Charles University

Faculty of Science

Ph.D. study program: Environmental Sciences

Mgr. Tomáš Telenský

Impact of Climate Change on Czech Bird Populations

Vliv klimatické změny na ptačí populace v České Republice

Doctoral thesis

Supervisor: doc. Mgr. Jiří Reif, Ph.D.

Prague, 2018

Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

Declaration:

Hereby I declare that I worked out this thesis independently, using the listed sources and literature. I have not submitted this thesis, or any significant part thereof, for the purpose of obtaining the same or any other academic degree.

In Prague, 31. 07. 2018

List of studies included in the doctoral disertation thesis

I: Reif J., Šťastný K., Telenský T. and Bejček V. (2009): Population changes of common birds in the Czech Republic: comparison of atlas mapping with annual monitoring data. Sylvia 45: 137-150.

II: Reif J., Telenský T., Šťastný K., Bejček V. and Klvaňa P. (2010): Relationships between winter temperature and breeding bird abundance on community level: importance of interspecific differences in diet. Folia Zoologica 59: 313-322.

III: Flousek J., Telenský T., Hanzelka J. and Reif J. (2015): Population trends of Central European montane birds provide evidence for adverse impacts of climate change on high-altitude species. PLoS ONE 10: e0139465.

IV: Telenský T., Cepák J., Klvaňa P., Jelínek M. and Reif J.: Impacts of climate change on long-distance migrants: a demographic framework. Global Change Biology (resubmitted manuscript).

Contribution of the student

I: Tomáš Telenský calculated bird population trends, contributed to the design of the analyses and commented on manuscript drafts.

II: Tomáš Telenský calculated bird population indices, designed statistical analyses and contributed to writing.

III: Tomáš Telenský calculated bird population trends, contributed to the design of the analyses and commented on manuscript drafts.

IV: Tomáš Telenský designed the study, developed population models, conducted statistical analyses and led writing.

As a supervisor and corresponding author of all studies listed above I approve the contribution of the student Tomáš Telenský as stated above.

doc. Mgr. Jiří Reif, Ph.D.

Abstract 5
Abstrakt 6
Introduction 7
Why birds? 7
Bird population changes 8
Climate change 9
Resident birds and impact of winter temperature 9
Long-distance migratory birds 10
Hypothesis 1: Trophic mismatch – impact of raising spring temperatures 11
Hypothesis 2: Droughts in sub-Saharan Africa 12
Impact of breeding or wintering grounds? 13
Montane birds 18
Conclusions 20
Acknowledgements 21
Epilogue 23
References 24
Attached publications .... **Chyba! Záložka není definována.**

Abstract

Climate change is one of the most important drivers of biodiversity. If it proceeds at current pace, it will lead to homogenization and pose a serious threat to biodiversity. Birds, as one of the most researched taxonomic groups, are successfully used as indicators of biodiversity of the whole ecosystems, and thus offer an excellent opportunity to study the overall impact of climate change. We use data from repeated annual monitoring programmes in Czech Republic, Breeding Bird Monitoring Programe, based on point counts, and Constant Effort Sites mist-netting ringing programme, capture-mark-recapture schema. We found that:

1. Population growth of 6 out of 37 resident species responded negatively to seasons with lower winter temperatures. The response was stronger in species feeding on animals.
2. Long-distance (LD) migrants' breeding productivity responds negatively to higher spring temperatures and advanced spring as indicated by earlier leaf unfolding of three tree species. Residents and short-distance migrants responded positively. This distinct contrast brings clear support for the trophic mismatch hypothesis.
3. LD migrants' adult survival was positively affected by moisture (AET/PET) in the Sahelian part of their non-breeding ranges. The effect was not present in the southern part. We found no support for the carry-over effect.
4. Spring climate explained 62% variability of the breeding productivity of LD migrants, whereas AET/PET in Sahelian part of their region explained 20% of the variability of adult survival. Climate on the breeding grounds was thus more important for migrant species than the on the non-breeding grounds. Nevertheless, survival was more correlated with population growth than breeding productivity; which suggests an important missing piece of its variability was not explained by climate. This study is likely the first one to make such comparable measurement across wide spectre and long-term data of long-distance migrant species.
5. Montane species moved upwards; species breeding at higher altitudes had more negative population trend; upward shift brought more benefit to lower breeding species, suggesting that higher altitude species already have nowhere to shift.

This thesis brings enough evidence for the impact of climate on bird populations, which is most severe for montane species and long-distance migrants.

Abstrakt

Klimatická změna je jedním z nejdůležitějších faktorů ovlivňujících biodiverzitu. Pokud bude postupovat současným tempem, povede k homogenizaci a bude představovat závažnou hrozbu pro biodiverzitu. Ptáci, jakožto jedna z nejvíce probádaných taxonomických skupin, jsou úspěšně využíváni jako indikátor biodiverzity celých ekosystémů, a tudíž poskytují skvělou příležitost zkoumat celkový dopad klimatické změny. V této studii jsme využili údaje z Jednotného Programu Sčítání Ptáků (JPSP) v ČR, který je založen na bodovém sčítání, a Constant Effort Sites, programu spočívajícím v odchytu ptáků do sítí a kroužkování metodou konstantního úsilí. Zjistili jsme, že:

1. Populační růst šesti z celkem 37 rezidentních druhů reagoval negativně na sezónu s nižní teplotou v zimních měsících. to lower winter temperatures. Tento vztah byl výraznější u druhů konzumujících živočišnou potravu.
2. Hnízdní produktivita dálkových migrantů reagovala negativně na vyšší jarní teploty a časnější nástup jara, měřeno datumem rozvíjení listů u tří druhů dřevin. Rezidenti a migranti na krátké vzdálenosti reagovali naopak pozitivně. Tento kontrast přináší zřejmou podporu pro mismatch hypotézu.
3. Meziroční přežívání dospělých jedinců dálkových migrantů pozitivně reagovalo na vlhkost (AET/PET) v Sahelské části jejich zimujícího areálu. Efekt nebyl prokázán v jeho jižní části. Vliv carry-over efektu nebyl prokázán.
4. Jarní klima vysvětlilo 62% variability hnízdní produktivity dálkových migrantů, zatímco AET/PET v Sahelské části jejich zimujícího areálu vysvětlilo 20% variability meziročního přežívání dospělých ptáků. Klima na hnízdištích bylo tedy důležitější pro populace dálkových migrantů než klima na zimovištích. Nicméně, přežívání bylo více korelováno s populačním růstem než produktivita, což naznačuje důležitou nevysvětlenou komponentu variability přežívání dospělých ptáků, kterou se nepodařilo vysvětlit klimatem. Tato studije je pravděpodobně první, která klade důraz na porovnatelnost relativní důležitosti jednotlivých faktorů na širokém spektru druhů na delší časové škále.
5. Horské druhy ptáků posunuly areály do vyšších nadmořských výšek; tyto posuny areálů se více vyplatily druhům, jejichž areály byly níže položené, což naznačuje, že druhy s výše položenými areály se již nemají kam posouvat. Druhy hnízdící ve vyšších nadmořských výškách měly negativnější populační trend.

Tato práce přináší dostatek důkazů pro vliv klimatické změny na ptačí populace, který je extrémně závažný zejména pro horské druhy a pro ptáky migrující na dlouhé vzdálenosti.

Introduction

Why birds?

Birds have always been among people's most favourite wild animals. Their song, their flight, their spirit itself has been an inspiration to human kind since the ancient times.They took place in mythology and romance (e.g. Mácha 1836 or Shakespeare 1597):

JULIET

Wilt thou be gone? It is not yet near day.

It was the nightingale, and not the lark,

That pierced the fearful hollow of thine ear.

Nightly she sings on yon pomegranate tree.

Believe me, love, it was the nightingale.

ROMEO

It was the lark, the herald of the morn,

No nightingale. I must be gone.

Birds' popularity might be due to the fact that they are the most conspicious animals in nature. They are the ones you can see or hear most frequently in the outdoors. Birdwatching has become a cult in a such extent that has no equivalent in other species groups. There are whole clubs, nationwide and international organizations and even contests dedicated just to birdwatching. This unique passion for birds is the reason why they are one of the most researched species groups. There are lots of skilled amateur ornithologists that have top-level knowledge on bird determination, and can be engaged into serious research activities. Organizations like Czech Society for Ornithology, czech partner of Birdlife International, are uniting people who love birds, allowing them to contribute to monitoring and research programmes.

Bird population changes

Population size is one of the most important characteristics of a species' population. It is crucial for species ecology, but also for assessment of conservation priorities (see e.g. IUCN Red List or Special Protection Areas). Thus, population ecology studies focused on changes in abundance belong to one of the most practical and applied research.

Population changes in many bird species' communities are alarming. Farmland birds are experiencing continual declines (Pe'er *et al.* 2014; Gamero *et al.* 2016). Long-distance migrants are declining (Sanderson *et al.* 2006; Heldbjerg & Fox 2008). Due to climate change, cold-loving and alpine birds are declining (Lemoine *et al.* 2007; Gregory *et al.* 2009). Nowadays, human induced pressure on the environment grows steeply. Birds, thanks to very good data availability and their position in the trophic pyramid, are great indicators of biodiversity of the whole ecosystems (Gregory *et al.* 2003, 2008; Lamb *et al.* 2009).

In order to have a proper and reliable information on bird abundance, which can be used for research and conservation purposes, periodic annual monitoring programmes with constant effort methodology are needed. For example, Breeding Bird Monitoring in Czech Republic (BBMP) held by Czech Society for Ornithology, is an example of such a programme. On the other hand, a lot of studies use data on population changes based on national breeding bird atlas mapping, which is held only once per cca 10-20 years to assess bird distribution and abundance. In **Paper I,** we have compared the data quality from this regular BBMP programme with the Czech Breeding Bird Atlas mapping. Despite the fact that BBMP data cover much less area than the Atlas, thanks to the unified methodology performed constantly every year, the BBMP data are much more reliable information relative abundance changes than Atlas mapping. For this reason, we chose regular monitoring programmes for our further research.

Climate change

Human induced climate change is more and more urgent and alarming topic (King 2004). Climate change is one of the most important drivers of biodiversity (Pimm *et al.* 2014). If it proceeds at current pace, it will lead to homogenization and pose a serious threat to biodiversity (Thuiller *et al.* 2011). There are various causes of bird population changes, but the climate change is on the top of the list and must be considered by any serious studies aiming to explain bird population changes (Vickery *et al.* 2014).

Climate and it's changes in time and space have been shaping bird populations since their evolution birth. For example, bird migration evolved as an adaptation to climate variability in space and time (Louchart 2008). Thus, it is not a surprise, that the same mechanism that led to their evolution is now threatening them, when the parameters of this mechanism – climate – are changed so rapidly as we observe in the past decades.

For this reason, we aim to focus on migration strategies and their challenges with changing climate. We also focus on a specific group, montane birds.

