The impacts of temperature on the long-term variation in migration and breeding performance of birds

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Contents

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IV Lindén, A., **Meller, K.** & Knape, J. (Submitted, under revision). An empirical comparison of models for the phenology of bird migration.

Table of contributions

	Original idea	Data handling & analyses	Manuscript preparation
Chapter I	ALE, AV	KM	KM, ALE, AV
Chapter II	ALE	KM, MP, JR, TH, ALE	KM, ALE, AV, JR, MP, TH
Chapter III	MP, ALE	KM, MP	KM, ALE, MP, AV
Chapter IV	ALI	ALI, KM	ALI, KM, JK

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ABSTRACT

As the climate of our planet is warming, there is an urgent need to understand how temperature changes affect nature and how the species are able to cope with the changing environment. In my thesis I used Finnish long-term monitoring data to examine the effects of fluctuations in temperature and other environmental variables on the migration behavior and breeding performance of birds.

I found that during warm springs birds started to breed earlier, which increased the length of the time period spent in the breeding area because the timing of autumn migration remained mostly constant (only the young from the latest broods migrated later). After warm springs productivity (the number of offspring per adult) was moderately but uniformly higher than after cold springs in the study community passerine birds. The annual productivities and population sizes varied synchronously among the species. Despite I found connections between the annual temperature, productivity and population size, the long-term population trends were not connected to changes in productivity. This implies that changes in survival during the non-breeding period would be driving the trends.

Mild winter temperatures caused higher proportion of partially migratory waterbirds to overwinter in Finland than in cold winters. Climate warming related lack of severe ice winters arguably was behind the steep increase in the proportion of resident in waterbirds, while there were no trends in terrestrial species during the study period. The annual wintering area choice of terrestrial species was little affected by temperature, but in several species the seed crop of trees had a strong impact.

Modelling the distribution of migration phenology is often essential for studying whether the temperature related adjustments in phenology are sufficient to cope with the effects of climate change. My comparison of methods showed that usually relative simple distributions describe the migration phenology well. I also provided a simple novel method to account for the day-to-day variation in migration data.

My findings indicate that the life-history traits of the northern bird species are responsive to the variation in temperatures, but there are differences between taxa and functional groups in the responses, which underlines the importance of studying numerous taxa in order to draw general conclusions and predict the effects of continuing climate change.

TIIVISTELMÄ

Ilmaston lämmetessä on ensiarvoisen tärkeää selvittää lämpötilavaihteluiden vaikutukset luonnossa ja arvioida kuinka hyvin lajit pystyvät sopeutumaan muuttuviin ympäristöoloihin. Väitöskirjassani tutkin suomalaisten pitkäaikaisseuranta-aineistojen avulla, kuinka lämpötilat ja muut ympäristömuuttujat vaikuttavat lintujen muuttokäyttäytymiseen ja pesintämenestykseen.

Tutkimuksissani selvisi, että lämpiminä keväinä linnut pesivät aikaisemmin, mikä pidensi yksilöiden pesimäalueilla viettämää aikaa, koska syysmuuton ajoittuminen pysyi enimmäkseen vakiona (vain kaikkein myöhäisimpien pesintöjen nuoret linnut muuttivat myöhemmin). Lämpiminä keväinä poikastuotto (nuoria / aikuinen) oli hieman parempi kuin kylminä keväinä liki kaikilla lajeilla varpuslinnuista koostuvassa tutkimusyhteisössäni. Sekä poikastuoton että populaatiokoon vuosittaisissa vaihteluissa oli lajien välistä synkroniaa. Vaikka vuositasolla lämpötila, poikastuotto ja seuraavan vuoden kannankoko olivat yhteydessä toisiinsa, pitemmällä aikavälillä muutokset poikastuotossa eivät aiheuttaneet kannanmuutoksia, mikä viittaa siihen, että muutokset pesimäajan ulkopuolisessa kuolleisuudessa olisi aiheuttanut kannanmuutokset.

Leutoina talvina suurempi osuus osittaismuuttajavesilinnuista talvehti Suomessa kuin kylminä talvina. Vesilintujen talvehtijaosuuden voimakas kasvu 25-vuoden tutkimusjaksolla johtui luultavasti siitä, että ilmaston lämpenemisen takia ankaria jäätalvia ei ollut. Maalinnuilla talvehtijaosuudet eivät muuttuneet eikä lämpötilat vaikuttaneet talvehtimisalueiden valintaan, mutta sen sijaan puiden siemensato vaikutti monen lajin talvehtimiskäyttäytymiseen.

Muuttofenologian jakauman mallintaminen on usein tarpeen sen tutkimiseksi, kuinka hyvin linnut ajoittavat muuttonsa suhteessa ilmastonmuutoksen aiheuttamiin muutoksiin ympäristössä. Eri menetelmien vertailu osoitti, että yleensä suhteellisen yksinkertaiset jakaumat kuvaavat hyvin muuttofenologiaa. Kehitin myös uuden yksinkertaisen menetelmän ottaa huomioon päivittäistä vaihtelua muuttajamäärissä.

Tulokseni osoittivat, että lämpötilat vaikuttavat pohjoisten lintujen muuttoon ja pesintään, mutta eri lajien ja toiminnallisten ryhmien välillä on eroja vasteissa. Tämä korostaa monia lajeja ja lajiryhmiä sisältävien tutkimusten tärkeyttä yleistettävien tulosten saamisessa ja ilmastonmuutoksen vaikutusten luotettavassa ennustamisessa.

SUMMARY

1. Introduction

1.1. Climate warming, observed general changes and effects

Anthropogenic climate warming has elevated the global temperatures since 1800s, and the warming has gotten faster during the past 40 years (IPCC 2013). The warming has been and is predicted to continue to be the strongest in the high latitudes. Depending on how fast the emissions of carbon dioxide and the other greenhouse gases are cut, the average global temperature is predicted to increase about 1.5 –- 6 degrees ºC during the 21st century. The temperature increase during winters in our high latitude study area, Finland, is predicted to be about 2.5 – 7.5 ºC (IPCC 2013).

The ongoing global climate change has great potential to affect both the temporal and spatial distribution of resource availability across the planet (Williams & Middleton 2008). The effects of warming are pronounced in the high latitudes where the length of the period with snow and ice is decreased due to increasing temperatures (Luomaranta et al. 2014).

