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THE EFFECT OF INCREASING ATMOSPHERIC TEMPERATURE ON THE BREEDING PHENOLOGY OF THREE BIRD SPECIES IN VILJANDIMAA COUNTY, SOUTHERN ESTONIA

Master's Thesis

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Information sheet

Increasing temperatures will be a driving force of ecological change. The issue is not only interhemispheric, but also local scale temperature asymmetry. One of the consequences is a mismatch between hatchlings and invertebrate food peaks. This may result in reduced fitness. However, the effect on birds with different migration strategies is not fully understood. There is mounting evidence that European passerine populations may respond differently. The aim of this study was to look at the relationship between temperature and phenological and breeding parameter data of three local songbirds with different migration strategies.

Expectedly, increasing spring temperatures resulted in earlier egg laying. Interestingly, temperature variability within spring periods also had an effect, causing delayed laying. As assumed, the Great Tit and the Common Starling showed no indication of mismatch between food availability and laying onset. As some studies contradict this, European local populations may respond differently. On the contrary, there was evidence that Pied Flycatchers have not advanced laying onset optimally and breeding success declined 8%. As predicted, long-distance migration may be the least favourable strategy for adjusting to increasing temperatures.

Key words: birds, temperature, breeding phenology, breeding success

Infoleht

Ökoloogiliste muutuste peamiseks põhjuseks on globaalselt tõusvad temperatuurid. Temperatuuri tõus erineb põhja- ja lõunapoolkeral, kuid ka lokaalselt. Üheks tagajärjeks on linnupoegade kasvatamise ja söögirohkuse perioodi fenoloogiline nihe, mis võib viia kohasuse languseni. Temperatuuri mõju erinevate migratsioonistarteegiatega lindudele ei ole üheselt mõistetav ning on põhjust arvata, et Euroopa linnupopulatsioonid reageerivad erinevalt. Käesoleva töö eesmärk oli uurida kolme erineva rändestarteegiaga kohaliku linnuliigi pesitsusandmeid seoses kevadiste õhutemperatuuridega.

Ootuspäraselt leiti, et tõusnud temperatuurid on põhjustanud munemisalguse nihkumise varasemaks. Huvitav on see, et kevadiste temperatuuride kõikumine põhjustab hilisemat munemist. Kooskõlas eeldatuga leiti, et rasvatihane ja kuldnokk kohandavad pesitsust vastavalt toidurohkuse varasemaks nihkumisele. Kuna on leitud ka vastupidist, võib eeldada, et Euroopa populatsioonid reageerivad erinevalt. Must-kärbsenäpp ei ole aga munemisalgust optimaalselt varasemaks nihutanud ning pesitsusedukus on langenud kuni 8%. Eeldustekohaselt, võib kaugmaaränne olla temperatuurimuutsutega kohanemiseks kõige kehvem strateegia.

Märksõnad: linnud, temperatuur, pesitsusfenoloogia, poegade edukus

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1. Introduction

1.1 Global temperature trends

The two most comprehensive climate change reports have shown that the world is facing an expanding global problem of increasing atmospheric temperatures that have a substantial effect on ecological interactions (IPCC Assessment Reports 2011, 2014). According to the IPCC Third Assessment Report (2011), the global mean surface air temperature increased by 0.6°C during the 20th century. The latest Fifth Assessment Report (2014) concludes that there is a continuous warming trend in the 21st century and its extent is mostly driven by the anthropocentrically released greenhouse gas concentrations in the atmosphere. In addition, the Earth's positive feedback mechanism involving the water circulation system also has a considerable effect (Stroeve *et al.,* 2012). Other authors have identified alternative natural forcers as the drivers of climatic change like the earth's orbit around the sun, but their effect on the temperature trends of the past 10 000 years remain ambiguous (reviewed in Thompson, 2010). Furthermore, when Foster and Rahmstorf (2011) looked at global temperature data from 1979–2010 and excluded three known factors on short-term temperature variations (El Niño, solar variability and volcanic activity), they still found a steadily increasing trend for the study period. The authors also emphasized the urgency needed to address this warming trend. The Fifth Assessment Report (2014) states that with the current mitigation measures in effect, the global mean surface air temperature is likely to rise by 3.7 to 4.8°C by the end of the 21st century. Therefore, it becomes evident that the increasing temperature is and will be an important abiotic factor that should be taken into consideration when explaining ecological phenomena.

1.2 Interhemispheric temperature difference

More importantly, this atmospheric temperature increase has not been globally homologous. The largest increase in the 20th century occurred over land area in the Northern Hemisphere where mean temperature peaks were considered highest in the past 400 years (Serreze *et al*., 2000). Some parts of Eurasia saw an increase as great as 0.5°C a decade from 1960 till the end of the century (Serreze *et al*., 2000). Largest increase in Eurasia was noted for the spring and winter seasons (Serreze *et al*., 2000). As a result, during 1955-2002 Northern Hemisphere experienced earlier spring warmth and first leaf date had advanced 1.2 days a decade (Schwartz, Ahas and Aasa, 2006). Friedman *et al*. (2013) looked at the interhemispheric temperature asymmetry trend between 1980 and 2000 and showed that the annual mean varied up to 0.8°C. Their model

predicts an even higher trend for the 21st century. As during the last century, the rise in the Northern Hemisphere independently is calculated to be above the global average and could increase up to 6°C by the end of the 21st century (IPCC, 2014).

Marshall *et al*. (2014) have suggested that the cause of this asymmetry is due to differences in ocean circulation at the two hemispheres and the ozone depletion over Antarctica that combined bring about delayed warming of the Southern Hemisphere. Additionally, Alexeev *et al*. (2005) demonstrated that during the past decade, the melting of Arctic sea ice and snow cover during the summer period has caused an increase in heat and moisture in the atmosphere, initiating further warming. Furthermore, ice cover of the Northern Hemisphere has an insulating effect, but the Earth is close to reaching a threshold where loss is greater than gain (Serreze and Francis, 2006). Another less studied phenomenon is the narrowing of the polar and sub-polar belt and widening of the tropical belt which may add to the feedback system but also has an effect on species climatic ranges (Seidel *et al*. 2008). Further studies are needed to understand to what extent this will affect species' climatic ranges. In conclusion, this information about interhemispheric temperature change, advanced spring and climatic range shifts is of paramount importance to biologists, as species will be affected by local and global trends.

1.3 Temperature trends in Europe and Estonia

Europe lies in the Northern Hemisphere where temperature increases noticeably faster compared to areas in the Southern Hemisphere. Walther *et al*. (2002) looked at global spatial temperature variability between 1976 and 1990 and showed that Europe is in the area where temperatures per decade have risen 0.7–1.0°C compared to <0.3–0.7°C near the equator. Although overall the change in Europe has been rather homogenous, it is spatially heterogeneous over the area of higher latitudes (reviewed in Walther *et al*. 2002). Estonia is part of the Northern European region in the subpolar climatic zone (Jaagus and Ahas, 2000). Jaagus (2005) analysed Estonian temperature change from 10 weather stations between 1951 and 2000 and showed that the annual mean temperatures rose by 1.0–1.7°C depending on the weather station. Therefore, the calculated global average for Estonia is even higher than is suggested for this region (Walthers *et al*., 2002). In a more recent study, Jaagus and Mändla (2014) assessed different climatic models in Estonia and concluded that the most accurate model for the years 2070–2099 predict a mean 3–4°C temperature rise. Due to this high trend, the effect of this on ecological interactions needs more attention.

Furthermore, Jaagus (2005) found that despite having a small land area (45,339 km^2), Estonia experiences rather significant temperature variability within the country. For example, depending on the weather station, temperature increased between 2.0–3.3°C during the spring season. This could partly be explained by Estonia's geographic location. It is surrounded by roughly 3800 km of the Baltic Sea coastline and approximately 700 km of land border. This results in a maritime climate in Western Estonia and gradually becomes more continental the more inward one reaches (Jaagus, 2005). Accordingly, spring temperature surge seems to increase from the coast towards the inland (Jaagus, 2005). Another factor could be the vicinity of human settlements to the weather stations. McCarthy, Best and Betts (2004) showed that cities create heat islands that exhibit temperature increases possibly exceeding the rate of local trends depending on the population size and growth. This difference between weather stations is important, as the ecological response may vary within the country due to these differences. This is supported by the study of Both *et al*. (2006) who identified areas within the Netherlands with different caterpillar peak dates, suggesting a lag in spring arrival between these areas. Taking this into consideration, it would be expected that temperature variation in Europe is more complex than Walthers *et al*. (2002) suggested for the region and as a result, it may become difficult to generalize ecological responses to increasing temperatures. This in turn emphasises the need to study local trends.

Therefore, Estonia would be an important study area to add to the knowledge about temperature variability within Europe and the consequences to ecological interaction. Especially, as it has been predicted that this overall warming in Europe will continue even with mitigating actions in practice (reviewed in Linden and Mitchell, 2009). Sala *et al*. (2000) have emphasized that climate will be the second main driver of biodiversity change in terrestrial ecosystems during the next 100 years. So, the effect of temperature on living organisms is an important study area to identify vulnerable species and interspecific interactions.

