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CLIMATE CHANGE EFFECTS ON AVIAN MIGRATION

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LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles, referred to in the text by their Roman numerals:

- I. Vähätalo, A.V., Rainio, K., Lehikoinen, A. and Lehikoinen, E. 2004: Spring arrival of birds depends on the North Atlantic Oscillation. - *Journal of Avian Biology* 35: 210-216.
- II. Rainio, K., Laaksonen, T., Ahola, M., Vähätalo, A.V. and Lehikoinen, E. 2006: Climatic responses in spring migration of boreal and arctic birds in relation to wintering area and taxonomy. - *Journal of Avian Biology* 37: 507-515.
- III. Rainio, K., Tøttrup, A.P., Lehikoinen, E. and Coppack, T. 2007. Has climate change affected the degree of protandry in migratory songbirds? - *Climate Research* 35:159-164.
- IV. Tøttrup, A.P., Thorup, K., Rainio, K., Yosef, R., Lehikoinen, E. and Rahbek, C. Avian migrants adjust migration in response to environmental conditions *en route*. – *Biology Letters*, published online. doi:10.1098/rsbl.2008.0290.
- V. Rainio, K., Lehikoinen, E. and Terhivuo, J. Similar arrival time responses of migrants to climate changes during warming and cooling periods - Manuscript

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CONTENTS

LIST OF ORIGINAL ARTICLES.....	3
1. INTRODUCTION	5
1.1. Trends in climate	5
1.2. General effects of climate change.....	5
1.3. Effects of changing climate on bird arrival	6
1.4. Aims of the thesis.....	6
2. Materials and methods	8
2.1. First arrival dates	8
2.2. Bird observatories	9
2.3. Climate data	9
3. Results and discussion	10
3.1. Effects of NAO on spring migration timing	10
3.2. Phases of migration	11
3.3. Changes in protandry	11
3.4. Climate change and the endogenous regulation of the yearly schedule	12
3.5. Long- term changes in arrival times	13
3.6. The distribution of arrival dates	13
3.7. Selection of explanatory variables in long- term studies	13
4. CONCLUDING REMARKS	15
ACKNOWLEDGEMENTS	16
LITERATURE CITED.....	17
ORIGINAL ARTICLES.....	21

1. INTRODUCTION

1.1. Trends in climate

Global climate has been warming rapidly since the 1970s (the Intergovernmental Panel on Climate Change, IPCC 2007). The recent warming is faster and globally coherent compared to earlier trends that have occurred for example in the North Atlantic region (Folland et al. 2001). Furthermore, the greenhouse gases emitted by man have been established as a major source of climate warming (IPCC 2007). Comparison of recent climatic trends with projections compiled in the IPCC:s previous report (2001), with observations up to January 2007, show that climate has recently changed more quickly than climate models indicate (Rahmstorf et al. 2007). European climate initially warmed in the beginning of the 20th century, after the cold period of 19th century (Little Ice Age, Holopainen 2006). Global temperatures too started to rise from about the start of the 20th century, but then levelled or slightly decreased for a period 1940 – 1970. After this, the rise has been steady for about three decades. Most data concerning arrival times of birds have been collected during the latest period.

1.2. General effects of climate change

Climate change has already affected biota worldwide. Reported changes linked to climate change range from changes in timing of life history events (phenology), range shifts and reproductive biology to changes in population dynamics, and community and ecosystem level changes, and ultimately to changes in extinction probabilities (Walther et al. 2002; McCarty 2001; Stenseth et al. 2002; Parmesan 2006; Møller et al. 2008). A general advance in spring events has been documented in all continents except the Antarctic (Parmesan 2006). Phenology changes in plants have been extensively studied in the context of climate change, which is crucial for understanding changes in higher trophic levels, dependent on plants as the basis of terrestrial food webs. In Eurasia, the growing season has lengthened about 10 days per decade (Zhou et al. 2001), due to both earlier onset of spring and later leaf fall in autumns. Plant phenology (flowering and leafing) has shown consistent changes with climate change (reviewed by Cleland *et al.* 2007). In an analysis concerning several phenophases across Europe, Menzel & al (2006) found an advance of 2.5 days per decade, matching the recent rising temperature trends. Differences in phenological responses between interacting species are also of concern (Harrington et al. 1999); for example breeding times of birds may be mismatched with the peak of food supply, such as peaks of occurrence in Lepidopteran larvae, causing decreased breeding performances (Both and Visser 2001; Visser et al. 2004; Visser et al. 1998).

