areas lay their eggs earlier in warm springs, and laying dates have advanced in many species and over vast geographical areas in response to the recent warming of spring temperatures (Crick & Sparks 1999, Dunn & Winkler 1999, Visser *et al.* 2003, Both *et al.* 2004, Dunn 2004). However, the increasing evidence for the decoupling of biological interactions at different trophic levels due to climate change has aroused concern among biologists (McCarty 2001, Walther *et al.* 2002). For example, in terrestrial ecosystems some long-distance migrants breed in increasing asynchrony with the availability of their food items (Visser *et al.* 1998, Both & Visser 2001, Sanz *et al.* 2003). Such mismatches may be due to insufficiently advanced spring arrival, which constrains the needed advance in the timing of breeding (Both & Visser 2001). Resident species too, however, may be driven to mismatch if the rate of phenological development in their food items is faster than they can respond to for example during the incubation period (Visser *et al.* 1998). Particularly in studies of the impact of climate change, it is therefore essential to consider changes in environmental conditions throughout the annual cycle, as they are predicted and observed to vary geographically (Easterling *et al.* 1997, Both *et al.* 2004, Hüppop & Winkel 2006).

1.3. Clutch size and breeding success

Recent studies have demonstrated that the reproductive traits of even small long-distance migrant passerine birds can be affected by environmental conditions at the wintering grounds and along the migration route (Marra *et al.* 1998, Sillett *et al.* 2000, Norris *et al.* 2004, Saino *et al.* 2004, Bearhop *et al.* 2004, Møller & Szép 2005). Respectively, resident species are affected by the harshness of winter at their breeding latitudes. As both the timing of breeding and clutch size depend in part on parental condition (Rowe *et al.* 1994), favourable conditions during winter and pre-breeding time should allow parents to time their breeding sufficiently early and lay larger clutches. In addition to environmental conditions, the number of competitors affects the sufficiency of food, nest sites and other resources during both breeding and non-breeding seasons. High densities will thus reduce clutch size and fledgling production in at least some bird species (Dhondt *et al.* 1992, Both 1998, Both 2000). Breeding density in turn is mainly affected by reproductive success and survival during preceding years, which are affected for example by food availability and climate (Jones *et al.* 2003). In temperate areas most resident species may benefit from climate warming, as milder winters will supposedly increase their survival over this critical period (Lack 1954, Berthold *et al.* 1998, Lemoine & Böhning-Gaese 2003, Sæther *et al.* 2004, Lemoine *et al.* 2007).

1.4. Natural selection

Natural selection can be considered to be a result of the fitness differences between individuals with different phenotypes. Traits favoured in one situation may turn disfavoured with changes in climate. The timing of reproduction and clutch size are two central characteristics affecting individual success (Martin 1995, Thomas *et al.* 2001). As breeding density affects resource availability and productivity in populations, it should also be considered as a possible factor affecting natural selection. Increasing selection for earlier breeding has also been observed in some populations that are facing an increasing mismatch between breeding time and the food availability peak (Visser *et al.* 1998, Both & Visser 2001, Both *et al.* 2006). The mechanisms behind these changes, however, have received little attention. In some studies, phenotypic plasticity – i.e. the ability of individuals to adapt to the changes they confront – has been found to sufficiently cover the rate of change that is observed at the population level (Przybylo *et al.* 2000). However, evidence for a direct connection between selection and observed change at the population level has only seldom been found (Gienapp *et al.* 2007), and only a few studies have examined whether selection for a life history trait has changed over time (Both & Visser 2001, Gienapp *et al.* 2006, Postma *et al.* 2007). Despite the great concern over the relationship between the timing of breeding and changing temperatures or environmental phenology, very few studies have yet examined whether selection in fact varies in relation to these environmental factors (van Noordwijk *et al.* 1995).

1.5. Interspecific competition

Since different species benefit from different circumstances, they may also respond differently to climatic changes, which may lead to changes in their interspecific interactions. It has been claimed that in interspecific competition residents should be favoured over migratory species, as they supposedly have a better chance to adjust to changes in their breeding environment (Berthold *et al.* 1998) and have a headstart in competition over common resources. Interspecific competition over a limited resource, such as breeding holes for hole-breeding passerines, is more likely to be expressed when the onsets of breeding in the competing species are close to each other (Slagsvold 1975), and obviously when the density of competitors is high. Climate change may affect both these factors, and thus also the competitive relationships between resident and migratory birds. As the timing of breeding is affected by a number of factors (see above), and resident and migratory species are exposed to different circumstances during their wintering and pre-breeding periods, their breeding times may also change differently. On the other hand, different conditions during the wintering period also determine the survival, breeding condition and breeding success of resident and migratory species, all of which may affect the competitive situation (Easterling *et al.* 1997, Berthold *et al.* 1998, IPCC 2007). Finally, variations in resource availability and population densities bring about variation in the limitedness of common resources for competing species.