1.4 The effect of increasing temperature on biodiversity

The biodiversity change due to increasing temperatures can manifest on individual, population, species, community, ecosystem and biome level (Bellard *et al.,* 2012). In addition, it affects phenology, range and physiology of taxa (Bellard *et al.,* 2012). The overall trends in responses to increasing temperatures have shown to mostly result in range and phenology shifts (reviewed in Parmesan, 2006). The mechanisms behind these disruptions are the narrowing and widening of habitat climatic ranges (Parmesan and Yohe, 2003; Chen *et al*., 2011); changes in the start and

duration of seasons (Parmesan, 2007) and desynchronization of responses of taxa to these changes (Thackery *et al.*, 2016). Considering range shifts, Chen *et al.* (2011) conducted a meta-analysis looking at latitudinal habitat shifts for 18 taxonomic groups from Europe, North-America and Chile and found trends many times higher than previously reported– movement to higher latitudes at a median rate of 16.9 km per decade compared to 6.1 km per decade shown by Parmesan and Yohe (2003). This could indicate species and/or location specific responses.

Taking into account the changes in seasons, during the period 1971–2000, spring in Europe had advanced on average 2.5 days per decade (Menzel *et al.*, 2006). Authors attributed this to increasing temperatures. As a result, 78% of all studied leafing, flowering and fruiting plants had advanced their vernal activity (Menzel *et al.*, 2006). Thackery *et al.* (2016) looked at the United Kingdom's marine, freshwater and terrestrial taxa over the period of 1960–2012 and found that the strongest responses were exhibited by plants (4.3 days earlier per 1°C) and insects (3.7 days earlier per 1°C) followed by birds (2 days earlier per 1°C). Parmesan (2007) found contradicting results when analysing taxa spanning the Northern Hemisphere. He found that birds are one of the most advancing and herbs and grasses, shrub and trees the least advancing. Two conclusions can be drawn from these studies. Firstly, the increasing temperatures will disrupt interspecific relationships as taxa advance at different rates. There is some evidence that this has a negative effect on fitness (Singer and Parmesan, 2010) but more studies are needed. Secondly, global trends can misrepresent local phenomenon as different locations exhibit different rates of change. This may become a problem when generalizations from studies are being made.

1.5 The effect of increasing temperature on bird populations

1.5.1 Range shifts

Birds have been experiencing range shifts and there is evidence that this is due to narrowing or widening of their climatic space (Gregory *et al.*, 2009). As a result, European species gaining range increase and the ones losing range decline in numbers (Gregory *et al.*, 2009). Especially vulnerable are Northern European populations who move northwards, but will be limited by finding suitable habitats (Brommer, Lehikoinen and Valkma, 2012). Virkkala *et al.* (2014) showed that 27 northern-boreal bird species in Finland had lost 27% of their range during 2006–2010 compared to 1974–1989. The same 27 species are projected to lose 74–84% of their historical range by 2051–2080 (Virkkala *et al.*, 2008). In addition, range shift can also manifest in the migratory behaviour of short-distance migrants. For example, milder winters in the

Netherlands correlate well with reduced migration distances to overwintering grounds of 12 species out of the 24 studied (Visser *et al*., 2009). Similar results have been demonstrated in the German population of the Eurasian Crane (*Grus grus*)– median distances shortened from 2088 km to 320 km between 1997 and 2007 (Nowald, Donner and Modrow, 2010). A proportion of the population stopped migration altogether.

A number of expectations could be formed. For example, it would be expected that with milder winters, more migratory birds stay on their European breeding grounds or shorten migration distances when conditions are suitable as migration is energetically costly (Wikelski *et al*., 2003). Some areas could lose historical species and gain novel ones. This means population decreases at one location may mean that the species as a whole have simply moved their range due to unsuitable climatic conditions. For this reason, more studies are needed to investigate the mechanisms behind species population trends.

1.5.2 Bird and their food phenology shifts

The most prominent and studied response to the changing temperatures on birds have been shifts in breeding phenology due to advancement of spring. The phenology of bird species food abundance has been used as an indicator of how much a species should be shifting due to increasing temperatures (Visser and Both, 2005). This is because food availability is an important factor in juvenile survival (Robinson, Baillie and Crick, 2007). The problem is that the advancement of phenology of taxa occurs at different rates (Thackery *et al*., 2016). Chmielewski and Rötzer (2001) looked at leafing dates of European trees and found that earlier spring during 1969–1998 advanced growing season by 8 days. Accordingly, caterpillars emerge earlier; failure to do so, will lead to reduced fitness (reviewed in Asch and Visser, 2007; Singer and Parmesan, 2010). In return, birds need to follow this advancement of their food objects (Robinson, Baillie and Crick, 2007). A possible mismatch occurs due to delayed egg laying, therefore, later hatching than is optimal to utilize food availability/quality (Both and Visser, 2005). For example, Visser, Holleman and Gienapp (2006) found that the mismatch between the Great Tit (*Parus major*) fledglings and caterpillar biomass food peaks is 10 days. This resulted in decreased fledgling numbers and reduction in their weight. This mismatch also affects adult birds that need to increase foraging effort and as a cost, their survival decreases (Thomas *et al*., 2001).

Synchrony is especially important for seasonally breeding birds that have their breeding season matched with a window of food availability (reviewed in Carey, 2009). Most affected are long-

distance migratory birds that breed at temperate zones but overwinter in the tropics. Some species have not advanced their arrival dates due to the interhemispheric temperature asymmetry but the phenology of their food has changed (reviewed in Carey, 2009). For example, Fontaine *et al.* (2009) looked at 200 North-American migrant bird species and found that the rate of temperature increase varies greatly between spring migration, summer breeding and autumn migration sites. The same phenomenon has been recorded in bird species breeding in Europe. For example, Cotton (2003) showed that between the period 1971 and 2000 the sub-Saharan temperature increase by 0.06°C did not correlate with the temperature increase in Oxford, England for the same time series. This is highly important as many long-distance migratory bird species spend their winter in the sub-Saharan region (Cotton, 2003). Importance of synchrony is supported by a study by Møller, Rubolini and Lehikoinen (2008) who showed that from the 100 European migrants considered in their study, the ones who did not show advancement of spring migration had declined in numbers between the years 1990–2000. The ones who did exhibit advancement had no change or increased in numbers. Furthermore, the temperature increase variation within European breeding and overwintering areas of short-distance migratory species, Common Starling (*Sturnus vulgaris),* has also been shown to be significant (Both and Marvelde, 2007). In order to understand the trends of bird population numbers of migratory and non-migratory bird species, it is important to regionally study the effects of temperature. It becomes evident that the right timing of spring arrival to their breeding grounds is of paramount importance.

One of the mechanisms behind this mismatch is the effect temperature has on the annual cycle of birds. The generalized cycle of birds comprises of physiological preparations for breeding and preparations for overwintering or preparations for spring and autumn migration for migratory birds (reviewed in Carey, 2009). The progress of the phases and therefore completion of the cycles are governed by two types of factors–exogenous and endogenous, and in addition, the interaction of both (Cohen, Moore and Fischer, 2012). Aspects of the cycle of the species that regulate the timing of migration by endogenous factors are more likely to become mismatched with food peaks. For example, it has been found that the circannual rhythms in birds are mostly governed by the length and/or intensity of photoperiod, which induces a response at the optimal time of the cycle for a given phase (Gwinner, 2003). This has been thought to be the most prevalent cue for long-distance migratory birds to start their migration to breeding grounds (Gwinner, 2003). As a result of interhemispheric temperature differences, long-distance migrants arrive to Europe later than is optimal. In addition, the endogenous mechanisms are also adjusted

by environmental cues (Gwinner, 1996). Birds are able to utilize environmental information in order to make decisions (Gwinner, 2003). This is beneficial to short-distance migrants and residents that are able to assess local environmental conditions. A meta-analysis carried out by Gienapp, Leimu and Merilä (2007) concluded that the change in migration patterns is due to a high phenotypic plasticity exhibited by birds. Therefore, it would be expected that birds have the mechanisms to adapt to the changing environment. Nevertheless, this phenotypic plasticity would be less beneficial to bird species which do not live long enough to carry out a number of migrations.

Furthermore, short-distance migrants and resident species exhibit a stronger phenotypic plasticity and are more receptive to environmental cues. This is supported by a 47-year Great Tit population study in United Kingdom (Charmantier *et al*., 2008). The authors found that the increasing early spring temperatures correlate well with earlier peaks in a winter moth's larval biomass, which in turn is related to advancement of Great Tit laying onset by 14 days during 1961 to 2007 (Charmantier *et al*., 2008). It should be noted that although some resident populations show successfull advancement of laydate compared to catepillar biomass, there are populations that despite advancement exhibit a mismatch (Visser, Holleman and Gienapp, 2006). This suggests a population or location specific response. Nevertheless, phenotypic plasticity seems to be a better form of adaptation than evolutionary change. It allows the species to account for the temperature variability between years and opt between strategies when spring comes early or is delayed (Charmantier *et al*., 2008; Nussey *et al*., 2005). Another strategy to synchronize hatch date and food peaks is to manipulate incubation period. For example, Cresswell and McCleery (2003) showed that Great Tits in the United Kingdom delayed the start of incubation in order to meet the food peak. As studies have shown, a significant temperature variability exists within Europe (Jaagus, 2005; Parmesan, 2007; Thackery *et al*., 2016) and the effect of this on short-distance migrants' phenology and synchrony with food peaks should be further examined.