1.3. Effects of changing climate on bird arrival

Climate change effects on birds have been increasingly studied during the last decade. Observed changes include advances in phenology, especially timing of spring arrival (Lehikoinen et al. 2004) and breeding (Dunn 2004), changes in reproductive performance (Dunn 2004), range shifts (Böhning-Gaese and Lemoine 2004), changes in population dynamics (Sæther et al. 2004) and microevolutionary responses (Pulido and Berthold 2004). Concerning avian phenology, good data exist for the timing of spring migration and subsequent breeding. Other parts of the yearly life cycle of birds have been less extensively studied. Timing of spring arrival has generally advanced during the last 30-40 years in Eurasian birds (Lehikoinen et al. 2004). The rate of advance in spring arrival has been 0.37 days per year. Similar patterns have been found in north-eastern North America where the overall advance in arrival was 8 days during the 20th century (Butler 2003), with short- distance migrants showing greater advances (13 days) than long-distance migrants (4 days).

First arrival dates (FAD) are the commonest type of data concerning bird arrival, since they are commonly collected by amateur ornithologists, and often published in local or national bird magazines. As a result, the first studies analysing changes in bird migration timing in the context of global climate change used FADs. Although FADs have been shown to be affected by climate warming (Huin and Sparks 2000), they may not honestly represent the behaviour of populations, being influenced by single individuals arriving “randomly” early (Lehikoinen et al. 2004). Sparks & al (2005) showed that although FADs and medians were quite well correlated, FADs were actually not good predictors of the latter. Thus it was recommended that when available, the total arrival distribution should be taken into account. Ensuing studies using north European bird observatory data showed that the early part of bird populations migrating via bird observatories has advanced more than median or late parts of the population and the early part is also more sensitive to yearly climate variation (**I**, **II**, Tøttrup et al. 2006; Jonzén et al. 2006)

1.4. Aims of the thesis

In my thesis, I have studied climate effects on changes in avian phenology. Using north European time series data on the timing of avian spring migration starting from the beginning of the 20th century, I demonstrate advances in avian spring migration which I discuss in the context of the recent global warming. First, I demonstrate that fluctuations in the dominant mode of climate variability in Europe, the North Atlantic oscillation (NAO), affect the timing of spring migration in birds. The effect is prominent especially in the early parts of each species’ migratory population (**I**, **II**). Moreover, NAO affects birds of all taxonomic groups studied (**II**). The effect of NAO variability was similar also between birds wintering in different areas (**II**). In paper **III** I studied whether

climate affects the degree of protandry, the difference between the arrival time of males and females of a species. Changes in protandry may lead to mismatch situations with other important aspects of the surrounding nature, e.g. food supplies, if both sexes do not respond at the same rate to the climate change. According to my findings, the four species studied show no temporal changes or climate effects in the degree of protandry (III). In paper IV I explore how the observed arrival time changes to Finland may have originated. This was done by comparing the timing of long-distance migrants at the two points of their migration through Europe: early migration stages are represented by the ringing data of Eilat, Israel; while the bird observatory data from Finland represent migration timing just before arrival to breeding grounds. The comparison indicates that the birds are able to speed up their migration in favourable conditions. In paper V my aim is to study whether the observed changes during the recent period of climate warming have been unique to that period, or if the observed changes are in fact typical and predictable responses to any kind of climate change. The results support the latter premise, showing similar responses to spring temperatures and NAO in two warming and one cooling periods of the 20th century.