Resident birds and impact of winter temperature

Winter temperature is amongst the most important predictors of bird distribution as shown by studies in Europe (Huntley *et al.* 2008) as well as in North America (Illan *et al.* 2014). Resident birds spend winter in their breeding ranges, so we might expect that their survival will be limited by climatic conditions in winter, namely temperature (Robinson, Baillie & Crick 2007).

To test the impact of winter temperature on annual population fluctuations, in the **Paper II,** we used the data from Czech Breeding Bird Monitoring Programme between 1982 and 2007. BBMP is a large-scale generic bird monitoring scheme based on fieldwork of skilled volunteers. All 335 census sites are scattered throughout the whole territory of the country and they form a representative sample of the Czech landscape (Reif et al. 2008a).

We modelled the inter-annual population growth as a function of temperature in different winter months. We then analyzed the responses according to diet and body mass. We found a significant positive response of population growth to January temperature in 4 species – out of the total 37 (*Streptopeila decaocto, Alcedo atthis, Troglodytes troglodytes, Turdus merula*), in

February in 4 species (*Anas platyrhynchos, Buteo buteo, Alcedo atthis, Troglodytes troglodytes*), and in December in 2 species (*Troglodytes troglodytes, Turdus merula*). We found that the response was stronger in species feeding on animals, potentially due to lower availability of prey (Rolstad & Rolstad 2000).

The effect of winter temperature is present, however, it is much weaker than we expected. This might be due to other influencing factors like land-use changes (Gregory *et al.* 2007; Reif & Hanzelka 2016), or due to the fact that, in contrast to e.g. Robinson, Baillie & Crick (2007) we did not study survival as a direct demographic parameter. For this reason, in our next study **(Paper IV)**, we focused on very detailed demographic analysis, which allows to disentangle various factors contributing to population changes.

Long-distance migratory birds

Species migrating over long distances are exposed to various adverse impacts in different regions, being thus under higher risk of extinction than non-migrants (Wilcove & Wikelski 2008). Although this pattern has been observerd across diverse taxonomic groups, ecoregions and habitats (Wilcove & Wikelski 2008), recent studies suggest this pattern is strongest in birds, whereas for example migratory mammals decline less than non-migratory (Hardesty-Moore *et al.* 2018).

In past decades, long-distance migratory birds are experiencing consistent declines in Europe (Berthold 1973; Winstanley, Spencer & Williamson 1974; Peach, Baillie & Underhill 1991; Berthold *et al.* 1998; Sanderson *et al.* 2006; Heldbjerg & Fox 2008) and North America (Ballard *et al.* 2003). Migratory birds experience declines not present in residents and short-distance migratory birds to such an extent, as has been shown by multiple studies from european countries (Lemoine *et al.* 2007; Heldbjerg & Fox 2008; Van Turnhout *et al.* 2010; Laaksonen & Lehikoinen 2013), as well as at the pan-European level (Sanderson *et al.* 2006; Vickery *et al.* 2014) and other continents (Bohning-Gaese, Taper & Brown 1993; Simmons *et al.* 2015). It is thus evident that long-distance migrants are under much stronger pressure than the other species. Although this pressure can be also attributed to non-climatic causes, including habitat loss or degradation, farmland intensification and other anthropogenic pressure on breeding, wintering and stop-over sites (Newton 2004; Calvert, Walde & Taylor 2009; Gamero *et al.* 2016), climate change stays on the top of the list (Vickery *et al.* 2014).

Climate affects long-distance migratory birds on the breeding and wintering grounds, as well as the stop-over sites. In the following two sub-sections, we will focus on two most prevalent hypotheses on long-distance migrant declines:

1) The trophic mismatch on the breeding grounds, which is a result of raising spring temperatures. Birds shift their breeding phenology slower than their food,

2) The impact of climate, droughts in particular, in sub-Saharan Africa, their wintering grounds.

Hypothesis 1: Trophic mismatch – impact of raising spring temperatures

The most discussed pressure on the breeding grounds is the trophic mismatch, general phenomena present accross many taxa. Changing climate, in particular raising spring temperatures (Schwartz, Ahas & Aasa 2006), results in phenology shifts, but these may differ among various trophic levels. Usually, higher trophic levels shift at slower pace than lower trophic levels. This means that the "predator" or "consumer" adapts their phenology slower than their food. This has been shown across many trophic pyramids:

- birds of prey - songbirds - caterpillars - trees (Both *et al.* 2009b)
- birds - caterpillars (Both & Visser 2005; Donnelly, Yu & Liu 2014)
- birds - plants (Ovaskainen *et al.* 2013)
- roe deer - vegetation (Plard *et al.* 2014)
- *Daphnia* - phytoplancton (Winder & Schindler 2004)
- in terrestrial ecosystems (Thackeray *et al.* 2010).

The bottom of the pyramid often does not catch up with the speed of changing climate itself (Duputié *et al.* 2015). It must be mentioned though that the opposite pattern - when lower trophic levels shift at slower pace - is also present (Visser & Both 2005), for example in marine and freshwater ecosystems (Thackeray *et al.* 2010), and trees versus invertebrate consumers (Both *et al.* 2009b; Donnelly, Yu & Liu 2014).