1.6 Current study

As shown, temperature has been increasing globally and characteristically exhibits interhemispheric asymmetry. Jaagus (2005) showed that temperatures have been increasing in Estonia, especially during the spring season, bringing about early spring. Early spring in Jaagus' (2005) and this study is defined as a season that starts when reaching and maintaining or going above a 0°C threshold. Similarly, spring's threshold is 5°C. The onset of early spring according

to 10 weather stations exhibits spatial variability and was between 19.6–44.1 days (Jaagus, 2005). This shift towards earlier spring in Estonia could bring about species' phenological shifts, which in turn affect synchrony of ecological interactions. Jaagus and Ahas (2000) showed that early spring is correlated with earlier phenological phases (foliation and blossoming) of plants in Estonia. This is supported by Menzel *et al*. (2006) who looked at phenological observations of vegetation from 21 European countries and concluded that plant development had advanced 2.5 days per 1°C during the period 1971–2000. Therefore, there is reason to expect that invertebrates have followed this shift.

Furthermore, studies have shown that long-distance migrants that breed in Estonia show less variability in arriving to breeding grounds in spring than short-distance migrants (Palm *et al*., 2009; Palm *et al*., 2017). The result of these migration timings in bird populations that breed in Estonia have not been investigated but would provide beneficial information for conservation work and making future predictions. Since plant phenological phases are correlated with spring temperatures, it could be expected that invertebrates follow this trend in their phenological phases. If long-distance migrants arrive to Estonia after the start of early spring, they may mismatch their hatching date with food abundance peaks. In addition, because there is a more varied temperature trend between locations in the Northern Hemisphere than was suggested by Walther *et al*. (2002), more local studies should be conducted in order to understand the extent in differences in responses. For example, the start date of climatic spring in Estonia exhibits great special variability within the country (Jaagus and Ahas, 2000). Relying on larger trends may lead to false conclusions when applied to explaining local phenomena.

The aim of this study was to investigate the relationships between the increasing temperatures at the study site and the response of local populations of three species that exhibit different migratory strategies–The Great Tit (non-migratory species), the Common Starling (short-distance migratory species) and the Pied Flycatcher (*Ficedula hypoleuca*) (long-distance migratory species). Furthermore, the Common Starling European populations are the least studied out of the three and iformation aboout their breeding phenology is valuable. The Great Tit and the Pied Flycatcher are insectivorous and the Common Starling mostly insectivorous species, therefore, expected to match their phenology with the phenological phases of their food. Breeding parameter data were used as a measure of response to temperature but also, since no data of invertebrate phenology for the study area and period were available, a measure of synchrony. It would be expected that with asynchrony breeding parameters decline. Data were

available for spring arrival time to the study site, breeding onset, clutch size and fledgling numbers for a 56-year period. It was expected that spring temperature at the study site has increased. The following hypothesises for each species were conducted:

- The Common Starling has advanced its arrival time and subsequently laying onset as they are more receptive to environmental cues (Gienapp, Leimu and Merilä, 2007). It has not increased or decreased its clutch size and exhibits no change in its fledgling numbers or success as they have advanced their breeding season in accordance to food peaks.

- The Great Tit has shown high phenotypic plasticity in response to environmental cues (Charmantier *et al*., 2008) and therefore, has advanced its laying onset according to spring temperature increase but exhibits no change in clutch size, fledgling numbers or success.

- The Pied Flycatcher has not advanced its arrival date as Sub-Saharan temperatures increase at lower rates (Cotton, 2003) and they depend more on internal cues to start their spring migration to breeding grounds (Gwinner, 2003). They have advanced their laying onset, as they need to meet the advanced food peak. Clutch size has decreased, as they arrive later in the season than is optimal and need to start laying earlier, therefore, having less time to lay large clutches. It is expected that fledgling success has decreased, as they do not meet the food peak that is necessary for successful breeding.

2. Materials and methods

2.1 Origin of the data

All data were obtained from external sources and not gathered by the author. The origin of temperature and first sighting data in spring is described under the subheadings 2.2 and 2.4. The bird breeding data were gathered by a local amateur ornithologist, Endel Edula, following strict methodological protocol compiled by a professional avian ecologist Sven Onno. The observation diaries were digitised by a number of people but mostly by Kaisa Telve (PhD student, Chair of Animal Ecology, Group of Avian Behavioural Ecology). All data were handled, sorted and analysed according to the objectives of this study by the author.

2.2 Study site

The study site was situated in Viljandimaa County, Estonia, 3 km south from the nearest town Viljandi, near Väike Närska farmstead (N 58° 18' 59", E 25° 36' 39") in a temperate mixed coniferous and broad-leaved forest. Between 1956 and 2012, there were 200 nest boxes distributed around the site. The tree species present during the study period were European aspen (*Populus tremula)*, wych elm (*Ulmus glabra)*, birch (*Betula spp.*), Norway spruce (*Picea abies)*, elder (*Sambucus spp.*), Scotch pine (*Pinus sylvestris)*, willow (*Salix spp.*), rowan (*Sorbus spp.*), lime tree (*Tilia cordata)* and European ash (*Fraxinus excelsior)*.

2.3 Bird phenology and breeding parameters

Data for laying onset date, clutch size and fledgling numbers were collected yearly. During the breeding season, nest boxes were routinely checked for eggs and later on in the season checked again for fledgling numbers. When necessary, the laying onset date was back-calculated from the number of eggs in the nest assuming one egg is laid per day. In addition, breeding success was calculated as the percentage of eggs producing fledglings in a given year. For statistical analysis, all parameters were used as yearly means.

2.4 Studied species

Breeding data of three cavity-nesting bird species was used: Pied Flycatcher (3344 clutches) and Great Tit (2320 clutches), which had entries for all years (1956–2012) and the Common Starling (628 clutches), which had no data entries for the year 1990. The Pied Flycatcher is a long-

distance migratory species that breeds in Estonia but over-winters in South-Africa (e.g. Guinea, Ghana, Nigeria, Gabon); the Great Tit can be considered as a non-migratory species that breeds and overwinters in Estonia with some exceptions which overwinter in adjacent countries; Common Starling is a short-distance migratory species which breeds in Estonia but overwinters in Western and Southern Europe (e.g. Belgium, Holland, Germany and Great Britain) (Palm *et al.* 2009; birdlife.org). Therefore, these species were considered relevant in order to study the relationship between temperature change and breeding phenology of birds with different migratory strategies.

Anomalous laying onset dates were classified, as the clutches started later in the season and therefore, determined to be possible second clutches and not appropriate for the objectives of this study. This was done so by examining the distribution of data and personal correspondence with M. Mägi. Accordingly, the Common Starling had data series for the period 20th April–17th June but included was the period 20th April–4th June, the Pied Flycatcher had data for the period 24th April–11th July but included was 24th April–23rd June, the Great Tit had data entries for 13th April–1st August but included was 13 April–20 May.

2.5 Temperature periods and spring arrival data

Daily mean temperatures for the years 1952-2012 for Viljandimaa County weather station were extracted from the Estonian Weather Service (www.ilmateenistus.ee). Firstly, in order to analyse the relationship between temperature and laying onset, clutch size, fledgling numbers and breeding success, relevant temperature periods were assigned, which could have an effect of the listed parameters. A summary of these periods can be found in Table 1. The first temperature period (TP I) was determined by the time after earliest spring arrival from overwintering grounds to Viljandimaa and before laying onset. This was considered the most critical period for the migrant species to adjust their breeding onset according to local temperature conditions (Källander *et al.*, 2017). The yearly average dates of first arrival sightings of the Pied Flycatcher and the Common Starling were obtained from records gathered by volunteers initially co-ordinated by the Estonian Naturalists' Society and later by the Estonian Ornithological Society. A detailed description of the methodology is described by Palm *et al.* (2009). Only the arrival data for Viljandi town were used as it is the closest observation area to the study site. Due to gaps in the data series, only the records for the years 1936–1940, 1948, 1950, 1952–1988, 1990 were used for the Common Starling and the years 1957–1975, 1977–1996 for the Pied Flycatcher. This was done so by selecting the earliest yearly records available to increase the

validity of the trends. Data gathered after 1996 were excluded as there was a change in methodology and the two data sets were not compatible for analysis. Palm *et al*. (2017) have described this methodological inconsistency in more detail.

The first sighting period of the Common Starling in Viljandi town spanned from 1st March to 6th April. Two sighting in 1953 and 1961 were in February and therefore excluded as these may have been overwintering individuals and not suitable to include. The Pied Flycatcher first sighting period was 16th April–10th May. Due to the short observation period that ends in 1990 for the Common Starling and 1996 for the Pied Flycatcher, it was decided to use wider and more inclusive periods. Subsequently, March–April and April–May served as TP I. As the Great Tit is a non-migratory species, TP I was chosen according to the laying onset data and selected to be March–April. Similarly, other authors have used a 30-day period preceding the start of egg laying for resident species (Källander *et al*., 2017).

 Secondly, the second temperature period (TP II) was assigned to be the temperature during laying onset. This information was obtained from the data gathered from the study site (see subheading 2.4). Since daily temperatures are dependent on each other, it was decided not to use specific dates but more inclusive periods, which would represent the characteristic temperature trends. Accordingly, TP II was assigned as April–May for the Common Starling and Great Tit and May–June for the Pied Flycatcher. Thirdly, the third temperature period (TP III) was chosen for the time the fledglings leave their nest boxes (M. Mägi personal correspondence) and was therefore only used to analyse the relationship between fledgling numbers, breeding success and temperature. For the Common Starling and the Great Tit this is 20th May–5th June, for the Pied Flycatcher 5th June–20th June.