2. MATERIALS AND METHODS

2.1. First arrival dates

In 1845, the Finnish Society of Sciences and Letters reorganised the collection of phenological records in Finland, originally started in 1750 by Professor Leche (Leche 1763; Haartman and Söderholm-Tana 1983). The initiative came from Carl von Linné, who had worked on plant phenological calendars (Linné 1757) and already in 1763 Johan Leche published data on bird arrival times (Leche 1763). The original aim of the study was to collect information in order to estimate when the best time to start agricultural activities was. In fact, phenological studies were a part of meteorology, which was a part of physics, and professors of physics were leading the phenology project until the end of 19th century. Data collection was organised so that a booklet was sent to the observers, who were mostly laymen. The booklet listed a series of phenological events which were to be observed; observers simply marked the first date of each event detailed in the booklets. Collection of this phenological data still continues, run now by the Finnish Museum of Natural History. I had the opportunity to use the bird arrival data set spanning the 20th century in paper V.

During the 1960s there was a ‘bird club boom’ in Finland. From the beginning, one of the main agendas of bird clubs was to collect and publish bird data, including first arrival dates. The Ornithological Bird Club of Turku was founded in 1966. In 1970 the club started publishing a magazine which concentrated on local bird fauna, including first arrival dates of spring migrants (Lehikoinen et al. 2003). The number of members of the club has been in steady rise ever since. Furthermore, several bird observatories were founded, including Jurmo bird observatory (1962, Lehikoinen et al. 2003), with an aim of standardized monitoring of migratory birds. As a consequence of the founding of ornithological clubs, birds and bird watching soon became very popular. With a rising number of observers the culture of bird watching changed too. More attention was paid to searching for arriving migrants, and the increasing use of telescopes in Finnish bird watching during 1970s (Lehikoinen et al. 2003) enabled the identification of many species at longer distances. In addition, changes in birding culture also resulted in increased observation skills of birdwatchers. While nowadays arriving passerines are found and identified already before they start singing, it can be assumed that old records consist mostly of singing individuals at their territories.

All these changes in observation effort are likely to influence the detection efficiency of first arriving migrants and thus may have generated some portion of the observed advances in first arrival times (V). Already between 1955 and 1965 the increase in numbers of birdwatchers raised the numbers of singing grasshopper warblers (*Locustella naevia*) and river warblers (*L. fluviatilis*) recorded in Finland (Eriksson 1969).

2.2. Bird observatories

Papers **I**, **II**, **III** and **IV** rely on data sets collected at bird observatories both in Finland and abroad. The strengths of bird observatory data sets are obvious; they include standardized bird counts, visual observation of migration and ringing from a diverse set of bird species. Thus, in addition to data on the first arrivals, data can also be extracted defining the median or mean day of migration as well as percentile dates better describing the start or end of migration season, for example dates when 5% or 95% of the birds have been observed, respectively. In Finland, the bird observatories were founded mainly in 1950s and 1960s. Jurmo bird observatory was founded in 1962 (Lehikoinen et al. 2003) and Hanko in 1979 (Lehikoinen and Vähätalo 2000). The papers **I** and **II** utilize data sets from these two observatories. There the timing of the first arrivals and that of the maximum number of birds (i.e. the migration peak) were determined as Julian days. The timing of the early, median and late phases of migration were defined as the dates when the season's cumulative bird sum reached 5%, 50% and 95%, respectively.

In paper **III** ringing data from three Finnish bird observatories, Långskär, Jurmo and Rönnskär, are compared with ringing data from Helgoland, Germany (Hüppop and Hüppop 2003) and Christiansø, Denmark (Lyngs et al. 1990) when studying changes in avian protandry. Paper **IV** expands the scope of this thesis outside Europe applying ringing data collected at the Eilat ringing centre, Israel.