2. AIMS OF THE THESIS

In this thesis, I examined the variation and trends in the timing of spring arrival (I) and breeding (I-IV), in clutch size (II, III, IV), in reproductive success ((III,) IV), in natural selection for laying date and clutch size (III, IV), and in interspecific competition (V). The study species used were the pied flycatcher (I, II, III, V) and the great tit (IV, V). Primarily, I wanted to better understand the factors affecting the breeding parameters of birds and how birds respond to changes in particular in climate-related determinants. I also revisit some earlier but reformulated approaches to climate change research, in order to arrive at more accurate analyses of possible explanatory variables contributing to the responses of birds. My third aim was to broaden the perspective of the study of climatic effects on bird populations on both a spatial and a temporal scale; for this purpose, I had a unique opportunity to make use of one of the longest-existing data-sets on the population biology of birds.

3. MATERIAL AND METHODS

3.1. The study system

This thesis is primarily based on one of the longest-existing data-sets on the breeding biology of birds. The data consist of two sets. The first was collected by Lars von Haartman at Lempisaari (in Swedish Lemsjöholm, the name mostly used in his articles) in Askainen, SW Finland (60º30'N, 21º45'E, Figure 1). This data, covering the years 1941-1994, contained information on altogether 2634 breeding attempts by the pied flycatcher (*Ficedula hypoleuca*), 1206 by the great tit (*Parus major*), 184 by the blue tit (*Cyanistes caeruleus*), 86 by the coal tit (*Periparus ater*) and 9 by the crested tit (*Lophophanes cristatus*). The second set of data was collected at Harjavalta (61º20'N, 22º10'E, Figure 1) by Tapio Eeva and Esa Lehikoinen during 1991-2005. The study was conducted in a wide area surrounding an industrial complex. I used only data collected more than three kilometres from the industrial complex, as heavy metal emissions from the complex have been shown to affect birds' breeding success at closer distances (Eeva *et al.* 1997, Eeva & Lehikoinen 2000). This data-set contained 4127 breeding attempts by the pied flycatcher, 2408 by the great tit, 482 by the blue tit, 112 by the coal tit, 51 by the crested tit and 13 by the willow tit (*Poecile montanus*). The main study species were the two most abundant species breeding in the nest-boxes, the pied flycatcher and the great tit; the others were only used to adjust the availability of nest-boxes in the analyses. The two study areas are located ca 95 km apart.

In both areas nest-boxes were checked during the breeding season at least once a week, and during egg-laying period usually more often. Based on the observed numbers of eggs and chicks, it was possible to calculate the first egg laying date, final clutch size and number of fledglings for most nests. In addition, information on dead flycatchers in the nest-boxes was collected as evidence of interspecific competitive conflicts. Only the first yearly nesting attempt per female was used in the analyses. The definition of subsequent attempts was based on ringed individuals or on the timing of laying in late new clutches that clearly deviated from the distribution of other laying dates of the year. Late breeding attempts were also often initiated shortly after nest desertion in a neighbouring nest-box. As an index for breeding density, I used occupancy rate of each species on all nest-boxes. I used such a measure instead of density per hectare as information on nest-box locations in Askainen was not available. I know, however, that the nest-boxes were situated in lines along paths with 40 metres intervals (minimum) and the locations remained the same from year to year. Thus I consider this index for breeding density to be a good alternative for the density per hectare. For the pied flycatcher, I also used another measure, the occupancy rate of the nest-boxes that were available after pairs of all tit species were settled to breed. This measure was used for taking into account the possible effect of interspecific nest-site competition. Ringing data for most adult pied flycatchers were available from 1941-1999, those for nestlings only from 1953-1999. Due to these reasons and some missing information, the numbers of observations used in individual analyses were lower than the total number of breeding attempts by each species. Although the two data-sets were collected in separate locations, the three years common to them showed that there was more variation between years than between study areas (I-V). In addition, the variables examined did not show any shift when one data-set changed to another. Thus I considered it safe to combine the two sets. Together with the breeding data, I used data on the spring arrival times of the pied flycatcher from the Jurmo bird observatory in the SW Finnish archipelago (Figure 1).