The organisms on earth have already been affected by the climate warming in several ways. For example, species distributions have shifted towards the poles and high altitudes (Thomas & Lennon 1999; Brommer, Lehikoinen & Valkama 2012), phenologies of many biotic processes have changed (Parmesan 2006) and population sizes have been altered (Knudsen et al. 2011). The extinction risks are predicted to increase during the next century in response to climate change (Maclean & Wilson 2011).

Birds have been one of the main groups studied in relation to climate change because of the ample amount of data available and due to their often strong responses to climatic variation. There are plenty of examples of both spring migration arrival and breeding of many bird species having generally advanced in mid- and high latitudes (Dunn & Winkler 2010; Lehikoinen & Sparks 2010). Other observed effects of increased temperatures include shifts of wintering ranges towards north (Maclean et al. 2008; Lehikoinen et al. 2013a), decreases in migration distance (Visser et al. 2009; Smallegange et al. 2010), and a mismatch between the peak abundance of caterpillar prey and the timing of breeding in some studies (Both et al. 2006, 2010).

1.2. Migration

One of the most important environmental variables affecting the migration strategies is temperature, which is exemplified by the increase of the proportion of migratory bird species towards the poles (Newton & Dale 1996; Somveille et al. 2013). The seasonal drop in temperature typically reduces food availability, leaving migrating to more southern areasas the only choice for many species in order to avoid starvation and survive. But if the environmental conditions in breeding, staging and overwintering areas change due to, for example, an increase in temperatures, the migratory animals often readily respond by adjusting their migration behaviour (Vähätalo et al. 2004; Visser et al. 2009).

The migration behaviour has developed and continuously adapts to maximise the lifetime fitness of the individuals, which in practice means maximising survival in relation to productivity (Griswold, Taylor & Norris 2010). Regarding the migration decisions, this probably usually means maximising the overwintering survival probability, but fitness of an individual can also be affected by migration decisions related to future productivity, like wintering as close as possibly to breeding areas in order to be the first to arrive in spring to obtain the highest quality territory (Kokko 2011; Johansson & Jonzén 2012). The optimal choice of migration behaviour can depend on the state of an individual, like the often inter-related social rank, age, sex or body condition, and can be affected by environmental conditions, population density, or the frequency of migrants relative to residents (Gauthreaux 1982; Taylor & Norris 2007; Kokko 2011). Switching the migration behaviour during the lifetime, for example from migrant to resident, may be an optimal solution for an individual as e.g. the social rank or the environmental conditions change (Kaitala, Kaitala & Lundberg 1993).

1.3. Migrants, residents and partial migration

Migratory populations are such in which all individuals migrate away from a breeding area to another area to spend the winter, while in a resident population all individuals stay the whole year at the same area. In many species the whole population migrates, but likely the most common migratory strategy in nature is the partial migration (Berthold 1999; Chapman et al. 2011). A population is partially migratory if it consists both resident and migratory individuals (Terrill & Able 1988). Partial migration emerges in a population where individuals face contradictory selection pressures concerning migration: a part of a population achieves on average higher fitness by migrating than by staying in the breeding areas during the non-breeding season, whereas the other part achieves on average higher fitness by staying resident year-around (Kaitala et al. 1993; Taylor & Norris 2007). The fitness consequences of overwintering in a certain place must be regulated by density dependence for partial migration to emerge because otherwise it would simply be most beneficial for all individuals to overwinter on the same area, i.e. either to migrate or to stay resident (Lundberg 1988; Kaitala et al. 1993; Taylor & Norris 2007).

1.4. Temperature on autumn migration

The climate warming and the interannual variation in temperatures can potentially have complex effects on the autumn departure migration, because it can be affected both indirectly by spring temperatures which affect the timing of breeding (Dunn & Winkler 2010), and directly by autumn temperatures, which may affect the timing of the seasonal decrease in food availability (Haila, Tiainen & Vepsäläinen 1986). Moreover, during autumn birds are not generally in a hurry to depart the breeding areas (but expectations exist, Jenni & Kéry 2003), unlike during spring when their arrival is more time-constrained (Johansson & Jonzén 2012).

The timing of autumn migration in relation to the timing of breeding affects the time-period an individual spends in the breeding area (or 'breeding area residence time', or BART, Thorup, Tøttrup & Rahbek 2007). An increase in BART may prolong the breeding season (Møller et al. 2010), but it is not necessarily always the case as birds can also allocate the extra-time for something else than breeding, like moulting or preparing for the migration. If species advance their autumn migration in correspondence with advanced breeding, as has been observed in some long-distance migrants (Thorup et al. 2007), then BART remains constant. If breeding advances with increasing spring temperatures, but the timing of autumn migration remains unchanged, then BART increases. This could provide more opportunities for second broods or renestings (Halupka, Dyrcz & Borowiec 2008), which could potentially increase productivity, but on the other hand, allocating the time for moulting could increase survival (Nilsson & Svensson 1996).

Early breeding has been shown to lead to early migration in many long-distance migrants (e.g. Sokolov, Markovets & Morozov 1999; Jenni & Kéry 2003), but also in some short-distance migrants (Morton & Pereyra 1994; Sokolov et al. 1999; Bojarinova, Rymkevich & Smirnov 2002). As would be expected based on the combination of early breeding causing early migration and advanced breeding times due to increased spring temperatures, the autumn migration dates have indeed advanced during the past decades in severals species, including both short-distance and long-distance migrants (e.g. Jenni & Kéry 2003; Tøttrup, Thorup & Rahbek 2006). On the other hand, in several species the autumn migration has been delayed (e.g. Jenni & Kéry 2003; Sokolov 2006; Lehikoinen & Jaatinen 2012), and in some timing of autumn migration has remained constant despite changes in temperatures, (e.g. (Sokolov et al. 1999; Gordo & Sanz 2006), so all in all the reported responses in autumn have been rather varied.

1.5. Temperature and wintering

Residence is a rare and migration a common strategy in the bird species breeding in high latitudes where between-season variability in food availability is large (Sol, Lefebvre & Rodríguez-Teijeiro 2005). In these areas of cold winters, a directional increase of winter temperatures usually should improve winter food availability and thereby survival of the resident individuals, which according to theoretical studies most often should increase the proportion of individuals utilizing the resident strategy in partially migratory populations (Berthold 1999; Taylor & Norris 2007). However, temperature changes can also have more surprising effects on the proportion of resident individiduals (hereafter PoR) depending on how productivity is affected in relation to survival, and whether these effects differ between residents and migrants (Taylor & Norris 2007; Griswold, Taylor & Norris 2011; Kokko 2011). This means that although an increase in PoR as the winter temperatures increase is probable, it is not inevitable.