2.3. Climate data

The North Atlantic oscillation (NAO) is used throughout the thesis as a variable explaining the timing of bird migration. NAO is a dominant mode of winter weather in the North Atlantic area, dictating climate variability from Western Atlantic to Siberia and from the Arctic to the subtropical Atlantic (Hurrell 1995; Hurrell et al. 2003). Using climate indices, such as NAO, in ecological studies reduces complex space and time variability into simple measures. Moreover, species are likely to respond to several climate variables simultaneously, thus using climate indices simplifies the analyses considerably (Stenseth et al. 2003). NAO indices were obtained from the website of the Climatic Research Unit at the University of East Anglia (<http://www.cru.uea.ac.uk/cru/data/nao.htm>) and corresponded to those used by Hurrell (1995). In **IV**, the normalised difference vegetation index (NDVI, <http://www.clarklabs.org>) was used to describe ecological conditions along the migratory partway. The index is a measure of the degree of absorption by chlorophyll in red wavelengths, which is proportional to leaf chlorophyll density (Pettorelli et al. 2005). In paper **V**, spring temperatures from Stockholm were also used, obtained from the website of the European Climate Assessment & Dataset (ECA&D) project (<http://eca.knmi.nl/>).

3. RESULTS AND DISCUSSION

3.1. Effects of NAO on spring migration timing

The results of studies **I** and **II** show that most migratory bird species arrived early after positive NAO winters, which indicate warm and rainy weather in northern Europe (Hurrell et al. 2003). Similarly, the timing of spring arrival of many terrestrial birds has correlated negatively with the NAO also elsewhere in northern Europe (Forchhammer et al. 2002; Hüppop and Hüppop 2003; Stervander et al. 2005; Sokolov and Kosarev 2003). In agreement with earlier studies concerning terrestrial species, study **II** shows that a majority of migratory birds, including shorebirds and waterfowl, are able to adjust their spring arrival in relation to a large-scale climatic oscillation.

The relationship observed between the NAO and the timing of migration has several, not mutually exclusive explanations: (1) in positive NAO years, the stronger than average SW-W winds over northern Europe (Hurrell 1995) provide tail-winds for migratory flight, (2) wintering birds are in good condition after positive NAO winters and are able to start their spring migration earlier (Møller 1994; Sæther et al. 2000), (3) in positive NAO winters the wintering regions are located closer to breeding regions than in negative, and (4) after positive NAO winters the development of spring is early (Post et al. 2001) and birds are able to migrate faster because the overall phenology is earlier and thus e.g. feeding conditions are good and birds may shorten their stopover times (Hüppop and Hüppop 2003). Explanations 1-3 fit only to some of the species studied. Winds from SW-W speed up the migratory flight of species arriving from those directions. Explanations 2-3 fit birds wintering in western and northern Europe, since in these areas the mild temperatures during positive NAO winters favour wintering birds and may shift wintering regions northwards. The early development of spring after positive NAO winters in northern Europe (Forchhammer et al. 1998; Post et al. 2001) can be expected to affect all the species studied.

Studies **I** and **II** show that the timing of all phases of migration correlate negatively with the NAO. Thus the results of studies concerning the arrival of the first individuals (reviewed in Lehikoinen et al. 2004) can be roughly extended to the behaviour of whole populations. In most species, the correlation between the NAO and arrival dates became progressively less negative, from 5% cumulative sums through the median to 95% cumulative sums. These results indicate that migrants respond to the NAO more sensitively in the early phases of migration.

3.2. Phases of migration

Many studies concerning changes in the timing of avian migration have dealt with single measures of migration, such as first arrival dates, mean or median migration times (reviewed by Lehikoinen et al. 2004). In papers **I** and **II** the passage of migration was described with three point estimates of migration, dates when 5, 50 and 95 % (phases of migration, **I**) of migratory populations had been recorded at bird observatories. Heterogeneity was found among the responses of several species groups. In most groups the degree of response weakened with the phase of migration, the early phase date of migration responding more strongly than the late phase date to the NAO.