All these trophic mismatches yield fitness consequences (Winder & Schindler 2004; Both & Visser 2005; Nussey *et al.* 2005). In case of birds, mismatch occurs between the phenology of the food and breeding of long-distance migrants. Due to rising temperatures, the spring onset advanced in last decades – earlier timing of budburst and leaf unfolding results in earlier hatching of caterpillars, most important avian food source in breeding period. Bird phenology advanced as well, however, long-distance migrants are not able to adjust their phenology as much as short-distance migrants or residents (Rubolini *et al.* 2007; Rubolini, Saino & Moller 2010; Saino *et al.* 2011; Kolarova & Adamik 2015), possibly due to constraints resulting from migratory strategy (Rubolini, Saino & Moller 2010). Long-distance (LD) migrants are thus unable to advance their phenology as fast as lower trophic levels (Ovaskainen *et al.* 2013; Donnelly, Yu & Liu 2014). This trophic mismatch results in lower breeding productivity (Both & Visser 2005; Clausen & Clausen 2013) and subsequent population decline (Both *et al.* 2006; Møller, Rubolini & Lehikoinen 2008). While this pattern is apparently very well described in local studies, it might be particular only to certain habitats (Both *et al.* 2009a; Dunn *et al.* 2011). The extent to which it affects populations of LD migrants in general is still unclear (Knudsen *et al.* 2011; Vickery *et al.* 2014).

Hypothesis 2: Droughts in sub-Saharan Africa

Climate also affects birds on passage and wintering grounds. In the case of European birds, long-distance migratory species are usually those wintering in sub-Saharan Africa. Famous is the relationship between precipitation in the Sahel and survival of LD migrants, which led to their severe population declines during the Sahel droughts in 70s and 80s (Winstanley, Spencer & Williamson 1974; Peach, Baillie & Underhill 1991). Similar pattern is observed at the American continent (Studds & Marra 2007). Recent situation is less clear. Precipitation in the Sahel has increased in last decades (see JISAO - Joint Institute for the Study of the Atmosphere and Ocean) and species wintering in the dry region of Sahel have recovered and are reported to have better trends than species wintering in the humid zone (Morrison *et al.* 2013; Atkinson *et al.* 2014). Nevertheless, water in sub-Saharan Africa is obviously still a limiting factor to some populations of LD migrants (Ockendon, Johnston & Baillie 2014; Johnston *et al.* 2016). Extent of the impact on populations is, however, still unclear and also most of these studies come from western Europe, mostly UK; studies from other regions of Europe are still lacking.

Climatic conditions in the wintering grounds may not only affect migrants' survival, but may also carry-over to affect the breeding season (Newton 2004; Norris & Marra 2007). Higher water availability in Africa may advance (Saino *et al.* 2004, 2007; Gordo & Sanz 2006; Gordo & Jose Sanz 2008), but also delay (Robson & Barriocanal 2011) migrants' arrival to the breeding grounds. The carry-over effect might also occur via the body condition after arrival (Smith & Moore 2003). Various studies have shown a positive link between moisture in the wintering tropical areas and breeding performace of both Old and New World LD migrants (Schaub, Jakober & Stauber 2011; Rockwell, Bocetti & Marra 2012; Norman & Peach 2013; Finch *et al.* 2014); in some cases, the carry-over effect was even stronger than the effect of climate in the breeding grounds (Schaub, Jakober & Stauber 2011; Norman & Peach 2013; Finch *et al.* 2014). Some other studies have found no such effect (Laaksonen *et al.* 2006; Pedersen *et al.* 2016), or even a negative one (Ockendon, Leech & Pearce-Higgins 2013). The population dynamics behind carry-over effect is more complicated, since the negative effect of conditions in wintering grounds might be also affecting the species positively via density dependence in the breeding grounds (Calvert, Walde & Taylor 2009). Caution is therefore needed in both analysis and interpretation.

Impact of breeding or wintering grounds?

As I sketched in the above two sections, both major hypotheses of how climate affects birds on breeding and wintering grounds have been pretty well described and confirmed. That being said, very little is known on their relative importance and contribution to the general population changes of long-distance migrants. Which one is the most important? Which one is the cause of the decline?

Let us see what we know from the literature. Global multi-species studies in Northern America and UK suggest breeding grounds having more impact (Bohning-Gaese, Taper & Brown 1993; Morrison *et al.* 2013), the same result is reported on *Setophaga caerulescens* and *Setophaga ruticilla* from a single site in New Hampshire (Holmes 2007). These studies, however, didn't compare relative contribution of breeding and wintering grounds. Some studies compared the impact of breeding versus wintering grounds, but only considered their impact on the productivity, not on the survival (Ockendon, Leech & Pearce-Higgins 2013; Finch *et al.* 2014). Only few studies directly tested the population dynamics. Pearce-Higgins *et al.* (2008) report more important contribution of survival compared to the productivity of *Actitis hypoleucos,* same pattern is reported on *Riparia riparia* (Norman & Peach 2013). Pöysä & Väänänen (2014) report more important contribution of temperature on the breeding grounds than precipitation in Sahel to the population growth.

As we can see, there are only few existing studies, which focus on comparison of different climatic impacts on LD migrants – and these only focus on single species from very small geographical area (usually single site or few clustered sites). But in fact, general, multi-species studies focusing on the comparison of relative importance of major factors and mechanisms shaping species populations are critical for understanding the causes of declines (Vickery et al., 2014). Without this understanding, prioritization and development of efficient conservation actions is hardly possible (Vickery *et al.* 2014)

For this reason, we designed a major study of this Thesis, **Paper IV**. In concordance with methodological Paper I, we decided to use as precise data as possible. We have chosen the Constant Effort Sites (CES) mist-netting scheme in the Czech Republic from 2004 to 2014. This bird ringing programme is based on annual collecting of capture-mark-recapture data for numerous species of small passerines using a network of skilled volunteers under a standard protocol. The idea behind CES is obtaining data on avian demography by repeated sampling of numerous sites over the course of the breeding season and to monitor each site for as many consecutive years as possible. Since the sampling effort is constant at each site across years, these data enable modelling reasonable estimates of demographic parameters (e.g. Johnston et al., 2016). Such CES programmes have been established in several European countries since 1990s (e.g. Robinson et al., 2009) and became an invaluable source of long-term avian demographic data (e.g. Johnston et al., 2016).