Table 1. Summary of the temperature periods used for each three species in order to analyse the relationship between temperature and laying onset date, clutch size, fledgling numbers and breeding success. Abbreviations as following: STU VUL is the Common Starling, FIC HYP is the Pied Flycatcher, PAR MAJ is the Great Tit.

Species	Spring arrival (TP I)	Laying onset (TP II)	Leaving nest boxes (TP III)
STU VUL	March–April	April–May	20th May–5th June
FIC HYP	April–May	May–June	5th June–20th June
PAR MAJ	March–April*	April–May	20th May–5th June

*The Great Tit is considered a resident species in Viljandimaa and TP I is the period before laying onset.

2.6 Data analysis

All data handling and sorting was performed using Microsoft Office Excel (Microsoft Corporaion, 2007) and statistical analyses were performed using STATISTICA 7 (StatSoft, Inc., 2004). All data met criteria of normal distribution. Temporal autocorrelation was tested with the Durbin-Watson test and d-statistic values measured against the Durbin-Watson significance table. No temporal autocorrelation was found ($p>0.05$). No additional steps with temperature data to further address temporal autocorrelation issues in climate change ecology (Brown *et al.*, 2011) were deemed relevant. This was decided after the guidelines of Ayazit & Önös (2009) – data had large sample size ($n \geq 50$) and high slopes of trend ($b \geq 0.01$). Linear and nonlinear regressions models were tested. All models were best described by a linear fit.

2.6.1 Analysis of Temperature data

Firstly, standard deviation (SD) was calculated for the assigned temperature periods (Table 1) for each year and used as an indicator of annual temperature fluctuation. The mean serves as a threshold and SD as the value of fluctuation from it. Linear regression analysis was then applied to see if the annual fluctuation has an effect on the annual means of laying onset, clutch size, fledgling numbers and breeding success. For TP III, only fledgling numbers and breeding success were used in the analysis.

Secondly, linear regression analysis was applied to identify trends in the temperature periods (Table 1). The total change for each period was obtained by multiplying the slope from the analysis with the number of years (after Jaagus, 2005). Then, SD for each period was analysed against year in order to see if the temperature fluctuation has increased, decreased or exhibited no change during the 54-year period.

2.6.2 Analysis of bird phenology data and breeding parameters

The mean arrival dates were analysed with a simple regression analysis against year to note trends in arrival times. Simple linear regression analysis was then applied to the following:

- Laying onset, clutch size, fledgling number, fledgling success against year;

- Laying onset against TP I and TP II (Table 1) relevant for each species;

- Clutch size against TP I and TP II (Table 1) relevant for each species;

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- Fledgling numbers and breeding success against TP I, TP II and TP III (Table 1) relevant for each species.

The total change for each year was obtained by multiplying the slope from the analysis with the number of years. The total change for each temperature period was analysed by multiplying the total temperature increase during the study period by the slope of each parameter analysis.

3. Results

3.1 Spring arrival

There was no statistically significant linear relationship between arrival date and year for the Common Starling (b=0.140 days per year, R^2=0.05, F_{48}=3.74, p=0.06). Similarly, there was no statistically significant trend for the Pied Flycatcher (b=0.015 days per year, R^2=-0.03, F_{37}=0.05, p=0.82). It is noteworthy that both trends are increasing. For the Common Starling this would result in an advancement by 5.7 days and for the Pied Flycatcher by 0.6 days.

3.2 Temperature trends

Temperatures in Viljandimaa for the periods March–April and April–May have increased on average 0.06°C per year and 0.04°C per year respectively (Table 2). During the years 1956–2012, annual air temperature for Viljandimaa has increased 3.08 °C for the period March–April. Months March and April contribute to the warming equally with March exhibiting a slightly steeper trend (March: b=0.057, R^2=0.04, F_{1765}=78.3, p<0.001; April: b= 0.054, R^2=0.04, F_{1708}=79.0, p<0.001). Temperature has increased 2.02°C for the period April–May. Both months show a statistically significant warming trend but May to a lesser extent (b=0.019, R^2=0.005, F_{1765}=9.7, p=0.002). No statistically significant change was observed for the periods May–June, 20th May–5th June and 5th June–20th June (Table 2).

Table 2. Annual warming trends during 1956-2012 in Viljandimaa. Results are from a simple regression model of the relationship between mean monthly temperatures and year. Statistically significant figures are indicated in bold.

Period	F	Slope	Df	R^2	P
March-April	20.38	0.055	55	0.26	**<0.001**
April-May	19.63	0.036	55	0.25	**<0.001**
May-June	0.99	0.009	55	-0.0002	0.32
20th May-5th June	0.62	0.015	55	-0.007	0.43
5th June-20th June	0.37	0.011	55	-0.01	0.55

All temperature periods exhibit yearly fluctuation from the mean (Fig. 1). When SD for each year for each period was analysed in a simple regression model against bird phenology parameter means, only SD of TP II had a positive linear relationship with laying onset of all species. It also had a positive linear relationship with the Great Tit fledgling numbers and breeding success (Table 3). The Pied Flycatcher and the Great Tit delayed the laying date 1.8

days per 1 °C of SD. Followed by the Common Starling which delayed the laying date 0.1 days per 1 °C SD. The Great Tit fledgling numbers increased by 0.6 fledglings per 1 °C of SD and the Great Tit breeding success increased 5% for every 1 °C of SD. When SD was analysed against year there was no statistically significant linear trend for any of the temperature periods (March–April: b=-0.001 ,R^2=0.02, F_{55}=0.01, p=0.90; April–May: b=-0.010 ,R^2=0.01, F_{55}=1.73, p=0.19; May–June: b=-0.012 ,R^2=0.04, F_{55}=3.33, p=0.07; 20th March–5th June: b= -0.014,R^2=0.03, F_{55}=2.49, p=0.12; 5th June–20th June: b= -0.011,R^2=0.03, F_{55}=2.64, p=0.11).

Table 3. Relationship between SD of each period and the bird phenology parameter means. Statistically significant values are indicated in bold. N/a indicates data not analysed. Abbreviations as following: S. VUL is the Common Starling, P. MAJ. is the Great Tit and F. HYP. is the Pied Flycatcher. For P. MAJ and F. HYP df is 55 and S. VUL df is 54.

| Species	TP	Laying onset				Clutch size				Fledgling numbers				Breeding success			
		slope	F	R^2	p	slope	F	R^2	p	Slope	F	R^2	p	slope	F	R^2	p
S. VUL	I	.001	.03	-.02	.85	.025	.30	-.01	.58	-.006	.006	-.02	.94	-0.532	.22	-.01	.64
	II	.069	6.88	.10	**.01**	.017	.08	-.02	.78	.072	.49	-.01	.49	1.342	.74	-.005	.39
	III	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	-.009	.01	-.02	.91	.053	.002	-.02	.97
P. MAJ	I	.012	.66	-.006	.42	.019	.15	-.02	.70	-.034	.04	-.02	.84	.137	.008	-.02	.93
	II	1.812	7.88	.11	**.007**	.121	3.37	.04	.07	.600	7.43	.16	**.009**	4.964	5.63	.08	**.02**
	III	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	.261	2.04	.02	.20	2.368	1.91	.02	.17
F. HYP	I	-.133	.08	-.02	.78	.013	.11	-.02	.74	-.009	.01	-.02	.91	-.642	.33	-.01	.57
	II	1.818	14.42	.19	**<.001**	-.072	2.71	.03	.11	.015	.02	-.02	.87	1.576	1.59	.01	.21
	III	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	.032	.12	-.02	.73	.860	.49	-.009	.49
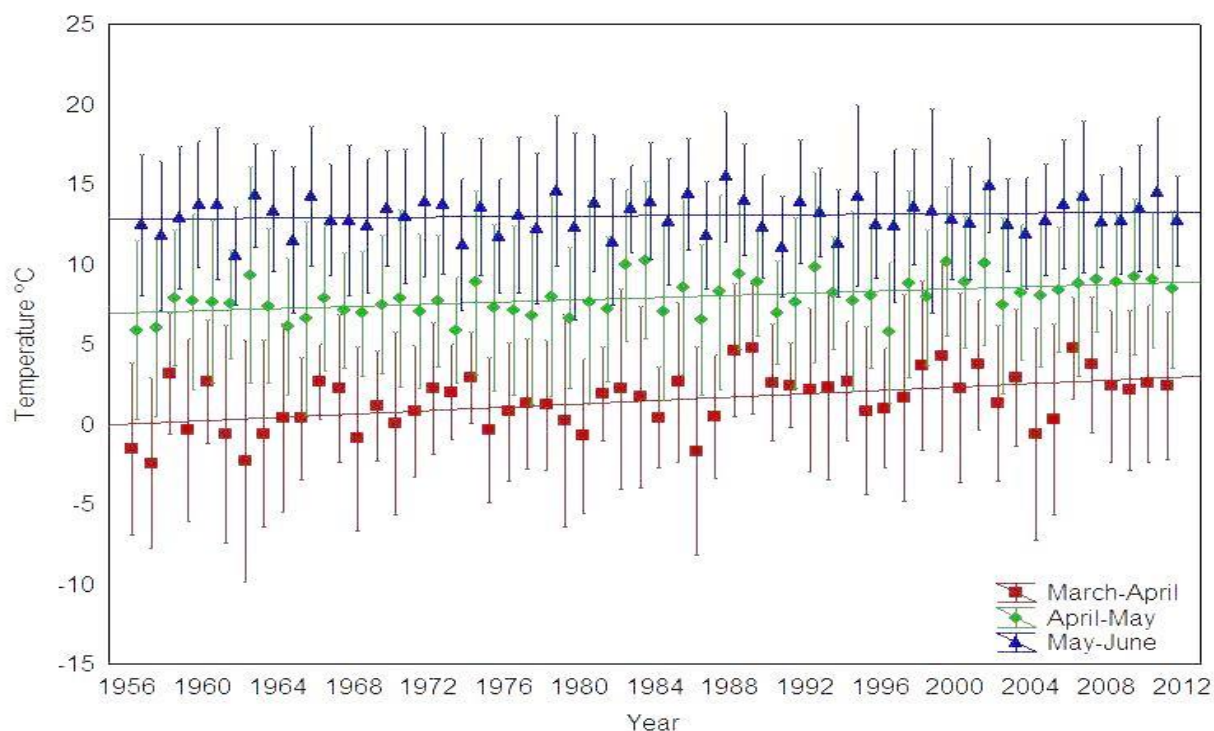
Figure 1. Fluctuation the three main temperature periods for the time series in Viljandimaa with their linear trends and standard deviations.