Wintering in high latitudes exposes the individuals to low temperatures, which increases the energy expenditure to keep warm (Saarela, Klapper & Heldmaier 1995; Swanson & Olmstead 1999). Nevertheless, the greatly insulating feathers together with metabolic adaptations and seasonal acclimatizations enable birds to survive in extremely low temperatures without freezing (Saarela et al. 1995), if enough food is available. Therefore, it is not surprising that a steep negative relationship between food abundance and autumn migration numbers (Fox et al. 2009; Lindén et al. 2011) and a positive effect of food abundance on wintering numbers have been found in the northern areas (e.g. Reinikainen 1937; Haila et al. 1986). Still, cold winter temperatures are known to cause decreased survival (Cawthorne & Marchant 1978; Robinson, Baillie & Crick 2007a; Zuckerberg et al. 2011), but it is usually not known to what extent the low survival is caused by the direct effect of the level of coldness exceeding the capacity of the individuals to warm themselves, or by the indirect effect of low temperatures decreasing the food abundance, or their combination.

Several species show interannual variation in their wintering numbers according to the winter temperature. (Musilová et al. 2009; Lehikoinen et al. 2013a), but others are unaffected (Eriksson 1970; Dalby et al. 2013). According to long-term records, the wintering abundances of many waterbirds have increased in the north-eastern and eastern Europe (Musil et al. 2011; Lehikoinen et al. 2013a), whereas in the western and south-western Europe the same species have declined (Crowe et al. 2008; Maclean et al. 2008; Lehikoinen et al. 2013a). indicating climate warming induced changes in the wintering behaviour.

1.6. Temperature, reproductive success and synchrony

A positive relationship between the spring or summer temperatures and reproductive success has been commonly observed in single-species studies, especially in the terrestrial species of high latitudes (reviewed in Pearce-Higgins & Green 2014). On the other hand, there are also examples of negative connections between temperature and reproductive success due to, for example, mismatches with peak food abundance after a warm spring (Watanuki et al. 2009), or due to high temperature related dry conditions decreasing the food availability (García & Arroyo 2001). Few studies have taken the next logical step and linked the trends of temperature affected productivity to the trends in population size (Julliard, Jiguet & Couvet 2004; Ludwig et al. 2006; Clausen & Clausen 2013; Sherry et al. 2015).

Usually the mechanisms behind the relationships between temperature and reproductive success are not known, but many different factors known to be important for breeding have been proposed to be affected by temperature and thereby to be potential explanations, including food availability (Kostrzewa 1989; Moss, Oswald & Baines 2001; Lehikoinen et al. 2013c; Eglington et al. 2015), mismatch between peak food abundance (Watanuki et al. 2009), viability of eggs (Cooper et al. 2005; Olsen et al. 2008), predation rate (Morrison & Bolger 2002; Dickey, Gauthier & Cadieux 2008), nest parasitism (Cox et al. 2013), foraging and thereby provision efficiency (Sergio 2003), nest site availability (Dickey et al. 2008) and thermoregulatory stress (Lehikoinen et al. 2013c).

Temporal synchrony, i.e. synchronous interannual variation in population size or in some demographic parameter, like productivity (the annual mean of offspring produced per adult), between the species in a certain area, has recently gained theoretical interest (Loreau & de Mazancourt 2008, 2013), and has been observed in several communities (e.g. (Mutshinda, O'Hara & Woiwod 2011; Lahoz-Monfort et al. 2013; Robinson, Dornelas & Ojanguren 2013; Vasseur et al. 2014). Weather conditions have been identified as the cause of temporal synchrony in one case (Hansen et al. 2013), but other external forcing, like a shared predation pressure or, in certain conditions, inter-specific competition, can also cause or contribute to it (Loreau & de Mazancourt 2013). In theory, temporal synchrony can destabilize communities and expose them to sudden changes (Loreau & de Mazancourt 2013), but its contribution to changes in species abundances or distribution is still largely unknown.

1.7. Methods for studying changes in migration phenology

Changes in bird migration phenology have been much studied during the last 10 - 15 years (e.g. (Vähätalo et al. 2004; Gordo 2007). These studies have mostly relied on simple statistics, like means, medians, quantiles, first arrival dates and last departure dates (Moussus et al. 2010, Knudsen et al. 2007). Some of these, like median, work rather well when long-term changes in the overall timing of migration are studied, but many potentially interesting aspects of migration dynamics are missed (two-peakedness of migration) or are not possible to study (phenological overlap of a species with its prey, Both et al. 2006; Lehikoinen 2011) using these simple approaches. Therefore, different methods of fitting distributions of varied shapes to describe the dynamics of the whole migration season have been proposed and also to some extent applied (Jonzén et al. 2006; Knudsen et al. 2007), but how well these different proposed approaches work relative to each other in describing the migration phenology dynamics is not known.

1.8. The motivation and the aims of the thesis

Our planet is experiencing climate warming at a rate that can potentially lead to level of extinctions similar to the five mass extinction events in the history of life (Bellard et al. 2012). Hence, there is an urgent need to understand how temperature changes affect nature and how the species are able to cope with the changing environmental conditions (Sæther, Sutherland & Engen 2004; Sutherland 2006; Sekercioglu et al. 2008).

In my thesis I examine the responses of species to interannual variation in temperature (and to lesser extent in other environmental variables) (**I**-**III**, Table 1). I also investigate the long-term changes in the variables of interest, and whether they are connected to changes in temperatures (**II**, **III**). The results provide basic knowledge on which future studies and predictions of impacts of climate warming can be based on. In addition, I contribute to the development of the methods for studying the changes in nature (**IV**, Table 1). Understanding how animals respond to temperature changes and variation is important, because in the future large number of species will be forced to adapt by altering their phenology, distribution or physiology, or a combination of these, in response to the global warming in order to survive (Bellard et al. 2012).

The effects of temperature on spring migration have been extensively investigated, but there are much less studies examining the effects of temperature changes on the potentially more complex autumn migration (Lehikoinen & Sparks 2010). The proportion of resident individuals (PoR in a partially migratory population is hypothesized to increase with the increase in winter temperatures (Berthold

Table 1. The study questions.