Birds were mist-netted at 43 sites around Czech Republic, during 9 visits in ca 10-day intervals covering the advanced breeding season (May - July) every year. Each site had at least 70 m of mist nets. The sites occurred mostly in wet and shrubby habitats (e.g. reedbeds, willow carrs, scrubland) and at forest edges. Each captured bird was determined and aged to distinguish adults from juveniles. Using these data allowed us to not only the population changes, but also key demographic parameters:

- **adult survival**: probability that adult resident bird will survive to the next year;
- **breeding productivity**: number of juveniles divided by number of adult population in a given year.

Our dataset provided results for 8 LD migrants, 8 SD migrants, 4 partial migrants and 1 resident species. Next, we used the following climatic variables:

- in the breeding grounds (Czech Republic):
    - mean monthly temperature in March – June;

   - GDD5 – Growing Degree Days – sum of daily temperatures above 5°C in March and April;
   - phenology of 3 tree species – Julian date of 10% leaf unfolding of *Tilia Cordata, Salix caprea* and *Sambucus nigra*;
- in the non-breeding grounds (sub-Saharan Africa):
   - AET/PET (actual to potential evapotranspiration) in species‘ individual non-breeding ranges. AET/PET ranges from 0 (no water at all) to 1 (100% saturation with water).

We did test the following hypotheses:

1. Breeding productivity of long-distance migratory birds will be negatively affected by spring temperature, GDD5, and earlier spring onset measured by leaf unfolding;
   a. for short-distance and resident birds we expect this effect to be neutral or opposite.
2. Adult survival will be positively affected by higher moisture (indicated by higher AET/PET ratio) in the non-breeding grounds. This effect will be stronger in the Sahelian part of their non-breeding range.
3. Breeding productivity will be positively affected by AET/PET in non-breeding grounds (carry-over effect).
4. Most importantly, we compared the strength of the above efects and their relative contribution to population changes.

The results clearly show that LD migrants' productivity indeed responds negatively to higher spring temperature and advanced plant phenology (see Figure 1 and Paper IV for more details). On the other hand, resident and short-distance (SD) migrant species responded significantly positively, partial migrants' response was also positive (though not significant). The distinct contrast between LD migrants and the other migratory strategies is a clear signal that the migratory strategy is what matters in response to spring temperature. Residents, SD and partial migrants can arrive earlier and thus can profit from earlier spring onset (Wright *et al.* 2009; Pearce-Higgins *et al.* 2015), whereas LD migrants, unable to advance their arrival to breeding grounds as much as residents (Rubolini *et al.* 2007; Rubolini, Saino & Moller 2010; Saino *et al.* 2011; Kolarova & Adamik 2015), respond negatively. This result and namely the contrast between migratory strategies is a support for the trophic mismatch hypothesis (see the reasoning above).