3.3 Bird phenology and breeding parameters

3.3.1 Laying onset

There was a statistically significant negative linear relationship between the year and laying onset, resulting in an advancement of the laying date per year, different for each species (Table 4). The relationships for the Pied Flycatcher and the Great Tit were less steep (about 0.1 days per year) than the Common Starling that advanced laying by about 0.2 days per year (Table 4). Overall, during the period 1956–2012 the Common Starling has advanced its laying onset 11.4 days, Great Tit 6.7 days and Pied Flycatcher 6.3 days. Furthermore, all species exhibited a significant relationship between the laying onset and TP I and TP II (Table 4). For the Common Starling and the Great Tit, the relationship between the laying onset and temperature is steeper at TP II, resulting in a 2.1 and 2.5 day earlier laying date per 1°C respectively. For TP I it was 1.8 and 2.2 day earlier laying per 1°C. For the Pied Flycatcher the relationship was steeper at TP I resulting in a 2.3 day earlier laying date per °C compared to 1.1 day earlier laying date per °C fpr TP II.

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Table 4. Linear relationships between mean laydate and year and temperature periods. Significant values are indicated in bold.

	Laydate vs year					Laydate vs TP I					Laydate vs TP II				
Species	slope	F	df	R^2	p	slope	F	df	R^2	P	slope	F	df	R^2	p
STU VUL	-0.207	79.69	54	0.59	**<0.001**	-1.792	54.22	54	0.49	**<0.001**	-2.199	27.88	54	0.33	**<0.001**
PAR MAJ	-0.121	12.52	55	0.17	**<0.001**	-2.199	125.73	55	0.69	**<0.001**	-2.454	33.56	55	0.37	**<0.001**
FIC HYP	-0.112	27.16	55	0.32	**<0.001**	-2.270	115.40	55	0.67	**<0.001**	-1.063	7.58	55	0.11	**0.008**

3.3.2. Clutch size

There was a statistically significant positive relationship between clutch size and year, TP I and TP II for the Pied Flycatcher (Table 5). During the study period, the Pied Flycatcher clutch size increased by 0.39 eggs. When TP I temperatures increase by 1°C, the Pied Flycatcher clutch size increases by 0.12 eggs. For a 56 year period this is an increase of 0.23 eggs. Similarly, when TP II increases by 1°C, clutch size increases by 0.09 eggs. This amounts to 0.04 eggs for the study period. The Great Tit had a statistically significant positive relationship between clutch size and TP II resulting in an increase by 0.19 eggs per 1°C. This amounts to an increase of 0.34 eggs during the study period.

Table 5. Linear relationships between mean clutch size and year, TP I and TP II. Statistically significant values are indicated in bold.

	Clutch size vs year					Clutch size vs TP I					Clutch size vs TP II				
Species	slope	F	df	R^2	p	slope	F	df	R^2	p	slope	F	df	R^2	p
STU VUL	0.002	0.33	54	-0.01	0.57	-0.053	2.77	54	0.03	0.10	-0.050	1.10	54	0.002	0.30
PAR MAJ	0.004	1.37	55	0.001	0.25	0.063	3.44	55	0.04	0.07	0.190	16.84	55	0.22	**<0.001**
FIC HYP	0.007	14.03	55	0.19	**<0.001**	0.116	18.74	55	0.24	**<0.001**	0.088	7.28	55	0.1	**0.009**

3.3.3. Fledgling numbers and breeding success

There was a statistically significant negative linear relationship between the Common Starling fledgling numbers and TP I (Table 6). When TP I temperature increases by 1°C, the Common Starling fledgling numbers decrease by 0.11 fledglings. For the study period, this amounts to a decrease of 0.34 fledglings. There was also a statistically significant positive linear relationship between the Great Tit fledgling numbers and TP II (Table 6). When TP II temperature increases by 1°C, the Great Tit fledgling numbers increase by 0.35 fledglings. For the study periods this amounts to an increase of 0.07 fledglings.

Table 6. Linear relationships between fledgling number and year, TP I and TP II. Statistically significant values are indicated in bold.

	Fledgling number vs year					Fledgling number vs TP I					Fledgling number vs TP II				
Species	slope	F	df	R^2	p	slope	F	df	R^2	p	slope	F	df	R^2	P
STU VUL	-0.004	0.51	53	-0.01	0.48	-0.109	4.43	53	0.06	**0.04**	-0.124	2.46	53	0.03	0.12
PAR MAJ	-0.004	2.14	55	0.02	0.15	0.003	0.00	55	-0.02	0.98	0.354	4.02	55	0.05	**0.05**
FIC HYP	-0.001	0.04	55	-0.02	0.85	0.075	1.32	55	0.01	0.25	0.125	3.0	55	0.04	0.09

There was a statistically significant negative linear relationship between the Pied Flycatcher breeding success and year (Table 7). This results in an overall 7.95% decrease in breeding success during the 56 year period.

Table 7. Linear relationships between fledgling success and year, TP I and TP II. Statistically significant values are indicated in bold.

	Breeding success vs year					Breeding success vs TP I					Breeding success vs TP II				
Species	slope	F	df	R^2	p	slope	F	df	R^2	p	slope	F	df	R^2	p
STU VUL	-0.142	2.29	53	0.02	0.14	-0.005	2.55	53	0.03	0.12	-1.647	1.93	53	0.02	0.17
PAR MAJ	-0.225	3.70	55	0.05	0.06	-0.005	0.27	55	-0.01	0.60	2.571	2.36	55	0.02	0.13
FIC HYP	-0.142	5.83	55	0.02	**0.02**	-0.718	0.68	55	-0.01	0.41	0.547	0.32	55	-0.01	0.57

In addition, there was a statistically significant positive linear relationship between the Great Tit fledgling numbers, breeding success and TP III (Table 8). When TP III increases by 1°C, the Great Tit fledgling numbers increase by 0.22 fledglings. For the 56 year study period, this is an increase of 0.19 fledglings. Breeding success increased 1.74% for every 1°C increase in TP III. For the study period, this is an increase of 1.46%. There was also a statistically significant positive linear relationship between the Pied Flycatcher breeding success and TP III (Table 8). For every 1°C increase in TP III, breeding success increases 1.01%. For the study period this is a 0.62% increase in breeding success.

Table 8. The linear relationships between the fledgling numbers, breeding success and TP II. Statistically significant values are indicated in bold.

	Fledgling numbers vs TP III					Breeding success vs TP III				
Species	slope	F	df	R^2	p	slope	F	df	R^2	p
STU VUL	0.037	0.96	52	-0.001	0.33	0.482	0.73	52	-0.01	0.40
PAR MAJ	0.221	7.41	54	0.10	**0.009**	1.738	5.05	54	0.09	**0.03**
FIC HYP	0.062	3.46	55	0.04	0.07	1.008	5.42	55	0.1	**0.02**

4. Discussion

4.1 Advancement of laying onset

As was hypothesised, the laying onset of all three species had advanced over the study period (Table 4). The number of days birds in Viljandimaa have advanced their laying onset is similar to other studies conducted in Europe. Findings for Great Tit (0.1 days per year) are similar to those found in Sweden (0.3 days per year, Källander *et al*., 2017), England (0.3 days per year, Charmantier *et al*., 2008) and Czech Republic (0.2-0.6 days per year, Bauer *et al*. 2010). Similarly, the rate of Pied Flycatcher laying onset advancement (0.1 days per year) agrees with records from the Netherlands (0.3 days per year, Both and Visser 2001) and Sweden (0.1 days per year, Källander *et al*., 2017). The Common Starling had the highest rate of advancement, 0.2 days per year. No adequate data were available from other studies for the Common Starling populations breeding in Europe.