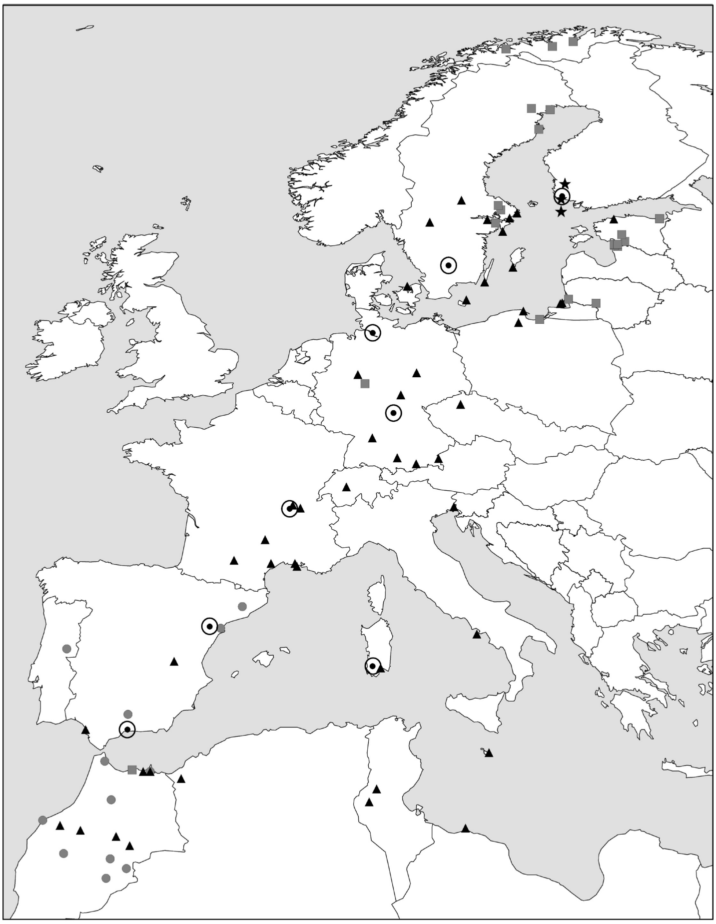

Figure 1. Origins of the data used in the thesis. Individual spring recoveries of pied flycatchers ringed in Finland during 1933-2002 are marked with grey dots (found during 28 February – 23 April), black triangles (24 April – 18 May) and grey squares (19 May – 27 June). Dotted circles mark selected weather stations along the migration route. Black stars in SW Finland (south to north) indicate the Jurmo bird observatory and the two breeding populations, Askainen and Harjavalta, of the pied flycatcher and the great tit.

3.2. Climate data

In explaining the different breeding parameters, data on daily mean temperatures and precipitation in Turku (60°30’N, 22°16’E), obtained from the Finnish Meteorological Institute, were used as base-data (I-V). The Sahel summer rainfall index was used to describe the wintering circumstances for the pied flycatchers (II). The Sahel data were derived from the Joint Institute for the Study of the Atmosphere and Ocean (website accessed 2 July 2008: http://jisao.washington.edu/data/sahel/). The winter (Dec-Mar) North Atlantic Oscillation index (wNAO) – a large-scale variable describing the mildness or harshness of winters, as well as springs in the case of Northern Europe – was also tested in explaining the arrival time, timing of breeding and clutch size of the pied flycatchers (I, II). The wNAO-data were provided by the Climate Analysis Section, NCAR, Boulder, USA (website accessed 2 July 2008: http://www.cgd.ucar.edu/cas/jhurrell/indices.html). For the arrival time (I) and timing of breeding (II) of the pied flycatcher, temperatures along the migration route were also used. First the spring migration route was determined on the basis of all spring recoveries of pied flycatchers ringed in Finland (Figure 1, I). Along the route, I selected weather stations and determined the relevant periods of explanatory mean temperatures for arrival and laying dates (Figure 1, I). The weather data for these stations were got from European Climate Assessment & Datasets (website accessed 2 July 2008: http://eca.knmi.nl/dailydata/index.php)