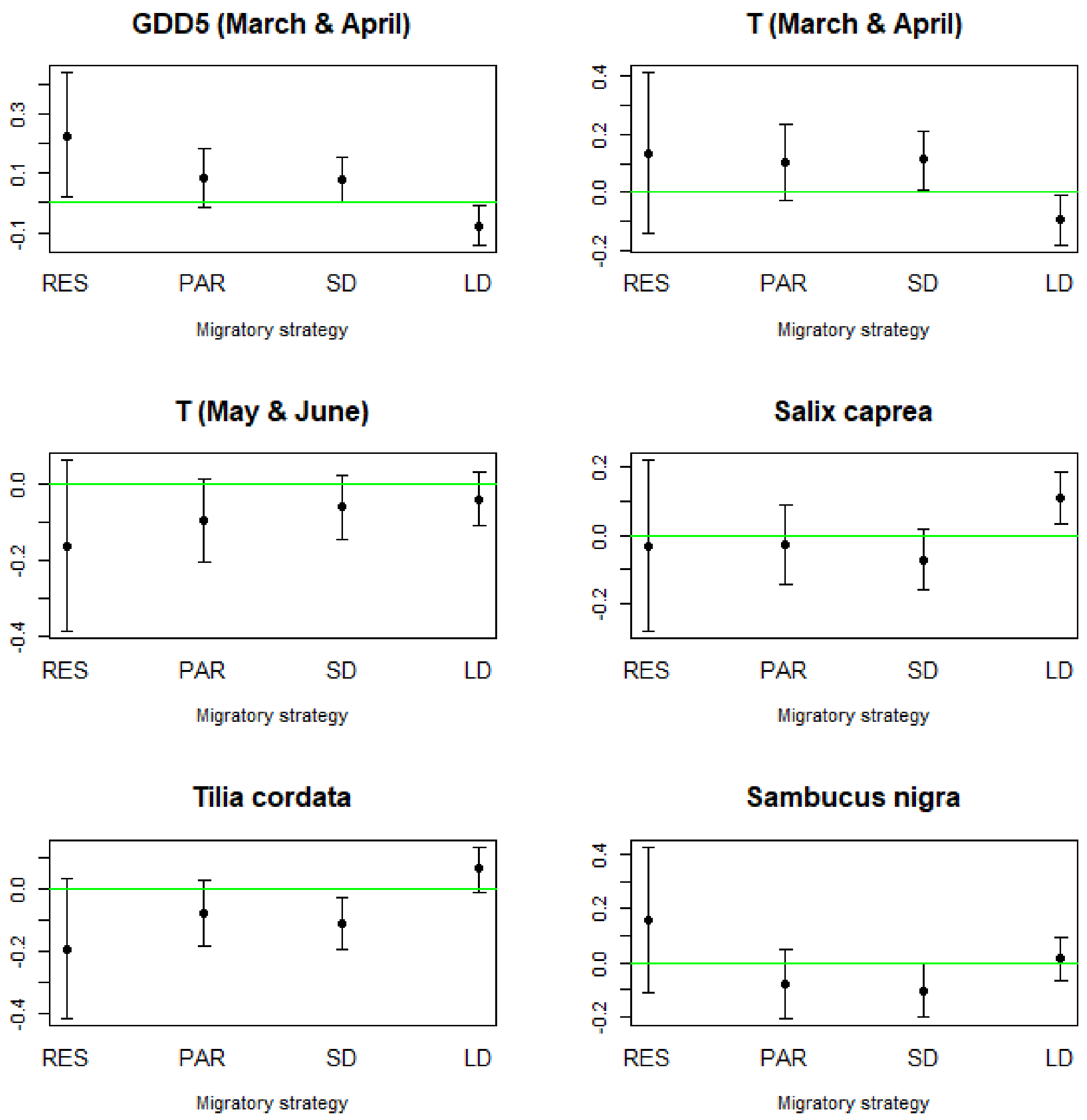

Fig. 1: Relationships between breeding productivity of bird groups defined by different migratory strategies and climatic variables reflecting spring phenology at breeding grounds. Each variable was tested in a single model taking also the potential effect of population density into account (see Table S4 in Paper IV for full results of each model). The relationships are expressed as mean slopes across species sharing a given migratory strategy with 95% confidence intervals (y-axis). Climatic variables: GDD5 – growing degree days, i.e. accumulated temperature above 5°C; T – mean temperature; *Salix caprea, Tilia cordata, Sambucus nigra* – Julian date of 10% leaf unfolding for a given plant species. Migratory strategy: RES – resident, PAR – partial, SD – short-distance migrant, LD – long-distance migrant. See Paper IV for more details.

We also did find support for the second hypothesis – survival of adult individuals was significantly positively affected by moisture – but only in the Sahelian part of their non-breeding ranges, not in the southern part. Stronger effect in the Sahel region could be expected for several reasons. First, it is a first stop after the Sahara desert in the autumn migration (Tøttrup *et al.* 2012), and also important refuelling station before crossing the Sahara desert in the spring migration (Risely, Blackburn & Cresswell 2015). Second, the Sahel region is very dry, so we can expect much more severe impact of water limitation on biota than in more moist regions of Africa (Hawkins *et al.* 2003). On a species level, this effect was significant for *Phylloscupus trochillus, Sylvia communis* and almost significant for *Acrocephalus schoenobaenus*, see Table S6 of Paper IV. Although this mechanism is very well known and described (Winstanley, Spencer & Williamson 1974; Peach, Baillie & Underhill 1991; Studds & Marra 2007), our study is, as far as we know, the first one that has studied this effect on survival on a wide range of species except for Johnston *et al.* (2016). In contrast to the impact of the African AET/PET on the survival, we did not see a significant carry-over effect; probably because this effect is much more indirect and complicated (Calvert, Walde & Taylor 2009).

Now, both hypotheses are confirmed, across species as well as on a species level. But which effect is stronger? Now, the most important and inovative part of our study comes into play.

Spring climate explained 62% variability of the breeding productivity (see Table 2 of Paper IV), whereas AET/PET (moisture) in Sahelian part of non-breeding ranges explains only 20% of the variability of the adult survival. As far as we know, our study is the first one to make such comparable measurement across wide spectre of long-distance migrant species, apart from few, very local studies (Pearce-Higgins *et al.* 2008; Norman & Peach 2013; Pöysä & Väänänen 2014). Interestingly, this finding contrasts with our analysis of population dynamics. Although survival was more correlated with population growth than breeding productivity, this relationship is probably caused by the fact that the breeding productivity is not a direct input to population growth – the produced young need to survive to become recruits to the adult population, i.e. to actually join the population of adults the next year. We could not incorporate juvenile survival into the analysis, because of low philopatry, and this is causing inevitably missing link in the population analysis. Interpretations of these correlations are also confused by the fact that the survival can be correlated with productivity with various limitations. For example, in density dependence situation, when populations fill the carrying capacity of their environment, higher spring productivity can be then negated (buffered) by lower juvenile survival due to competition on resources either between juveniles, or among adults (Calvert, Walde & Taylor 2009). On the other hand, lower adult survival can allow more recruitment of one-year birds (last year juveniles) due to lower pressure on the breeding grounds. In the situation, where populations live far below the carrying capacity, the productivity and survival can be correlated positively, and both be positively correlated with population change, as in case of *Acrocephalus scirpaceus* (see Table S7 in Paper IV). More sophisticated Jolly-Seber type of model would be needed to answer these questions. We can conclude that climate has much more direct and significant impact on the breeding grounds than on the non-breeding grounds, and the survival, which is more correlated with population growth than the breeding productivity, apparently contains large component that we have not explained by moisture in Africa – either due to poor localization of their wintering grounds, or other factors affecting adult or juvenile survival that come into play – land use change in sub-Saharan Africa (Zwarts *et al.* 2009) or more complex dynamic involving the mentioned negative density dependence (Calvert, Walde & Taylor 2009).