There are various explanations why the early part of the migrating population responds more strongly to the NAO than median or late parts. It may be that 1) the result arises from increasing protandry, i.e. males arrive increasingly earlier than females since they are under a stronger selective pressure for early arrival (e.g. Møller 2004); 2) only individuals in good condition are able to speed up their migration; 3) non-breeding individuals are not in a hurry and arrive independently of the NAO; 4) wintering ranges extend during mild winters so that the birds' northern range limit lays more to the north (Root 1988; Valiela and Bowen 2003; Austin and Rehfishch 2005) and 5) birds, whose goal area is at higher latitudes where the advancement of spring is postponed, migrate later through the study area. At present, there is not enough detailed information about arrival in breeding areas to distinguish between these alternatives.

The phase date differences in responses to the NAO suggest that the distribution of migration timing will expand if global temperatures continue rising, as previously observed in Pied Flycatchers (Ahola et al. 2004). This could have fitness consequences if, for example, males arrive earlier but later migrating females do not.

3.3. Changes in protandry

In the context of bird migration, the term protandry refers to the time difference between male and female arrival (Morbey and Ydenberg 2001). Avian protandry is positively associated with sexual dichromatism (Rubolini et al. 2004) and sexual size dimorphism (Kissner et al. 2003). The degree of protandry has also been shown to be associated with levels of extrapair paternity, suggesting that males arrive relatively more in advance of females in species with high sperm competition where sexual selection through female choice is intense (Coppack et al. 2006). Climate change might affect breeding performance of birds through changes in protandry. For example, if climate change affects earlier arriving males more than females, a mismatch between breeding time and time of food peak may emerge. The effects of advancing female arrival times are more difficult to predict but it could cause, for example, situations where the males have not

yet established their dominance hierarchies at breeding sites when females arrive, and thus the pair formation may not be optimal.

In paper **III**, I explored whether the degree of protandry has changed during a period of climatic warming using long-term phenological data collected at five North European bird observatories. We show, for four sexually dichromatic songbird species, that spring migration has generally advanced but that the degree of protandry has not changed. Moreover, variation in NAO did not affect the degree of protandry. The parallel shift in the timing of male and female migration may be due to similar phenotypic plastic responses of males and females to climatic changes or reflect a correlated selection response in males and females.

3.4. Climate change and the endogenous regulation of the yearly schedule

Birds can respond to environmental changes both behaviourally (phenotypic plasticity) and through microevolutionary changes in the gene frequencies of bird populations. Both phenotypic plasticity and microevolution are involved in determining the timing of phenological events in birds (Przybylo *et al.* 2000; Pulido *et al.* 2001). Phenotypic plasticity allows birds to adjust their behaviour according to real-time environmental cues, which they experience at wintering grounds, or during the progression of migration. Microevolution may change the timing of migration over a few generations (Berthold *et al.* 1992; Pulido *et al.* 2001), but it requires that selection acts consistently in one direction. It has traditionally been assumed that birds wintering close to the equator rely more on endogenous regulation for starting migration, and that would make the long-distance migrants more vulnerable to climate change. However, it has also been shown that long- distance migrants respond to changes in climate at their breeding grounds or along the migratory journey, and even temporal advances have been reported (Hüppop and Hüppop 2003; Tøttrup *et al.* 2006; Stervander *et al.* 2005, **II**). Jonzén *et al.* (2006) argued that the advance they found in the Mediterranean would reflect evolutionary change in the timing of the start of migration in African wintering areas. However, to tease apart the portion of microevolution in the observed advances would require individual data concerning selection on arrival times (Both 2007). Moreover, climate changes may also enhance the conditions in the sub-Saharan Africa. For example Oba *et al.* (2001) found a positive correlation with the NAO and the vegetation cover in Sahel (measured with the Normalized Difference Vegetation Index, NDVI), thus partially explaining the earlier arrival of long-distance migrants after high-NAO winters. Further, in paper **IV** we show that migrants travel more rapidly through Europe in favourable conditions, thus supporting the idea presented by Hüppop and Hüppop (2003) that long distance migrants speed up their migration when the overall phenology of the environment has advanced.