3.3. Determination of relevant time periods for explanatory mean temperatures

To determine the most relevant periods the temperatures of which would explain the variation in timing of arrival, timing of breeding and breeding success of the pied flycatcher and the great tit, a pinpointing method was used (I, III, IV, V). First, the mean temperatures of largely overlapping three-week periods through spring and summer were correlated against the response variable. Adjacent periods in this step overlapped by 18/21 days; in other words, each period started three days after the start of the previous one. For pied flycatcher arrival time, the adjacent periods with the highest correlations were chosen; together, they formed a period of explanatory temperature (I). This procedure was carried out for the temperatures recorded at all the weather-stations chosen, to compare their relative importance for arrival times observed in SW Finland (I). For timing of breeding (V) and fledging success (III, IV, V) the procedure was further developed: the three-week period with the highest correlation was used as the starting point in pinpointing the relevant period for the explanatory mean temperature, after which the base period was shortened or lengthened –from its start, its end or both – in steps of three days (V) or one day (III, IV). At each step, the yearly mean temperature for the period was calculated and regressed against the yearly mean laying date. This procedure was continued until the period was found whose mean temperature best explained the variation in the response variable according to the coefficients of determination (AdjR^2). The temperature for this period was used as an explanatory factor in subsequent analyses.

3.4. Environmental phenology

In addition to the mean temperatures of periods preceding and during breeding, thermal sums were used to describe the stage of phenology in the breeding environment. The thermal sum is the cumulative sum of daily mean temperatures exceeding +5°C after 1 March. The achievement dates of certain thermal sums were used to compensate for the absence of data on caterpillar or other food availability to the study species. This approach was seen as a good alternative, since the accumulation of thermal sums is known to determine the phenology of the most common deciduous tree, the silver birch (*Betula pendula* Roth); the insect fauna that rely upon these trees, and are important food for birds during their breeding season, are strongly selected to follow them in synchrony (Feeny 1970, van Dongen *et al.* 1997). The date when a thermal sum of 50 was reached was chosen for comparison with the mean laying date of the great tit, as it coincided on average with the overall mean laying date. By the same logic, the date when a thermal sum of 150 was reached was chosen for the pied flycatcher. Thus these indexed stages of the environment match on average with the yearly average laying date of each species. Therefore by comparing these indices to the yearly laying dates, I could measure the timing of breeding in relation to the phenological stage of the breeding environment.

3.5. Measures of natural selection (III, IV)

Standardized selection differentials (SSD) were used to measure natural selection on laying date and clutch size in each year. The standardized selection differential measures how much and in what direction the average value of a breeding parameter in a whole population differs from the average value of those that are selected to produce offspring to next generations. For the pied flycatcher, number of recruits (offspring returning to breed in their natal population) was used as the measure of productivity. For example, in calculating the standardized selection differential for the pied flycatcher laying date ($\mathrm{SSD}_{\mathrm{LD}}$), the following formula was used:

$$SSD_{LD} = \frac{LD_W - LD}{StdLD}$$

Here LD_W is the mean laying date, weighted for the number of recruits produced in each nest; LD is the untreated mean of all laying dates during the year and $StdLD$ is the standard deviation of laying dates. Selection differentials for the clutch size of the pied flycatcher (SSD_{CS}) were calculated similarly. For the great tit, adult trapping intensity and thus recapturing probability was low. Therefore the number of fledglings produced was used as the weight variable instead of the number of recruits.

4. MAIN RESULTS AND DISCUSSION

4.1. Timing of spring arrival and breeding (I, II, IV, V)

During 1970-2002 the arrival period of pied flycatchers in SW Finland, i.e. the time interval between the arrival of early migrants (first 5 percent of all) and late ones (95 percent), lengthened by almost one week (I). This was due to early migrants significantly advancing their arrival while late migrants did not. The advancement of the median arrival date was indicative, and the timing of breeding did not change. As a consequence, the time interval between the medians of arrival and laying also increased, indicating that in the late 20th century pied flycatchers waited longer to start breeding after arrival (I). During the longer data period (1943-2002; II) the timing of breeding tended to be delayed. These trends differ from most published earlier, as during the last few decades climate warming has advanced the timing of both arrival and breeding in many species (Lehikoinen *et al.* 2004, Dunn 2004, Jonzén *et al.* 2006, MacMynowski *et al.* 2007).