Chapter	Study question
I	Does spring temperature affect the timing of hatching?
	Does the timing of hatching affect the timing of autumn migration?
	Are there differences between the species and between tits and hawks in the responses?
II	Do winter temperatures or tree seed abundances affect the inter-annual variation in the proportion of resident individuals (PoR) in partially migratory birds?
	Have PoR increased or decreased between 1987 – 2011?
	Are there differences between the species and between the functional groups of waterbirds and terrestrial birds in the responses environmental variables or in trends?
III	Does spring temperature affect the annual productivity, and does annual productivity affect the population size of the next year?
	Is the interannual variation in productivity or in population sizes synchronous within the community?
	Is the synchrony in productivity caused by the common response to spring temperature, and is the synchrony in population size caused with a time lag by the synchronous productivity?
	Have productivity and population size increased or decreased between 1987 – 2013?
	Are the trends in population size related to the trends in productivity?
	Are there differences between the species and between short- and long-distance migrants in the responses, synchronies or trends?
IV	How well do parametric models compared with additive models perform compared with each other in describing bird migration data?
	Can inclusion of covariates in the model account for the large day-to-day variability in migration, and does it alter our conclusions about phenology?
	Does any of the models fit the data reasonably well?
	Are there differences between groups of species in which model is the most suitable for describing migration data?

1999; Taylor & Norris 2007), but there are few single-species studies which have investigated the changes in PoR in general (Adriaensen, Ulenaers & Dhondt 1993; Hebblewhite & Merrill 2011) and only two have tried to link the changes to temperatures (Nilsson et al. 2006; Vliet, Musters & Keurs 2009). There are no studies including more than one species, or combining the effects of temperature on the interannual variation in PoR with the long-term trends in PoR.

I aim to fill these gaps in knowledge by examining the dynamics of autumn migration in three chapters (**I**, **II**, **IV**) of my thesis. First, I examine whether the timing of breeding is explained by spring temperatures, and then whether the exact timing of hatching affects the timing of autumn migration on an individual level in three tit species and two hawk species (**I**). These questions have been examined on the level of individual responses in the wild, to our knowledge, only twice before. Both studies analyze single species (Vilbaste 1975; Lehikoinen, Hokkanen & Lokki

2011), so my study provides the first multi-species investigation of this subject.

Second, I analyse whether the interannual variation in PoR is affected by winter temperatures of the same and previous year (**II**). Also the seed crops of three tree species are included as explanatory variables to compare the relative importance of direct food availability in seed-eating species with the effect of winter temperatures. In addition, the trends in PoR and their relation to temperature changes are examined.

Third, I compare different methods for modeling the whole distribution of migration phenology (**IV**). When studying the impacts of temperature variation and climate warming, it is important to use the methodology that most accurately describes the changes in nature. The results of the comparison can be used as a guideline for choosing the best method for analysing bird migration data, or any phenology data with daily or other regular interval counts within a season. Weather variables are known to affect migration intensity (Richardson 1978), but they usually have not been included in the modeling of migration phenology. In addition to the comparison of modeling approaches, we also introduce a simple novel method to account for the effects of weather, and compare it to another proposed method of autoregressive models (Alerstam 1978).

In chapter **III**, I first examine the effects of interannual temperature variation on the productivity of species. There is much variation between the studies in both how productivity has been measured and which time-period(s) is used for examining the effect of temperature, making between-species and between-studies comparison of the found relationships somewhat difficult. Our approach of examining the effects of temperature of fixed time period (spring) on productivity in a community of 20 species residing a common area (Finland), provides a reliable comparison of the effects of temperature across the species. To our knowledge, no prior study has examined the effects of temperature on any measure of productivity in nearly as many species. This approach also enables us to easily investigate whether there is temporal synchrony in productivity or in population sizes, and whether spring temperature causes the synchrony, providing more empirical examination of this emerging, but so far relatively little studied subject.

Productivity has potentially profound effect on population size variation and trends, but is largely unknown how commonly productivity regulates or limits population sizes in migratory species (Pearce-Higgins & Green 2014), or, a related question, what is the relative importance of the environmental changes in the breeding areas compared with the changes in the non-breeding areas (Vickery et al. 2014). Therefore, we examine whether long-term trends in productivity are connected with the trends in populations size, which would imply that changes in productivity would had caused or contributed to the changes in population size.

Comparing the responses between taxa or functional groups can provide insight on how the effects climate warming vary depending on the traits or behaviour of the species. Therefore, we compare the responses between small-bodied and potentially multi-brooded tits (**I**), between waterbirds and terrestrial birds (**II**), between short-distance and long-distance migrants (**III**), and between different taxonomic groups (**IV**).

2. Materials and Methods

2.1. Study area and climate

All chapters were based on data collected in Finland. The northern location (between 60 and 70 latitude) of Finland causes winters to be cold and summers mild. The mean temperatures of the coldest (February) and warmest (July) months calculated over the whole country between 1991-2000 were -9.1 ºC and 15.1ºC , respectively (Venäläinen et al. 2005). Birds wintering in Finland are exposed cold temperatures, but occasional sub-zero or near zero periods occur even in May - June, meaning also breeding birds and nestlings are occasionally exposed to low temperatures. The variation in temperature both between and within years is larger in winter than in summer in Finland (Mikkonen et al. 2014).

2.2. Data description and statistical methods

All chapters are based on long-term monitoring data, great majority of which was collected by volunteer amateur birdwatchers (Table 2). In the analyses I utilized and combined data from about eight different bird monitoring schemes, temperature data and tree seed crop data (Table 2).

Our choices of the time periods over which temperature estimates used in the analyses were averaged were based on using the same or similar time-periods which were in prior studies found to affect the variables we were studying (**I**, Lehikoinen et al. 2009, **III**, Eglington et al. 2015), or using a physically relevant period of when temperatures vary around zero degrees affecting the annual timing of freezing and snowfall (**II**).

Most of the data used in the thesis were time-series data, meaning that they were successive measurements made over a regular time interval of one year. The analyses in **II** and **III** included examining the relationships between the interannual variation of variables. In analysis like this the time-series properties of the data must be taken into account or otherwise one may find apparent but spurious connections between the variables of interest due to correlated long-term trends in the variables. Therefore, the variables in these analyses were first detrended and then the relationships between the residuals were analyzed. We also

Table 2. The datasets used in the thesis. FMNH stands for The Finnish Museum of Natural History, LUKE is Natural Resources Institute Finland, Tringa is the birding society of Helsinki region and FMI is The Finnish Meteorological Institute.