3.5. Long- term changes in arrival times

Many of the studies reporting climate effects on bird migration timing concentrate on the last three decades of rapid increase in global temperatures (Lehikoinen et al. 2004). Longer time-series data sets provide an opportunity to compare the climate responses between periods of different climatic trends, for example periods of cooling and warming. In **V**, we studied the trends in first arrival dates of 13 Finnish bird species during three periods, two of warming (1910-1940 and 1970-1999), and one of cooling (1940-1970). We found that birds reacted to yearly variation in climate measured as spring temperature and NAO. The responses were independent of the underlying climatic trend. However, we found that during the most recent warming period, arrival times were at an earlier level, thus indicating earlier arrival due to modern climate warming.

Earlier arrival times documented in the most recent warming period may also be explained by the increased effectiveness in finding and documenting first arrivals. Firstly, the number of observers has increased recently and secondly the culture and expectations of bird watching is different from the earlier periods. Part of these differences between the two older periods and the new period may stem from increased observation skills of birdwatchers; nowadays arriving passerines are found and identified already before they start singing. It can be assumed that old records consist mostly of singing individuals at their territories.

3.6. The distribution of arrival dates

Climate change may affect the arrival distribution of bird populations in several ways. In the simplest scenario, all parts of the population advance at the same rate with unchanging population distribution in arrival date. But, for example the stronger rate of advance in the early part of the population would lead to a left- skewed distribution, thus affecting also the median. Meanwhile the late part of the population could remain unchanged and so the distribution would also be wider. Ahola *et al.* (2004) showed that because climate change has been strongest during the early part of the migration of the pied flycatcher, early part of the population has advanced whereas the median and late parts have not. In my thesis, I show that this bias towards the stronger advance in the early parts of migratory populations applies to a larger number of other species too (**I**, **II**). It is therefore recommended that when possible, the whole arrival distribution should be studied when studying climate change effects on avian migration timing.

3.7. Selection of explanatory variables in long- term studies

Ornithologists readily use climate indices or more local weather variables in explaining observed patterns in the timing of avian migration. However, explanatory variables need

to be carefully chosen for each data set under investigation. Local temperatures have been commonly used in different phenological studies. While they are excellent in explaining patterns seen in e.g. as plants or non- migratory birds, they may not be representative when migratory birds are concerned. Migratory birds travel through vast land areas with different patterns in local climate, and are thus affected by climate change in a more complex way than non- migratory ones. The arrival time changes should be explained also with climate along the migratory route, for example using data from several weather stations (Ahola et al. 2004; Hüppop and Winkel 2006). Then, however, analyses soon turn very complex and difficult to interpret. Using large-scale climate indices (NAO, ENSO etc.) is one way of getting rid of these difficulties, as they compress several climate variables into a single measure of climate variability (Stenseth et al. 2003).

4. CONCLUDING REMARKS

The results of this thesis give new information for the study field concerning climate change effects on avian migration. According to my results birds are able to rapidly respond to climate fluctuations, be it through phenotypic plasticity or microevolution (**I**). I extend the traditional scope of studying only first arrival dates (**V**) to other measures of migration, such as the median migration date and show that the timing of early parts of migratory populations are more sensitive to climate changes than later parts (**II**). In (**III**) I investigated, whether changes in protandry, the difference in arrival times of males and females, are behind this observation. However, I found that both sexes seem to be able to respond to climate changes at the same rate. I also show that birds are able to speed up their migration when the conditions are favourable, thus supporting the view that mainly phenotypically plastic responses are behind the observed advances in avian spring migration (**IV**).

In conclusion, my results suggest that many species are able to follow climatic changes at least to some extent, advancing arrival in earlier springs. However, results obtained from single species or even larger sets of species do not necessarily generalize to every species or even all populations of a single species (Rubolini et al. 2007). Furthermore, it is difficult to assess how closely migrants should be able to follow phenological changes in other trophic levels in order to maintain synchronization with e.g. peaks of food availability. Thus the threats of climate change remain topical, and future work will hopefully identify those species that need our attention most; to apply the conservation measures needed to prevent their decrease or even extinction (Møller et al. 2008).

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