Montane birds

As shown in the previous chapters, climate change already affects bird populations. Warm loving species increase, cold-loving species decline (Lemoine *et al.* 2007; Gregory *et al.* 2009). This is also case of mountain species (Lehikoinen *et al.* 2014). In general, cold-loving species can adapt by shifting their ranges northwards (La Sorte & Thompson 2007; Huntley *et al.* 2008). On the other hand, mountain species without access to higher elevations are especially vulnerable, since they have nowhere to shift (Şekercioğlu *et al.* 2008). Especially sensitive are species in the tropics (Şekercioğlu, Primack & Wormworth 2012). Ironically, the same process that resulted in such a spectacular diversity of tropical montane bird species – elevational specialization along the altitude gradient, along with geographical barriers created by lower altitudes (Fjeldsa, Bowie & Rahbek 2012) – the very same process is now reason why many of these species are extremely vulnerable as a result of climate change (Laurance *et al.* 2011). Not only montane birds are threatened; the same pattern has also been described in butterflies (Forister *et al.* 2010) and plants (Lenoir *et al.* 2008). Although several studies predicted the impact of these threats according to future climate conditions (Chamberlain *et al.* 2013), empirical evidence for these impacts remains limited due to the lack of long-term data on species' distribution and abundance at high altitudes (Chamberlain *et al.* 2012). For this reason, we decided to take opportunity of unique dataset of our friend Jiří Flousek, and bring more knowledge about alpine birds population changes **(Paper III)**. Our Aim is to:

- Determine how montane species cope with climate change:
    - Test if their population trend is dependent on altitude and life history traits.
    - Test if they adapt by shifting their altitudinal range and how much this adaptation actually helps them to improve their population trends

Our dataset consists of point counts held from 1984 to 2011 in Giant Mountains in Czech Republic, 10 transects in total, 6 – 27 points each. For each species, we computed population trend, as well as mean annual altitudinal range shift. Next, we ran a linear model, one species as one data point, trend as a response variable, with the following explanatory variables:

- mean altitude
- altitudinal range shift
- migration strategy
- life history strategy (fast/slow resp. r-/K- strategy)
- European climatic niche (Reif *et al.* 2013).

Temperatures in the breeding season increased 0.04 – 0.08°C/year, depending on the station. Species moved upwards during the study period. Species breeding at higher altitudes had more negative trend. Moreover, the interaction of mean altitude and altitudinal range shift has shown that altitudinal range shift correlated with more positive trend in lower altitude species than higher altitude species. All these findings are in concordance with our expectations. Raising temperatures causes birds to track their climatic optima and shift upwards (Chen *et al.* 2009; Grytnes *et al.*). Species breeding at higher altitudes have nowhere to shift, which results in their declines. On the other hand, species breeding at lower altitudes, which shifted their range upwards, had more positive trend.

Our study thus brings an important evidence on a long-term, multi-species dataset, and confirms that if the climate change progresses at the current speed, montane birds are in urgent trouble. We suggest that conservation efforts should be made to protect their habitats in order not to add further pressure on their populations.

Conclusions

In **Paper I**, we have compared the data quality from the regular Breeding Bird Monitoring programme with the Atlas mapping. Despite the fact that BBMP data cover much less area than the Atlas, thanks to the unified methodology performed constantly every year, the BBMP delivered much more reliable information on relative abundance changes than Atlas mapping. For this reason, we chose regular monitoring programmes for our further research.

In **Paper II**, we found that six out of 37 resident species, for which the data was available, responded negatively to lower winter temperatures. The response was stronger in species feeding on animals, potentially due to lower availability of prey.

In **Paper IV,** we found that long-distance migrants' breeding productivity responds negatively to higher spring temperatures and advanced spring indicated by earlier leaf unfolding of three tree species. Residents and short-distance migrants responded positively. The distinct contrast between the response of long-distance migrants and the other migratory strategies brings a support for the trophic mismatch hypothesis. In other words, residents, short-distance and partial migrants can arrive earlier and thus can profit from earlier spring onset, whereas long-distance migrants, unable to advance their arrival to breeding grounds as much as residents, respond negatively.

We also found that survival of adult individuals of long-distance migrants was positively affected by moisture (AET/PET) in the Sahelian part of their non-breeding ranges. The effect was not present in the southern part. This suggest that the conditions in the Sahel have overall great importance on the populations of long-distance migrants, whether they actually do or do not spend whole winter in that region. We found no support for the carry-over effect.

We found that spring climate explained 62% variability of the breeding productivity, whereas AET/PET (moisture) in Sahelian part of non-breeding ranges explains 20% of the variability of the adult survival. Thus, climate on the breeding grounds is more important for migrant species than the climate on the non-breeding grounds. On the other hand, survival was more correlated with population growth than breeding productivity. This suggests that either the single unknown component of population dynamics – juvenile survival – is buffering the effect of productivity via density dependence, or is affected by other factors that we do not explain by climate, like land use change. As far as we know, our inovative study is the first one to make such comparable measurement across wide spectre of long-distance migrant species.

In **Paper III**, we found that montane species moved upwards to higher altitudes. Species breeding at higher altitudes had more negative population change. Moreover, the altitudinal range shift brought more positive population change to species living in lower altitudes. This suggests that species breeding at higher altitudes have nowhere to shift, which results in their declines.