Dataset	Organised by	Data collected by	Chapters	Reference
Winter bird monitoring scheme	FMNH	Volunteers	II	Koskimies & Väisänen 1991
Breeding period line transect counts	FMNH	Mainly by volunteers	II	Lehikoinen 2013
Breeding period point counts	FMNH	Volunteers	II	Lehikoinen 2013
Inland waterbird census	FMNH & LUKE	Mainly by volunteers	II	Pöysä *et al*. 2013
Archipelago waterbird census	FMNH & LUKE	Mainly by volunteers	II	Hario & Rintala 2011
Nestling ringing	FMNH	Volunteers	I	Valkama et al. 2013
Constant effort site ringing	FMNH	Volunteers	II, III	Piha & Haapala 2012
Hanko bird observatory (HBO) ringing	FMNH & Tringa	Volunteers	I	Lehikoinen et al. 2011
HBO migration and staging counts	Tringa	Volunteers	IV	Lehikoinen & Vähätalo 2000
Daily mean temperature	FMI	Professionals	I, II, III	Venäläinen *et al.* 2005
Seed crop of birch and spruce	LUKE	Professionals	II	Hokkanen 2000

checked, and if needed accounted for, if there were any temporal autocorrelation left after detrending.

I used a variety of statistical tests and approaches in order to model the relationships and processes as realistically as possible, and to account for different potential sources of biases in the results. Basic null hypothesis tests, like linear regressions, analyses of variances and Pearson's correlation tests were used in all chapters. Linear mixed-models (Pinheiro et al. 2014; Bates et al. 2015) were used to account for the differences among the species in **II** and **III**. Generalized additive models (GAM, Wood 2011) were used for detrending (for few species) with more complex trends in **II** and **III**, and also for modeling the migration intensity in **IV**. In **II**, TRIM-software, which has been especially developed for analysing bird monitoring data (Pannekoek et al. 2005), was used for modeling the annual indices for wintering and breeding period abundances. An informatic theoretic approach based on Akaike's information criterion for a small sample size (AICc, Burnham & Anderson 2002) was applied in **II**, **III** and **IV** in order to compare and find the best model(s) among a set of models. Normal distribution was used as an error variance in chapters **I**, **II** and **III**. This was appropriate even though **II** and **III** were based on count data, because the analyses in these chapters were done with the values averaged over all annual observations, which apparently had transformed the originally probably different distributions to normal distributions, as central limit theorem predicts. In **IV** a negative binomial error distribution was used to account for the residual overdispersion typical to migration data (Lindén & Mäntyniemi 2011).

2.3. The effects of hatching date on the timing of autumn migration

We studied whether the timing of hatching is related to spring (April) temperature, and whether it affects the timing of autumn migration in five species with individuals that had been ringed as nestlings around southern Finland and were then controlled during the autumn of the same year in Hanko Bird Observatory located in southwestern Finland (**I**). Three of these species were tits (great tit, blue tit and coal tit), which have the potential to breed twice in a summer, and two were hawks (sparrowhawk, goshawk), which breed only once in a summer. All species are partially migratory, so therefore the study concerns only the migrating part of the populations. The pool of study species was decided by the fact that these species were the only ones with enough suitable observations.

2.4. The effects of winter temperatures on the interannual variation and long-term trends in PoR

I examined in 27 partially migratory species whether the mean temperatures of two different time-periods, just before the winter bird census season (November – December, census season 25.11 – 7.1.) and previous winter (December – February), affected PoR (**II**). The reasoning behind selecting these two time-periods was to measure if the choice of whether to migrate or not (i.e. PoR) was more affected by the direct effect of early-winter temperature, indicating phenotypic plasticity in the migration behaviour, or by the delayed effect indicating a larger proportion of individuals with innate inclination to remain resident due to adaptive selection or learned behaviour after a successful overwintering when the previous winter had been mild (and vice versa). PoR was calculated as the proportion of the annual index of winter abundance to the annual index of breeding period abundance.

We also included estimates of the annual seed crops of spruce, birch and rowan in the analyses. We expected the seed crops to directly affect the food availability and thereby the wintering possibilities of the species which commonly exploit them. We also examined the effects of temperatures on only those terrestrial species whose PoR was not affected by seed crop, because it was assumed that species exploiting seeds could be less affected by temperatures than other terrestrial species. Productivity (**III**) was also included in the analyses for those species we had the data (11 terrestrial species) to find out if it affects PoR, because only adults were counted in the bird censuses used to estimate the annual index of breeding period abundance, and the amount of juveniles born after the counts could to bias the estimate of PoR, if the juveniles significantly contribute to the resident population.

We also analysed the long-term trends during the study period (1987-2011) in PoR and all explanatory variables: winter temperatures, tree seed crops and breeding success. We performed all analyses to all species together and to all species individually, and for the two functional groups of waterbirds, including six ducks and three gulls, and terrestrial species, including 18 passerines. We defined the individuals observed inside Finnish borders during the winter census as residents, while migrants were the individuals which had migrated away from Finland and therefore were not observed during the winter census.

2.5. Spring temperature, productivity and population trends

The annual productivity indices were calculated based on the proportions of adults and juveniles caught in the constant effort site ringing scheme following the methodology described in Peach, Baillie & Balmer (1998) and Robinson et al. (2007b) (**III**). We examined whether spring temperatures (mean temperature of April, May and June) affect the interannual variation in productivity in 20 passerine species, and whether productivity in one year affected the population size of the next year. Furthermore, we analysed whether there were trends in productivity and in population sizes, and whether trends during the study period (1987 – 2013) in productivity were related to population size trends. We also analysed the among-species temporal synchrony with the community.sync function from synchrony package in R (Gouhier & Guichard 2014), which applies the method developed by Loreau & de Mazancourt (2008).

In all analyses we compared the responses and trends between short-distance and long-distance migrants. We classified the species which mainly overwinter in Europe and Mediterranean region as short-distance migrants and the species which migrate either to sub-Saharan Africa or to south-east Asia as long-distance migrants.