The local temperatures of the relevant locations and the periods preceding each event played an important role in explaining the timing of arrival and breeding. The pied flycatchers' arrival time in SW Finland was best explained by the mean temperature for the period 20 April – 25 May in Hamburg (northern Germany). The timing of breeding was explained by the mean May temperature (earlier in warmer years), the median arrival date of females (earlier breeding with earlier arrival) and year (delaying trend; I). When determined more accurately, the period best explaining the timing of breeding was 5 – 28 May (1953-2005; V). The different trends in early and late migrants and in timing of breeding were due to differences in the temperature trends of short within-spring periods. The spring temperatures in Central and Northern Europe during 1970-2002 have risen markedly only at the end of April, just prior to the arrival of early pied flycatchers in SW Finland. An examination of the timing of other pied flycatcher populations in Europe showed that the period with the strongest warming is prior to the breeding time for a Dutch population (Both & Visser 2001, I). For a Spanish population (Sanz *et al.* 2003) the rise in spring temperatures has been more uniform through the whole spring, but less intense than the warming at higher latitudes at the end of April. These results demonstrate that the effects of climatic changes should be studied at the appropriate time and geographical scale for the species or population concerned (I). My results also showed that although the winter North Atlantic Oscillation -index is a good large-scale measure of the favourability of spring conditions (Hüppop & Hüppop 2003, Vähätalo *et al.* 2004, Stervander *et al.* 2005, Rainio *et al.* 2006), migrant birds seem to follow the local temperatures they encounter (I).

In the analysis of the long-term data (II) the Hamburg temperature affected the timing of breeding (earlier in warmer years) as a proxy for arrival time, which was not available until 1970. Laying dates of the pied flycatcher were early when the Hamburg temperature was high. There was also a trend of increasing among-year variation in the mean and skewness of the laying date. The mean and skewness of the laying date were linked: in warm springs most of the population began to breed early and quite synchronously, but a right tail was formed by individuals starting to breed after the majority of the population. Similar pattern was found in skew of arrival times in 1970-2003: in years with high migration time temperatures in northern Germany, there was a tail of later arriving females in SW Finland. The skews of laying dates and arrival times were also positively correlated indicating that the right tail in laying dates was partly formed by birds arriving late from their spring migration. Thus the conditions along the migration route affected both the timing and distribution of the laying dates (I, II).

The great tit laying date did not change in relation to calendar dates during 1953-2005, although it was strongly determined by the temperature of the species-specific pre-breeding period (2 April – 7 May), which increased significantly (IV). Due to the rise in early spring temperatures the accumulation of the thermal sum was accelerated; thus, while the laying date was unchanged in terms of calendar dates, it was markedly delayed in relation to the thermal-sum-based index of environmental phenology (IV). According to the multiple regression model, the variation in great tit laying dates was best explained by the mean temperature of the pre-breeding period (earlier in warmer years), year (later in recent years) and suggestively by the breeding density of the great tits (earlier at higher density; IV, V). As the trend persisted after other explanatory factors were taken into account, it still remains to be examined why the laying dates of the great tit have not followed the advancement of spring phenology, especially since they are largely determined by the pre-breeding temperature in this and other populations (Slagsvold 1976, Dhondt & Eyckerman 1979, McCleery & Perrins 1998, Ardia *et al.* 2006)

4.2. Clutch size and reproductive success (II, IV)

The clutch size of the pied flycatcher decreased mainly during the first half of the period 1943-2002. Interestingly, the intra-annual standard deviation of the clutch side also decreased until 1980, resulting from the loss of the left tail from the clutch size distribution. The Sahel rainfall index appeared to explain this pattern. In years with a high rainfall index, indicating good wintering conditions, there was an increase in the proportion of small clutches. The tail probably represents low-quality individuals that in worse conditions would not survive or achieve breeding condition. After favourable winters, high-quality individuals may also produce larger clutches and thus have an increasing effect on the mean clutch size (II).