It should be noted, that although the advancement of days per year has been fairly similar between countries, longer time spans would amount to larger variation between locations. For example, assuming the rate is constant in time, in a 60-year time span, Viljandimaa Great Tits would have advanced their laying by 6 days in total, but Swedish populations by 18 days in total. Consequently, there is a need for local studies in order to draw more accurate conclusions about the extent of these trends locally and globally. Many authors have attributed this laying onset advancement to increasing temperatures in breeding areas (Both and Visser, 2001; Visser and Marvelde, 2011; Källander *et al*., 2017).

4.2 The effect of temperature on advanced laying onset

As was expected, the temperature in Viljandimaa has increased during the 56 years. The results of analysis applied to temperature data from the three periods (Table 2) are overall in concordance with those of Jaagus (2005). Jaagus (2005) studied mean monthly temperature data from 10 weather stations in Estonia during 1951–2000. He showed that the highest increase in temperature has occurred during the spring season (March, April, May), especially March (3.0–5.0°C during 50 years) and April (1.7–3.0°C during 50 years). No statistically significant increase was detected for the summer season (June, July, August). Similarly, it was shown in this study that the highest increase was typical for spring periods March-April and April–May (Table 2). March exhibited the highest increase, followed by April and May. No increase was noted for

May–June, 20th May–5th June and 5[th]June–20th June (Table 2), which could be considered as the summer periods. It should be noted that these periods still exhibited an increasing trend and with longer time spans may become statistically significant. Overall, these findings also agree with annual trends in Europe (Xoplaki *et al*., 2005). During the last 100 years, the greatest change in Europe has occurred in spring (Xoplaki *et al*., 2005). Although all spring months contribute to this, March has seen the strongest warming trend (Xoplaki *et al*., 2005). This demonstrates that ecological phenomena occurring in spring experience the highest increasing temperatures.

More importantly, these warming trends coincide with the Common Starling, the Great Tit and the Pied Flycatcher's TI I and Common Starling and Great Tit's TP II. Although, the Pied Flycatcher's TP II was not statistically significant, it exhibited an increasing linear trend. The inclusion of mean temperature period data to the analysis showed a significant relationship between TP I, TP II and laying onset for all three species (Table 4). This suggests that the advancement of egg laying could be due to increasing temperatures. Since TP I had a bigger effect on laying onset than TP II (according to R^2 values, Table 4), it seems like the temperature during spring arrival is a more important cue for birds to adjust their laying onset. This agrees with previous studies on the relationship between laying onset and 30 day period preceding it. Källander *et al*. (2017) found similar values for Swedish Great Tit populations that exhibited 2.2–2.5 day advancement per 1°C compared to 2.2 days per 1°C found in this study. Similarly, Källander *et al*. (2017) found that Pied Flycatcher had advanced their laying onset 1.7 days per 1°C compared to 2.3 days per 1°C shown in this study.

The effect of temperature on laying onset is suggested to be indirect. The increasing spring temperatures bring about advancement of plant phenology (leafing and blossoming), that is followed by that of invertebrates (start of development) and in turn insectivorous birds (Both and Visser, 2001; Visser and Marvelde, 2011; Källander *et al*., 2017). This has been found for Great Tit populations in England and Czech Republic, where the birds have advanced their laying roughly the same rate as caterpillars (Charmantier *et al*., 2008; Bauer *et al*. 2010). No loss of fitness was noted for these populations. On the other hand, there are studies that show a mismatch between the Great Tit populations resulting in reduced fitness (Visser, Holleman and Gienapp, 2006). Studies with Pied Flycatchers in the Netherlands and Spain have shown that caterpillars have advanced their phenology, but the birds to a much lesser extent (Both and Visser 2001; Sanz *et al*., 2003). This resulted in reduced fitness. For example, Sanz *et al*. (2003) found that this mismatch caused reduction of Pied Flycatcher adult energy expenditure. This

reflected in reduction of nestling growth and survival of fledged young. Ahas (1999) concluded that in Estonia, during the 20th century phenological advancement of plants had occurred and predicted increasing trends for the future. Therefore, it can be suggested that the studied species, like that of other European populations, have advanced their laying onset due to advancement of food peaks. Unfortunately, due to data limitations on Estonian vegetation and/or invertebrate phenology trends, there is no accurate measure to quantify the success of this advancement (as suggested by Visser and Both, 2005).

A possible reason why the Common Starling has advanced the most is that its diet composes of a variety of invertebrates. Therefore, it can start feeding as soon as weather conditions allow to find suitable food objects from the ground. Temperature has a direct effect on snow cover (Jaagus, 2005). In addition, soil temperature correlates well with spring mean temperatures (Qian *et al.*, 2011). This may mean that with increasing temperatures, the Common Starlings are able to access food earlier. This may have lead to advancement of its laying onset. Furthermore, other authors have noted that some migratory species have changed their migratory strategy and become residents or shortened their migration distance (Sutherland, 1998; Visser, *et al.* 2009). It could be that due to milder winters in Estonia (Jaagus, 2005) the Common Starlings in Viljandimaa have shifter their migratory strategy. Possible residency could also partly explain the high rate of laying advancement. They would be able to accurately follow snow cover loss and warming of the soil. The Pied Flycatcher and Great Tit are mostly insectivorous and are probably more limited to the availability of certain insect prey like caterpillars (Mägi *et al.*, 2009; Sisask *et al.*, 2010). Therefore, these species depend more on the synchrony between plant and caterpillar phenology and are limited by suitable prey availability in their laying advancement.

4.3 The effect of temperature on breeding parameters

4.3.1 The Pied Flycatcher

Contrary to the hypothesis, the Pied Flycatcher's clutch size has increased during the study period and the greatest effect was on TP I. Overall, this resulted in an increase by about 0.4 eggs (Table 5). On the other hand, as hypothesised, there was an overall decrease in breeding success by about 8% (Table 7). Some populations of Pied Flycatchers have shown to increase clutch sizes with increasing temperatures (Winkel and Hudde, 1997). Both and Visser (2005) suggested that the Pied Flycatchers can optimize their life-history traits according to the yearly

environmental conditions. They showed that Pied Flycatchers that lay early in the season, increase their clutches. Individuals laying later in the season, decrease their clutches. They proposed this is due to earlier, but shorter food peaks in years that have earlier spring. The ones advancing their laying, invest in future reproductive success, as their offspring have a higher chance of survival by meeting the food peak. Therefore, in warmer springs the selection is for birds that lay early, but in colder springs for the ones who lay later. As the Pied Flycatchers at the study site have advanced their laying onset and exhibit significantly increasing trends in clutch size, it could be expected that there is a food peak in Viljandimaa. This peak has advanced with earlier spring and selection is favouring earlier laying onset and larger clutches. This, with the evidence by Both and Visser (2005), indicates that Pied Flycatcher populations breeding in Europe are more phenotypically flexible than has been suggested for long-distance migrants (Gwinner, 2003). To further investigate this phenomenon it is suggested to study separately the individuals who lay earlier and later in the season and their clutch size respectively.

Nevertheless, the 8% decrease in breeding success may be an indicator of a slight mismatch with food peaks. This is supported by a study carried out in the Netherlands where Pied Flycatcher populations have experienced a decline where brood rearing period missed the food peak (Both, 2006). Interestingly, TP I nor TP II had an effect on breeding success. Since there seems to be a selection towards earlier laying onset and larger clutches that indicate a food peak, it is plausible that fledgling success is affected by temperature periods other than the ones assigned in this study. Similarly, it could also be speculated that selecting temperature periods spanning two months may be too broad to represent temperature conditions during fledging of the Pied Flycatcher young. There is evidence that the Pied Flycatcher chicks reach higher weights when reared on higher proportion of caterpillars in their diet (Burger *et al*., 2012). Therefore, it may be that this caterpillar abundance occurs in a narrower time span than is indicated by the selected temperature periods for this study. It is supported by the fact that overall Pied Flycatcher TP II is not statistically significant but May exhibits a statistically significant warming trend. It is plausible that higher caterpillar abundance occurs in May and the Pied Flycatcher brood is in slight asynchrony from it resulting in breeding success decline. It is advised to study shorter time periods to identify this.

It may be that Pied Flycatchers do not arrive to Viljandimaa early enough to optimally adjust their laying onset as laying onset, clutch size and brood rearing is constrained by a distinct breeding season. Since there is a difference in the rate of temperature increase between Europe

and sub-Saharan Africa (Cotton, 2003), Pied Flycatchers may start spring migration later than is optimal for breeding success. Temperature en-route to breeding grounds may be a cue of changed environmental conditions (Hüppop and Winkel, 2006). Hüppop and Winkel (2006) looked at the migration route and time of the Pied Flycatcher from their overwintering grounds in sub-Saharan region to breeding grounds in central Europe and found a strong correlation between temperature regimes en-route and arrival times. They found strong regional temperature variability and suggested that western route of migration would be the most beneficial in terms of more accurate temperature cues (Hüppop and Winkel, 2006). Unfortunately, it is not known which migration routes birds breeding in Viljandimaa use and it may be possible that individuals from the same population use different routes. Information on migration routes combined with data on bird laying onset would provide beneficial information for predicting future trends.

Alternatively, breeding success in Viljandimaa may have decreased due to reasons other than a mismatch between food peaks. One of the reasons could be population size and competition for resources (Ahola *et al*., 2012). Furthermore, this decline at the study site is important as with longer time spans this could amount to even higher decrease. Overall Pied Flycatcher populations breeding in Estonia have declined during 1980–2012 (Elts *et al*., 2013). Therefore, it is important to identify the cause of this decline. From the data available for this study, it is not clear what may have caused this.