2.6. A comparison of approaches for modeling migration phenology

We compared different methodological approaches for describing migration dynamics in 75 species, with or without covariates to take into account the effects of weather on the day-to-day variation in migration intensity (**IV**). The modeling techniques compared were, from the simplest to the most complex: fitting a normal distribution to data containing daily migration counts, fitting a skew-normal distribution capable for describing higher migration intensity in the beginning or the end of the migration season, fitting a combination of two normal distributions for two-peaked or otherwise more complex migration patterns, and fitting a generalized additive model (GAM) with 2, 3, 5 or automatically optimized amount of degrees of freedom. Into the comparison we included two covariates for indirectly take into account for the effects of weather has on the daily variation in migration intensity: a novel approach of using the daily migration intensity of related species with similar migration strategy, or a conditional autoregressive model (Zeger & Qaqish 1988) to examine if the consecutive days are more similar (or dissimilar) than by chance (Alerstam 1978). We also examined if there were differences between taxa or between spring and autumn in which models were preferred.

3. Results and Discussion

3.1. Temperatures during the study period

Spring or winter temperatures did not significantly increase during the study periods of **II** and **III** (i.e. in 1987 – 2011/2013), but the study period as a whole was warmer than the previous time-periods of similar lengths (Tietäväinen, Tuomenvirta & Venäläinen 2010). Therefore, the climate warming was most probably ongoing also during the study period. The large interannual variation in temperatures largely caused us not to detect the increasing trend in temperatures within the study periods, but on the other hand the large variation offered a good opportunity to study the effects of interannual variation in temperature on the different variables of interest.

3.2. Spring temperatures, timing of hatching and autumn migration (I)

The timing of hatching was affected by spring temperatures, which was expected as it has been commonly observed in prior studies. This means that the effects of timing of hatching on the timing of autumn migration are connected to the spring temperature variation.

The timing of hatching affected the timing of autumn migration only when the hatching date was distinctly late, i.e. in juvenile tits which were from presumed second broods. The effect was significant only in blue tit and coal tit, both of which had considerable amount of late-hatched birds. Also in great tit there seemed to be a similar tendency, as was found by Vilbaste (1975), but the small amount of late-hatched birds made it impossible to confirm the pattern. Even though the presumed second brood individuals migrated later than the presumed first brood individuals, they still migrated at a younger age, i.e. the time-period between hatching and migrating was not constant.

The late migration of the late-hatched individuals could be due to allocating time for moulting and migration preparation beyond the optimal timing for migration of the less time-constrained early-hatched individuals. Still, second-brood juveniles moult less than first-brood juveniles (Bojarinova et al. 2002), meaning the later migration does not fully compensate for the short time-period between the hatching and the migration. This implies that the timing of migration of late-hatched juveniles would be a compromise between allocating time for moulting and migrating before the environmental conditions deteriorate too much. The reduced moulting has been linked with lower survival (Nilsson & Svensson 1996; Siikamäki

1998), which could reduce the fitness value of the second clutch individuals to the parents. Therefore, it is not inevitable that the increase in spring temperatures would automatically increase the proportion of second clutches in multi-brooded species. Indeed, while in some species they have become more common (Halupka et al. 2008), in others they have even decreased (Husby, Kruuk & Visser 2009).

Based on these results, the length of the time-period between hatching and autumn migration (BART) is expected to increase along with the predicted increase in spring temperatures. If autumn temperatures increase simultaneously with spring temperatures, as is expected to happen, it should postpone the seasonal deteriorating of environmental conditions, which should reduce the pressure to migrate early, and potentially further increase the time-period between birth and migration, potentially helping especially the second-brood individuals.

3.3. Interannual variation and long-term trends in PoR (II)

Mild early-winter temperatures caused high PoR in waterbirds, but did not generally affect PoR in terrrestrial species (positive effect only in one species). The strong relationship between temperature and the amount of ice (Luomaranta et al. 2014) is the most probable causal mechanism for the observed pattern, as the waterbirds obtain most or all of their food from water. High abundance of tree seeds caused high PoR in terrestrial species. If the seven species whose PoR was found to be affected by the abundance of tree seeds were removed from the group of terrestrial species, winter temperatures still did not affect PoR in the remaining 11 terrestrial species. The reason for the lack of temperature effect in terrestrial species is probably due to their food availability not being affected by temperature (Hildén & Koskimies 1969), allowing them to compensate the increased thermoregulatory stress caused by coldness by increasing their feeding activity. Therefore, our results support the view that the effects of temperature on the wintering possibilities are mainly indirect and are mediated through the effect temperature has on food availability.

The previous winter's temperature did not affect PoR in any species, suggesting that there were no temperature related wintering success induced changes in the proportion of individuals with an innate inclination to remain resident (i.e. no potential evolutionary response due to temperature related survival). This implies that the decision to overwinter would be based on phenotypically plastic response to annually varying proximate factors like the environmental conditions during autumn and early-winter.

PoR increased steeply in waterbirds but there were no general changes in terrestrial birds (decrease in one species). The lack of trends in PoR in terrestrial species was probably due to lack of trends in the abundances of tree seed crops (Wallenius 1999; Lindén et al. 2011). Winter temperatures did not increase during the study period, but the study period as a whole was warmer than the preceding period of similar length. The lack of severe ice winters during the study period (Luomaranta et al. 2014) is the most probable explanation behind the increasing PoR in waterbirds.

Despite not finding an effect of previous winter's temperature on PoR, the continuous increase of PoR in waterbirds suggests that there still could had been selective response (or learned innate inclination) towards residency going on. The explanation for these conflicting results could be that our statistical method of trying to find a relationship between PoR and winter temperature variation within range of temperatures occurring during the study period would had been unable to detect any effect if the winter temperature constantly remaining above threshold of successful overwintering. Also the long time-period with many possible confounding factors between the previous winter and winter census period probably made observing the potential effect of previous winter's temperature more difficult than the effects of early-winter temperature or tree seed crop.

The predicted increase of winter temperatures will decrease both the length of the ice-season and the extent of ice-coverage (Luomaranta et al. 2014), which most probably will improve the wintering possibilities of waterbirds, so their PoR is expected to continue to increase. According to the results, PoR of most currently common terrestrial wintering species in Finland would be unaffected, unless the increasing temperatures affect the seed crops of the trees, as might happen (van der Meer, Jorritsma & Kramer 2002), but generally there are large uncertainties about how the climate warming will affect boreal forests (Lindner et al. 2010; Ge et al. 2012).