In the great tit, both clutch size and fledging success decreased during the period 1953-2005. In addition, both were reduced by high breeding density, and fledging success also by a low breeding time temperature. The temporal decrease in the productivity of the population, however, was not reflected in population density. A probable explanation is the higher proportion of low-quality individuals, due to the increased survival rate resulting from milder winters and the increased additional food supply by humans. While compensating for the lower productivity of the population, the increased contribution of low-quality individuals to the breeding population would also explain the lack of advancement in the mean laying date with the increase in pre-breeding temperatures. Higher density and lower breeding time temperature may also mean lower availability of food during the breeding season, which obviously reduces fledging success. Similar effects of breeding density and breeding time temperature on fledging success were also found in the pied flycatcher (M. Ahola *et al.*, unpublished).

4.3. Natural selection (III, IV)

According to recruit production, the selection in the pied flycatcher shifted towards selection for later laying dates and smaller clutch sizes during 1954-1999 (III). The trend toward selection for smaller clutch size remained after the effect of selection for laying date was taken into account. Long-term trends in the yearly mean laying date and clutch size were in the same direction as the changes in selection trends, i.e. towards later laying (suggestively) and smaller clutch size (II). However, it could not be determined whether these changes in the phenotypic means were caused by natural selection. The selection patterns were not connected to pre-breeding or breeding-time temperatures or to the earliness of spring. Selection for laying date, on the other hand, was connected to the breeding density of the pied flycatcher: selection for an earlier laying date was stronger when breeding density was high (III). The density-dependence of selection has been a focus of theoretical interest since MacArthur's (1962) paper, but in the wild it has only seldom been found (Moorcroft *et al.* 1996); probably for this reason it has been ignored in most recent studies.

In my work a density effect was also found in the great tit, when selection was measured according to fledgling production. In addition, selection for an early laying date was stronger when the breeding-time temperature was high. These findings suggest that at high densities and in warm summers late broods may suffer from food depletion, probably because of the more efficient depletion and accelerated development of their food items (e.g. Visser *et al*. 1998). There was no temporal trend in selection on laying date, but selection for larger than average clutch size increased while the phenotypic mean of the population decreased. The result that the trends in mean clutch size and selection differentials for clutch size were contradictory in the great tit differed from the parallel trends in respective variables in the pied flycatcher. However, the increasing selection for larger than average clutch size, together with the decreases in mean clutch size and fledging success, supports the idea that the proportion of less fit individuals has probably increased. This may have happened due to milder winters and the increased additional food supply for tits from humans during recent decades, which may have increased the survival especially of less fit individuals (IV).

I used two standardized selection differentials for measuring the strength and direction of natural selection. The measures of selection were based on 1) recruit and 2) fledgling production. As the local recruitment rate in this population of pied flycatchers is low, there is presumable some error in the recruit-based selection differentials. However, the clear connections between recruit-based selection differentials and independent explanatory factors are unlikely to appear randomly but, in my opinion, they rather indicate real causalities. Another question is whether the surviving young that recruit to breed in their natal area represents the whole surviving cohort regarding to their breeding time or clutch size. As in this case a significant proportion of young obviously disperse out from their natal population, it must be taken into consideration which part returns in. The observed patterns in recruit-based selection differentials may indicate the true natural selection at the population level but also changes in post-fledging survival and natal dispersal distance. This is an unavoidable problem in every study in which a proportion of offspring disperse outside of the study area.

When using the selection differentials based on the fledgling production the problem caused by possibly biased natal dispersal is avoided, but quality of fledglings and their post-fledging survival can not be taken into account. There is evidence that fledglings from larger clutches have smaller body size and lower recruitment rate than those from small clutches (Kruuk *et al.* 2001, Sheldon *et al.* 2003, Tinbergen 2005). However, lower recruitment does not necessarily mean lower fitness for the parents, as it might just be a result of longer natal dispersal distance of the offspring from large clutches (Nilsson 1989, Tinbergen 2005).

4.4. Competition over nest-holes (V)

As a sign of nest-hole competition, killed pied flycatchers were found more often in great tit nests when the density of either tits or pied flycatchers was high and when the interval between the laying date medians of the two species was short (V). These results support earlier findings by Slagsvold (1975). The laying date interval was to a great extent explained by the difference between the temperatures of the separate pre-breeding periods of the two species, and the breeding densities of tits and pied flycatchers showed divergent trends (V). Furthermore, there can be within-spring differences in warming trends (I), and different changes in the climatic circumstances of African and Scandinavian wintering grounds may obviously affect the survival of the two species differently. Thus, while there was no clear temporal change in competitive conflicts between great tits and pied flycatchers, these results indicate that the competitive relationships between resident and migratory birds may be affected by climatic change.