4.3.2   The Great Tit

Contrary to the hypothesis, TP II had an effect on clutch size resulting in an increase by 0.3 eggs. Similarly, TP II had an effect on fledgling numbers resulting in an increase by 0.07 fledglings. Some studies have found that the Great Tit clutch size does not change with earlier laying dates (Winkel and Hudde, 1997). On the other hand, Saino *et al*. (2004) looked at the effect of temperature on eggs in Barn Swallow (*Hirundo rustica)* and found that increasing temperatures induce higher concentrations of antioxidants and antibacterial immune factors. It may be that higher temperatures during the Great Tit laying onset may indicate that there is food abundance and/or high quality of food, which in turn increase female reproductive ability. Furthermore, better female condition may lead to improved egg composition and in turn fledgling health.

Contrary to the hypothesis, TP III had an effect on fledgling numbers and breeding success. This resulted in an overall increase by 0.2 fledglings and breeding success by 1.5% during the study period. This may indicate that feeding conditions in Viljandimaa during the time fledglings leave

their nest boxes are optimal. Higher temperatures during this period may result in faster development of caterpillars which are the main food resource for fledglings (Mägi et al., 2009). Since the Great Tits at the study site have advanced their laying onset, it could be hypothesised that they have been successful in meeting the food availability. Otherwise there would have been a decrease in breeding parameters. This is supported by overall population trends in Estonia which show no decrease (Elts et al., 2013). Similarly Great Tit populations in England and Czech Republic have advanced their laying onset optimally (Charmantier *et al*., 2008; Bauer *et al*. 2010). Furthermore, it shows that the Great Tits are phenotypically flexible and susceptible to environmental cues enabling them to adjust to changing temperatures.

4.3.3 The Common Starling

On the contrary to the hypothesis, TP I had a negative effect on fledgling numbers. This resulted in an overall decrease by 0.3 fledglings during the study period. Interestingly, overall trends in Estonia during 1980-2012 show no increase or decrease in the Common Starling breeding population (Elts *et al*., 2013). One of the explanations for this slight decline may be the fact that the Common Starlings feed on a variety of food objects on the ground and high temperatures may cause invertebrates to hide, making them harder to detect. Since no other breeding parameter showed an increase or decrease this hypothesis is inconclusive and further studies are needed. On the other hand, as hypothesised, the Common Starling clutch size or fledgling numbers show increase or decrease. This may be an indicator of successful synchrony with prey species.

One of the available studies with Common Starling's breeding parameters and temperature looked at populations breeding in Canada (Williams *et al*., 2015). The study showed that mid-winter, not spring temperatures were correlated with laying onset and clutch size. The authors suggested that these temperatures are cues by their prey species to synchronize development with plant phenology the following growth season. The mechanisms by which the birds translate this temperature cue are not known. Although, the study was carried out in Canada, it may be that the Common Starlings breeding in Europe also depend on their prey availability. Furthremore, it may be that they use temperature cues from seasons not investigated in this study. As they are short-distance migrants and exposed to local conditions in Europe, they could utilize information other than spring temperatures. Since the Common Starling populations in Europe are understudied more research is needed to draw conclusions about the effect of increasing temperature.

4.3.4 Conclusions about bird food dynamics in Viljandimaa

There are few studies in Estonia investigating caterpillar abundance. For example, Mägi *et al.* (2009) studied the Great Tit food preference in southwest Estonia in 2004. They showed that there was no change in caterpillar abundance during the brood rearing period in a deciduous forest. Studies with the Pied Flycatcher food preference in southwest Estonia have shown similarly results (Sisask *et al.*, 2010). No food peak in a deciduous forest, but caterpillar abundance increased during the second broods in a coniferous habitat. No studies in a mixed coniferous broad-leaved forest, like the study site, have been conducted. Since there is no evidence that the Great Tit or the Common Starling have reduced fitness, it may be that the study site does not have a distinct food abundance period. On the other hand, it may also indicate that the populations have adjusted their phenology according to possible food abundance. Furthermore, the increased clutch size but reduced breeding success of the Pied Flycatcher may indicate that later on in the season there may be distinct food peak that may be in slight asynchrony with the Pied Flycatcher broods. Although, some conclusions can be drawn from breeding parameters they are inconclusive. More studies are needed on caterpillar availability and biomass to understand the interaction between populations, their food resources and temperature. This information will also indicate how successful are breeding parameters in predicting food dynamics.

4.4 Effect of temperature fluctuation on laying onset

Another effect of temperature found in this study was the effect of high temperature fluctuation (SD) on laying onset (Table 2). High temperature fluctuation from the mean results in postponed laying onset. It could be hypothesised that postponed laying is a strategy to synchronize the hatching date with delayed food peaks. High temperature fluctuation may indicate a delayed primary production that has an effect on invertebrate life cycle. This hypothesis is partly supported by the findings of Nilsson (1944) and Crasswell and McCleery (2003). The first author established that when Blue Tit (*Cyanistes caeruleus)* laying onset was experimentally advanced, they delayed the start of incubation. Similarly, Crasswell and McCleery (2003) found that Great Tit respond to high temperature fluctuations by opting for strategies that help synchronize hatch date with food peak of that given year. Interestingly, this happens after the eggs are layed not before, like in the current study. They found that over a 39-year period in the United Kingdom, Great Tits significantly increased their incubation period. They suggested that Great Tits start laying eggs as soon as conditions are suitable. This means they can invest in larger clutches.

When there is a high temperature fluctuation, they delay the start of incubation in order to meet the delayed food peak. The data available for this study cannot be used to test delayed incubation hypothesis, but the results do show that birds have advanced their laying onset and delay it with high temperature fluctuations. It may be possible that birds can delay the start of incubation only to an extent, before it becomes harmful for the developing embryos. It may be plausible that delayed laying onset and delayed incubation onset are part of the same mechanism. Alternatively, limited food availability may be a constraint for the adults. More studies are needed to confirm or reject the hypothesis of synchronisation mechanisms in birds.

Interestingly, the temperature fluctuation of TP II had a positive effect on the Great Tit fledgling numbers and breeding success. This may be due to the fact that this temperature fluctuation causes the insects to develop at different times intermittently and not as one distinct food peak. Since the Common Starlins feed on a variety of invertebrates they would be less affected by this. The Pied Flycatcher population breeds later in the season and this intermittent development of caterpillars may have ceased. More studies are needed to understand this pehnomena.

4.5 Spring arrival trends

On the contrary to the hypothesis, there was no statistically significant trend for the spring arrival of the Common Starling or the Pied Flycatcher. This is inconsistent with observations from other studies (Cotton, 2003; Kullber et al., 2015). It would be expected that due to the temperature increase in Viljandimaa, the short-distance migrants advance their arrival. This is necessary to meet the earlier foraging conditions for breeding adults and to adjust laying onset optimally. For example, Kullberg et al. (2015) looked at short- and long-distance migratory bird species data separately for historical (1873–1917) time series and present day (1984–2013) time series in southern and central Sweden. They found that short-distance species including the Common Starling have advanced their arrival to breeding grounds to a greater extent than long-distance species. Both and Visser (2001) looked at the Pied Flycatcher and found that the spring arrival has not advanced. Although the results of arrival for the Pied Flycatcher and the Common Starling from this study contradict other author's findings it should be noted that the trend for the Common Starling was much steeper than for the Pied Flycatcher. If significant, the trend for the Common Starling would result in a 6 day advancement during the 41 year period. The high p-value may be due to the nature of the data (Palm et al., 2009, Palm et al. 2017). For example, population size and sampling effort may affect the first spring arrival data.

4.6 General implications

The findings of this study are important assets to the knowledge about how different bird populations respond to global and local increasing temperatures. It seems like the long-distance migrant has a disadvantage in adapting to change, making long-distance migration the least favourable strategy for adjusting to increasing temperatures. On the other hand, the short-distance migrant and resident species seem to utilize local cues more accurately and respond more optimally, making these strategies more favourable. It's noteworthy that although the rate of change between populations in Viljandimaa and some other countries seem similar, these similarities may amount to big differences in longer time spans. Analysis on bird breeding parameters seems an adequate means of interpreting the relationship between increasing temperatures, food dynamics, bird phenology and breeding parameters. Studies on food peaks are needed to further confirm this.

In general, most studies seem to agree that the Pied Flycatcher exhibits a mismatch between its brood rearing season and food peaks, resulting in reduced fitness. This is important from the perspective of conservation action. The Great Tit populations seem more variable with some showing synchrony and others asynchrony with their food peaks. To make generalizations on a wider scale, this disparity needs further attention. Since there is a lack of studies about the Common Starling, the findings of this study are valuable. For example, they may be shifting their migration to residency and they may be using temperature cues from other seasons than spring. It also seems likely they may be less dependent on a certain food peak, but more on invertebrate availability under snow cover.

Furthermore, temperature fluctuations in spring may be an important cue for birds to adjust their breeding onset. As the evidence for synchronization mechanisms in birds is a new study area, this is an important addition and further studies are needed to investigate this phenomenon. Nevertheless, it should be noted that increasing temperatures are not the only factors having negative effect on bird populations and synergistically may hinder their capability to adapt efficiently. Since anthropocentric temperature forcing has a part in increasing temperatures, it demonstrates well the need for human attention and intergovernmental action.