3.4. Temperature effects, trends and synchrony in productivity (III)

In our study community of 20 passerine species, productivity was better across the species when spring temperature was warm, and vice versa. The strength of the effect moderate. Unlike in some studies done in more southern areas, we found no indication of productivity decreasing during the years of highest temperatures. This indicates that in Finland the study species reside below the temperature optimum for productivity (Eglington et al. 2015).

Productivity in one year had a positive effect on the population size of the next year in long-distance migrants, but not in short-distance migrants. Neither productivity nor population sizes on average changed during the study period in the whole study community or in the groups of short-distance or long-distance migrants. There were clearly fewer species with increasing or decreasing trends in productivity during the study period (3) than species with trends in population sizes (12). The lack of significant increase in spring temperature combined with its moderate effect on productivity caused spring temperatures not contributing to the trends in productivity.

Despite finding a connection between the interannual variations in productivity and population size in long-distance migrants, the trends in population size did not correlate with the trends in productivity, indicating that population trends were mainly driven by changes in other factors than productivity. The most probable explanation is survival changes during the non-breeding period, which could had been caused by changes in land-use or climatic conditions in the overwintering and staging areas, as has been proposed to have caused many population size changes both in Finland (Laaksonen & Lehikoinen 2013) and in European level (Siriwardena, Baillie & Wilson 1998; Newton 2004; Grosbois et al. 2006; Robinson et al. 2007a).

We found a moderate level of temporal synchrony in both productivity and population sizes. Despite the uniform moderate positive relationship with spring temperatures across the species in the community, the temporal synchrony was only little affected by the common response to spring temperatures, contradicting the prior finding of weather mediated synchrony (Hansen et al. 2013). This indicates that some other factor, like interannual variation in shared predation pressure, would cause the synchrony (Loreau & de Mazancourt 2013).

Our results suggest that productivity would increase across the study species as spring temperatures increase due to climate warming. Whether this prediction holds is dependent on whether a directional increase in temperatures has similar positive outcome as the warmer years among generally stable temperatures, which is not necessarily the case. Directional warming could change distributions of prey species and introduce southern bird species to compete for resources, or could otherwise alter the environment either to be more or less suitable for successful breeding for the study species (Gilman et al. 2010).

3.5. Comparison of approaches for modleling migration phenology (IV)

Fitting two normal distributions was found to be the best way to model migration dynamics when the number of degrees of freedom in GAM was restricted to be comparable with the other modeling approaches (i.e. to 2, 3 or 5). If GAMs were allowed to estimate the annual numbers of degrees of freedom during the fitting process, as GAMs are most often applied in practice, then it became the modeling approach with the best fit in most cases. Ultimately, the choice between fitting GAMs or two normal distributions (or some other of the compared distributions) depends on the properties of the data and the purpose of the analysis. GAM could be preferred e.g. for purely descriptive purposes, especially if the expected migration dynamics are unknown, but the other, more strictly defined and shaped distributions could be preferred if there is e.g. a good reason to expect a certain underlying distribution of migration intensity, or when predicting the migration intensity beyond the truncated data collection period (Jonzén et al. 2006).

Including a covariate of daily migration activity of related species generally improved the model fit, which means that this novel method proved to be a convenient indirect way to account for the effects weather has on the daily migration activity of a species. Therefore we recommend including such a covariate into future analysis of migration dynamics whenever suitable data of several species with similar migration behaviour exists. Naturally, modeling the effects of weather directly would provide information about the actual conditions affecting the migration, but if the goal is just to remove or decrease the effects of weather on the variation in daily migration intensity, our approach works well as a handy shortcut. Autoregressive models did not generally improve model fits, so they are clearly less useful for trying to account for the effects of weather on daily migration activity.

Using these modeling approaches, a wide variety of different migration patterns can be described and analysed. The results indicate that usually fairly simple models are sufficient for describing the migration, but in some cases, e.g. due to several populations, age-classes or sex-classes passing the migration observation point at different times, GAMs with higher amount of degrees of freedom are preferred.

There were some differences between the taxa in which approach was the best. The most interesting of these was that GAMs were more preferred in passerines than in other groups, which could be due to multiple breeding attempts causing longer autumn migration season with more peaks, as the results of Chapter I implied.

More complex models were preferred in spring than in autumn, which was a little surprising, because we expected the opposite due to the known sex- or age-dependent differences in the timing of autumn migration in many species (e.g. Lehikoinen et al. 2010). The explanation for this could be that the shorter and more hurried migration period combined with protandry (males arriving before females, Rainio et al. 2007) producing more distinctly separate peaks of between the sexes (or between different populations) spring than during autumn migration. Despite the potentially larger number of groups with differences in timing of migration in autumn due to juveniles migrating in addition of males and females, the less hurried nature of autumn migration could cause the migration timing of these groups to overlap more than in spring, causing the overall migration intensity to have less complexity, potentially even a shape best described by a normal distribution.

3.6. Cross-chapter observations of the results

If second broods become more common due to an increase in spring temperatures (**I**), it could decrease PoR (**II**), because late hatched individuals are more prone to migrate (Smith & Nilsson 1987). Similarly, if an increase in spring temperatures improves productivity (**III**), it could also decrease PoR if the winter survival of residents does not improve correspondingly, as increased post-breeding population size would cause migrating become the optimal strategy for a larger proportion of individuals (Griswold et al. 2011). Then again, we did not find much evidence of productivity actually affecting PoR (**II**), so changes in productivity would probably have to be quite substantial to have an effect, but so far there were almost no changes at all in the productivities of species included in both **II** and **III**. Interestingly, the only species with changes in both PoR and productivity was greenfinch. Both changes can probably be attributed to a trichomonosis epidemic, which has severely affected the population sizes of the species for several years (Lehikoinen et al. 2013b).

According to the results, the predicted increase in spring temperatures would cause both better productivity (**III**) and prolong the period between hatching and migration thereby offering more time for e.g. moulting and fattening (**I**), potentially increasing both the annual amount and average survival of juveniles. Therefore, an increase in population sizes could be expected, but if population size is indeed limited by conditions during the non-breeding season (**III**), then these assumed improvements during the breeding season may not have effects on the population sizes.

Based on the results of **I**, the population level changes in the timing of autumn migration could be dependent on the changes in the proportion of second broods. Also the proportion of individuals from a certain age- or sex-class which migrate could change as the climate gets warmer (**II**). Changes like these could cause changes to the shape of the migration distribution, like two-peakedness or wider distribution, which would be easily observed with the methods of **IV**, but could be missed using more simplistic methods.