5. CONCLUSIONS

This thesis revealed a number of patterns in the breeding parameters of the migratory pied flycatcher and the resident great tit which were linked to variation in climatic and/or population-intrinsic factors. Basic causalities, such as earlier spring arrival and breeding when preceded by warmer temperatures, or decreasing clutch size with delayed laying date were clear. However, this detailed study of two sympatric hole-breeding passerines also revealed a number of factors suggesting that the connections and mechanisms underlying such causalities are not always simple or straightforward. The thesis emphasizes the importance of a detailed examination of both breeding parameters and their determinants, in order to explain the variation and temporal changes observed.

According to my results, conditions indicated by ambient temperature along migration route to a large extent determine the migration speed and thus the arrival time of migratory pied flycatchers (I). This result is consistent with the fact that warm weather usually means favourable tailwinds for northward migrants (Alerstam 1990). The development of spring temperatures, however, is not just a matter of steady warming, but a series of cooler and warmer periods following each other. Annual variation in the occurrence of these periods can lead to within-season differences in temperature trends. As early and late migrants are influenced by temperatures at different times, their arrival times may also change differently (I).

Just as ambient temperatures along the spring migration route affect the pied flycatchers' arrival time, pre-breeding temperatures at the breeding grounds strongly determine the timing of breeding (I, V). However, the migratory pied flycatchers seem to be unable to follow the phenological advancement of their breeding environment which has taken place due to warming before their arrival. The sub-optimality of the actual laying dates may be supported by the fact that the pied flycatcher clutch size decreased more than can be explained by the change in their timing of breeding (II). The selection, indicated by the recruit-based standardized selection differentials, also shifted to favour smaller clutch size during the study (III). Alternatively, it would not be beneficial for pied flycatchers to follow the advancement of their breeding environment, as indicated by the disappearance of selection for earlier than average laying during the study period (III). However, conditions at the wintering grounds may also have weakened the pre-breeding condition of individuals, leading both to inability to advance their breeding time and to a lower reproductive investment. In the case of clutch size distribution, the effect of wintering conditions was obvious: the tail of small clutches was lacking after harsh winters, indicating an inability of low-quality individuals to breed (II).

Like the migratory pied flycatchers, the resident great tits bred early when their pre-breeding period was warm (IV, V). On the other hand, they did not advance their breeding over the years 1953-2005, despite the warming trend in the pre-breeding temperature (IV, V). This presumably resulted from increasing survival due to milder winters and increased additional food supply by humans, which have evidently increased the proportion of low-quality individuals in the breeding population. These low-quality individuals obviously breed later, and have both lower reproductive investment (clutch size) and success (fledging success). This could also logically explain the increasing selection for larger than average clutch size along with the decrease in the phenotypic mean (IV). Another explanation to the observed changes may be that birds now invest less in one breeding attempt as their probability to reproduce several times has increased due to increased survival (Dijkstra *et al.* 1990). The two proposed explanations do not exclude each other, but can both be true in this system. Decrease in both mean and 90th percentile of clutch size fit to the lower investment –option while the increase of low-quality individuals is supported by increase in standard deviation of the clutch size due to small clutches getting smaller.

The effect of density on the appearance of competitive conflicts was assumed and also found (V). The effect of the laying date interval between the two species was also previously known (Slagsvold 1975). However, there was no temporal change in this interval, even though one has been expected from the different temperature trends in the pre-breeding periods of the two species. Rather, the population changes in the migratory pied flycatcher and the resident tit species were different, and conflicts were documented most frequently when the density of pied flycatchers was highest (V). The factors determining population size, and the as yet unexplained year effects, remain to be thoroughly examined in future work on these data.

This thesis has highlighted the importance of a population-intrinsic factor, breeding density, on fledging success and on natural selection on timing of breeding. The importance of being early appeared to be emphasized when the density was high, but there were no climatic factors affecting selection measures. Thus both population-intrinsic and environmental factors should be taken into account in future studies, especially when examining temporal patterns of selection. This detailed examination has shown few different trends and new causalities in reproductive traits or in selection in and between the resident great tit and the migratory pied flycatcher compared to earlier studies. The both spatially and temporally wider perspective, and consideration of the effects of population-intrinsic factors on breeding parameters, shed some more light on the field of climate change research. These findings may make things more complex, but more importantly they improve our understanding of the processes at work in bird populations.

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