Summary

Temperatures are increasing globally, but the Northern Hemisphere is warming with a higher rate than the Southern Hemisphere. Temperature trends also exhibit local variation. Most importantly, temperature increase in Europe is highest during spring climatic season, bringing about earlier spring and affecting ecological phenomenon occurring in spring. One of the consequences is a mismatch between songbird fledglings and caterpillar peaks due to mistimed laying onset. Short-distance migrants and resident species are known to be more susceptible to external cues and exhibit higher phenotypic plasticity. Consequently, some European songbirds have advanced their phenology the same rate as their main prey species have advanced their phenology. Due to local temperature variation birds can misinterpret cues. On the other hand, long-distance migrants are more dependent on internal cues and arrive to their European breeding grounds later than is optimal. As a result some species have been declining in numbers.

This study looked at the relationship between breeding phenology and temperature of three species with different migration strategies- Great Tit (resident), Common Starling (short-distance migrant) and Pied Flycatcher (long-distance migrant). All three species are mostly insectivorous and therefore expected to be dependent on their invertebrate prey availability and abundance in a limited breeding and brood rearing period. Data was gathered during a 56-year study period in a location in Viljandimaa. As there was no available data on invertebrate phenology in Estonia, breeding parameters were suggested to show some insight into available food dynamics. The effect of three temperature periods on laying onset, clutch size, fledgling numbers and breeding success was analysed with a simple linear regression model for each species. In addition, temperature increase, yearly fluctuation and bird first spring arrival data were analysed.

It was found that all three species had advanced their laying onset and temperature had a significant effect. Temperature has been increasing in Viljandimaa in accordance to local and global trends. It is suggested that the most important period for birds to obtain relevant cues from the environment for adjusting their breeding, is the time before laying onset. The Common Starling had advanced the most (11.3 days), followed by the Great Tit (6.7 days) and the Pied Flycatcher (6.3 days). There is evidence that there is a food peak second half of spring when the Pied Flycatcher eggs hatch. This is indicated by a selection towards earlier laying and increased clutch size. Surprisingly, the Pied Flycatcher breeding success has decreased, but temperature had no effect. It remains unclear if it is the result of a slight mismatch with food peaks due to later laying onset than is optimal; or other reason not identified in this study.

There is a positive effect of temperature during laying onset on The Great Tit clutch size and fledgling numbers. This may show good breeding condition of females due to food abundance. This combined with the positive effect of temperature during fledglings leaving nest boxes on fledgling numbers and breeding success may indicate that the Great Tits have advanced their laying optimally. Nevertheless, there is a possibility that there is no food peak during the Great Tit first broods. As expected, the Common Starling exhibited no change of most breeding parameters As they had advanced the most, it may be that they are less dependent on distinct food peaks. They start breeding activity as soon as food becomes available after the snow melts. The negative effect of temperature period before laying onset on fledgling numbers may mean that higher temperatures cause their invertebrate prey to hide and decrease availability. More studies are needed to confirm this. Overall, it is suggested that the Common Starling has adjusted their laying onset optimally.

Interestingly, temperature fluctuation has an effect on laying onset. This may be a part of synchronization mechanisms utilized by birds to delay their breeding when there is high temperature fluctuation. This may have an effect on invertebrate phenology and therefore, timing of food abundance. Overall, it seems that long-distance migration is the least favourable strategy to adjust to increasing temperatures. More studies are needed on invertebrate food peaks to quantify the success of laying advancements more accurately.

Kokkuvõte

„Temperatuuritõusu mõju kolme linnuliigi pesitsusfenoloogiale Lõuna-Eestis, Viljandi maakonnas.”

Temperatuur tõuseb globaalselt, kuid põhjapoolkera soojeneb kiiremini kui lõunapoolkera. Peale selle erinevad temperatuuritõusud ka lokaalselt. Oluline on see, et Euroopas tõuseb kõige kiiremini kevadine temperatuur, mille tulemusena saabub kevad varem ja see omakorda mõjutab ökoloogilisi nähtusi. Üks tagajärgedest on linnupoegade ja röövikute rohkuse perioodi fenoloogiline nihe, sest linnud hakkavad valel ajal munema. Lühimaarändurid ja paigalinnud on teatavasti vastuvõtlikumad eksogeensetele faktoritele. Lisaks on nad fenotüübiliselt plastilisemad. Mõni Euroopa populatsioon on pesitsusfenoloogiat oma toiduobjekti fenoloogia järgi edasi nihutanud. Siiski lokaalsete temperatuurierinevuste tõttu võivad linnud keskkonnamuutusi valesti hinnata. Kaugmaarändurid sõltuvad rohkem endogeensetest faktoritest. Seetõttu jõuavad nad Euroopa pesitsuskohtadesse hiljem, kui oleks optimaalne. Selle tulemusena on mõnede linnuliikide arvukus langenud.

Selle töö raames uuriti temperatuuri seost eri migratsioonistrateegiaga kolme linnu pesitsusfenoloogiale. Rasvatihane on paigalind, kuldnokk lühimaarändur ja must-kärbsenäpp kaugmaarändur. Kõik kolm liiki on peamiselt insektivoorsed. Seega võib eeldada, et oma pesitsuse ning poegade kasvatamise perioodil sõltuvad nad selgrootute kättesaadavusest ja rohkusest. Andmeid koguti 56 aasta jooksul Viljandimaal. Kuna Eesti selgrootute pesitsusfenoloogia kohta andmed puuduvad, siis kasutati pesitsusparameetreid, et toidudünaamikat hinnata. Kolme temperatuuriperioodi mõju uuriti munemise algusajale, kurna suurusele, lennuvõimestunud poegade arvule ja lennuvõimestumise edukusele. Analüüsina kasutati lineaarset regressiooni. Peale selle uuriti temperatuurimuutusi ja temperatuuri aastast kõikumist ning lindude esmasaabumiskuupäevi.

Leiti, et kõik kolm liiki nihutasid oma munemisaega varasemaks ja temperatuuril oli sellele oluline mõju. Temperatuur Viljandimaal on tõusnud kooskõlas lokaalsete ja globaalsete trendidega. Võib eeldada, et lindude jaoks kõige olulisem periood keskkonnamärkide interpreteerimiseks on periood enne munemise algust. Kuldnokk nihutas oma munemisaega edasi kõige enam (11,3 päeva), talle järgnes rasvatihane (6,7 päeva) ja seejärel must-kärbsenäpp (6,3 päeva). Tulemuste põhjal on põhjust arvata, et Viljandimaal on toidurohkuse periood hiliskevadel, kui kärbsenäppide munad kooruvad. Sellele viitab varasem munemisaeg ja suurem

kurn. Veel leiti, et must-kärbsenäpi lennuvõimestumise edukus langes. On ebaselge, kas selle põhjus on väike erinevus munemise alguse ja toidurohkuse perioodi vahel või mõni muu põhjus, mida see uuring ei võimaldanud tuvastada. Ootustele vastavalt ei olnud kärbsenäpid esmasaabumiskuupäeva varasemaks nihutanud. See võib olla ka põhjuseks, miks munemisaega piisavalt optimaalselt ettepoole ei nihutata.

Munemise algusaja temperatuuril on positiivne mõju rasvatihase kurna suurusele ja lennuvõimestunud poegade arvule. See võib tähendada, et emaste olukord on hea, mis omakorda võib viidata toidurohkusele. Peale selle on positiivne mõju temperatuuriperioodil, mil pojad pesakastidest lahkuvad, lennuvõimestunud poegade arvule ja lennuvõimestumise edukusele. See kõik võib viidata sellele, et rasvatihased on oma munemise algust kohandanud optimaalselt toidurohkusega. Samas võib ka arvata, et rasvatihase jaoks ei ole toidurohkuse perioodi. Selle selgitamine vajab edasisi uuringuid. Nagu eeldatud, ei olnud kuldnoka pesitsusparameetrites muutusi, välja arvatud negatiivne mõju lennuvõimastunud poegade arvule temperatuuriperioodil, millal linnud munemist alustavad. See võib tuleneda asjaolust, et kõrgemate temperatuuride juures on lindude toiduobjektid varjus ja raskemini kättesaadavad. Sellest tulenevalt on emased halvemas konditsioonis, mis kandub üle munadele. Tulemustest järeldub, et ka kuldnokk on oma munemisaega optimaalselt edasi nihutanud.

Lisaks on kevadise temperatuuri kõikumise ja munemise alguse vahel oluline seos. Temperatuuri kõikumise tulemusena munetakse kurnad hiljem. See võib olla osa sünkronisatsioonimehhanismidest, mida linnud kasutavad, et munemisalgust nihutada, kui olud ei ole sobivad. Seda seetõttu, et suured kõikumised võivad mõjutada ka selgrootute fenoloogiat. Kokkuvõtvalt võib öelda, et temperatuur on oluline faktor, mis mõjutab lindude fenoloogiat ja pesitsusparameetreid. Lisaks on kaugmaaränne kõige kehvem strateegia kohanemaks tõusva temperatuuriga. Toidurohkuse dünaamikat on vaja rohkem uurida, et täpsemalt munemisaja nihkumise edukust hinnata.

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