4. Conclusions and conservation implications

In my thesis, I found that temperatures affect important life-history traits, like reproduction (**III**) and migration behavior likely connected to the overwinter survival of the individuals (timing of autumn migration **I**, whether to migrate or not **II**). I found indication that survival would be more important for population size changes than productivity (**III**), which suggests that adjusting the migration behavior to the environmental changes like climate warming is most likely relevant for the future population projections.

One of the strengths of my thesis is that it includes 94 species of 9 orders, and in all chapters I was able to compare the responses across species and in three out of four chapters also across orders (Table 3). The main finding from these comparisons was that there were clear differences between the species (**I**, **II** and **IV**), orders (**I**, **II** and **IV**) and functional groups (**II**) in the responses of migration behaviour to temperature and other environmental factors, but the responses related to productivity (**III**) were really similar between the species. On the other hand, in **III** only passerines were included, so it might be that the main differences in the responses of productivity to spring temperatures are between higher taxa or between functional groups.

The message emerging from the results is that widely generalizable interpretations of the effects of climate warming across the species cannot be deduced from studies concentrating only in single species, order or functional group. If only one species from each study would had been studied, as it is the case with most scientific studies, quite contrasting conclusions about the effects of temperature and other factors, or the patterns observed in general, could had been reached depending on which single species I would had studied. This stresses the need for multi-species studies when scrutinizing the effects of temperatures or climate change on species, preferably including many different functional groups and taxa, obviously also others than birds.

The observed and predicted changes in the proportion of individuals migrating (i.e. the increase of overwintering individuals in Finland, **II**) and in the timing of autumn migration (**I**) mean that the relative responsibilities between different countries for protecting the species during the non-breeding season also changes. This means that protection area networks should be updated (Pavón-Jordán et al. 2015), and for the hunted species, like many waterbirds studied in this thesis, the hunting regulations should be updated (Lehikoinen & Jaatinen 2012). The result of productivity not affecting population trends (**III**) implies that the potential conservation and habitat restoration efforts of declining species should not be targeted only to breeding areas, but also, or even mainly, to non-breeding

Table 3. The amounts of species, families and orders included in the chapters of the thesis.

	Species	Families	Orders
Chapter I	5	2	2
Chapter II	27	10	3
Chapter III	20	6	1
Chapter IV	75	24	9
Thesis	94	26	9

habitats. In migratory species this is in practice quite difficult, because the areas used and their relative importance are often unknown, and the migration route can span over many countries and thousands of kilometres, but anyhow more attention should generally be given to the importance of the non-breeding habitats in the annual cycles of birds.

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When I started my PhD work with Aksu in 2011, I was the only on besides him in our "group". During the years more people came and a proper group, the Helsinki Lab of Ornithology was born. The more the merrier, and the latter part of my PhD has definitely been more fun thanks to all the great people joining the group. Therefore, great big thanks for all the friends in HelLO, both present and former, and in the extended lunch group! You are all great people and made working a more pleasant experience. You were also always ready to help with anything. So thanks Aksu, Vilppu, Sara, Diego, Ed, Andrea, Noora, Juan, Päivi, Jarkko, Sanna, Hanna, Pepe, Filipa, Dominique, William! Thanks also for all the present and former graduate students in Luomus!

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Friends! It is always difficult for me to send invitations to or list my friends, because I tend to consider pretty much everyone I have talked at least twice as my friend. And I hate discriminating between who I consider as my friends, or close enough friend with some strange criteria to be listed here. Therefore I don't mention any names here, so you have to imagine your name here as it most probably should be here. Anyhow, I salute my floorball buddies who keep me moving, especially my team mates in FBB, Biko and Gintonico (we don't always win that many games, but the spirit always stays good), my birding buddies, Halias people, the knowledge workers' sailing club members, beer brewing buddies, secret wine and cheese society members, Symbioosi comrades (both past and present), Batumi raptor count people, and all you friends who do not fall into these categories! Friends, you are the best, thank you for existing! Lately I haven't been very social and haven't seen most of you as nearly often as I should had, but I promise to try to be more active now on.

Paloma, Ville-Veikko, Aatos and Toivo, I have had and continue to have the privilege to live with you, for which I am very thankful! The last few months haven't been the easiest ones for me, but your support, both directly through discussions and indirectly by just being there, have been very important. Kiitos! Watching the

kids grow and start to play together has been a wonderful thing! Hopefully now as my PhD is finished I will spend less time in the front of the computer inside Rontti's room and be more social again. I also promise to clean my fridge and wipe some dust. And special thanks to Ville-Veikko for making the cool cover of my thesis!

Mom and dad, Äiti ja Isä, I wouldn't be here today defending my thesis without you. Growing up I got to see and experience nature with you, and despite often showing more interest in playing computer games and floorball than, for example, birdwatching, probably still the fact that you always told which bird or plant species the ones we encountered were had some effect on me. Plants I still don't know, but at least nowadays I know something about birds. Still, much more important was that you always lovingly supported me through all the highs and lows in my life, and let me search my own way of doing things. Thank you for being such great parents!

Anna and Antti, you have been the best sister and brother for me! Thank you for everything! Tuomas and Matias, it has been great to see you grow up to be such great fellows. Thank you for still not always beating me up, too badly at least, in Mario Kart! Thanks to Ritu, Hexi, Lotta and Ilkka for welcoming me to be a part of your family and always treating me well! I hope to see you often also in the future, not only as Mummi, Pappa, Täti and Eno, but also as friends.

Laura, thank you for all the years together! You were the one who the most had to share the difficulties of my Phd-work and largely were the only one who knew the deepness of the low periods, but continued to support me throughout the process. Now a couple of journeys are coming to an end, but we have only begun the long journey of bringing up a new human being together. I think we have so far done a great job, and I am confident that regardless to which directions life takes us, our solid teamwork will continue and everything will go well.

Vanamo, you were born one and half years ago and immediately reset the priorities in my life. Suddenly my PhD did not feel nearly as big thing as before. Following you grow up and learn new skills is just the best, and I think trying to be a good and responsible parent has made me a better person. Just to hear you laugh makes everything so much better and easier. Thank you, I love you!

Once again, thank you all, I love you, and my apologies and big thanks also to everyone I forgot to mention! Cheers!