Overall, our study, encompassing wide species spectrum and long-term dataset, confirms serious impact of climate change on populations of Czech birds. If the climate change progresses at the current speed, mountain birds and long-distance migrants will be in trouble. We suggest that conservation efforts should be made to protect their habitats in order not to add further pressure on their populations.

Acknowledgements

First, I would like to thank to my advisor, Jiří Reif. Our cooperation on the research started more than two years before I entered the studies. One day he asked „don't you want to do this as a PhD study?". „Yes!", I replied. I hope he does not regret his question :) I don't. That being said, I lost lots of illusions during the studies. Namely:

1. **I can construct a bayesian model that will model everything!** Oh no. The perfect models were so slow they would run for weeks and still not converge. Besides, they do not work on real data ;)

2. **I will find proof for this or that idea about birds!** Wrong. Every time I was chasing this illusion I was dissappointed. The nature is always more complicated than I expected, and the message is rarely a nice simple story, as all those articles in high impact journals pretend :)

Jiří is one of the best people I cooperated with. When I met him, which wasn't so often, because I was very slow with my research, he was always so enthusiastic into my progress, that he brought me new motivation. He always believed in me and my abilities. This was very motivating and it was a very pleasant atmospehere of cooperation. Thank you, Jiří!

Thanks to Meah, for using her gifts and abilities to support me in my last few months and weeks. Without her, I would probably not be able to finish.

Many thanks belong to Marc Kéry for his charismatic introduction into Bayesian modelling which caught me completely and gave me the freedom in modelling. Thank to him for consultations on population modelling and for the for giving me excellent books Kéry & Schaub (2012) and Kéry & Royle (2016), which have been very helpful many times during the work. Thanks to all my PhD. colleagues for friendship and help, namely Jan Hanzelka for help and cooperation.

I would like to thank to many other people for cooperation and for helping me in various ways during my studies: Petr Voříšek, Petr Procházka, Jaroslav Koleček, Zdeněk Vermouzek, Jan Hanzelka, Arco van Strien, Alison Johnston, Marc Anton, Carmen Recansens, Sergi Herrando, Lluís Brotons, Henk Sierdsema, Jiří Flousek, Michael Schaub, Matt Denwood, Jaroslav Cepák, Petr Klvaňa and Miroslav Jelínek.

I would like to thank to all open-source projects that made my work possible: R (R Core Team 2016), JAGS (Plummer 2003), MARK (www.phidot.org/software/mark/), RMark (Laake 2013), QGIS, R package runjags (Denwood 2016) and many others.

This work was only possible due to fieldwork of hundreds of volunteers; I am very grateful for their annual consistent work. Part of the work was supported by the Czech Science Foundation (project no. 13-06451S), the Grant Agency of Charles University in Prague (project no. 633212), the Institute of Vertebrate Biology (institutional support RVO: 68081766) and the Charles University (PRIMUS/17/SCI/16).

Epilogue

My illusions about conquering science with simple, beautifly and perfectly modelled answers abount nature are gone. I think I found more about myself than I found about nature.

I must think of what my ex-girlfriend Alena told me: „You don’t have to understand me, you just have to love me!“ Perhaps it’s the same with nature. If I can’t understand it, I will probably stop trying to do so. I will just love it.

References

Atkinson, P.W., Adams, W.M., Brouwer, J., Buchanan, G., Cheke, R.A., Cresswell, W., Hewson, C.M., Hulme, M.F., Manvell, A., Sheehan, D.K., Small, R.D.S., Sutherland, W.J. & Vickery, J.A. (2014) Defining the key wintering habitats in the Sahel for declining African-Eurasian migrants using expert assessment. *Bird Conservation International*, **24**, 477–491.

Ballard, G., Geupel, G.R., Nur, N. & Gardali, T. (2003) Long-term declines and decadal patterns in population trends of songbirds in western north america, 1979–1999. *The Condor*, **105**, 737–755.

Berthold, P. (1973) On the severe decline of populations of the Whitethroat and other song birds in Western Europe. *Journal of Ornithology*, **114**, 348–360.

Berthold, P., Fiedler, W., Schlenker, R. & Querner, U. (1998) 25-year study of the population development of central European songbirds: A general decline most evident in long-distance migrants. *Naturwissenschaften*, **85**, 350–353.

Bohning-Gaese, K., Taper, M.L. & Brown, J.H. (1993) Are Declines in North American Insectivorous Songbirds Due to Causes on the Breeding Range? *Conservation Biology*, **7**, 76–86.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.

Both, C., Turnhout, C.A.M.V., Bijlsma, R.G., Siepel, H., Strien, A.J.V. & Foppen, R.P.B. (2009a) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20091525.

Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. & Visser, M.E. (2009b) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, **78**, 73–83.

Both, C. & Visser, M.E. (2005) The effect of climate change on the correlation between avian life-history traits. *Global Change Biology*, **11**, 1606–1613.

Calvert, A.M., Walde, S.J. & Taylor, P.D. (2009) Nonbreeding-Season Drivers of Population Dynamics in Seasonal Migrants: Conservation Parallels Across Taxa. *Facteurs hors reproduction intervenant sur la dynamique des populations de migrateurs saisonniers : analogie entre divers taxons.*, **4**, 71–97.

Chamberlain, D., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A. & Zbinden, N. (2012) The altitudinal frontier in avian climate impact research. *Ibis*, **154**, 205–209.

Chamberlain, D.E., Negro, M., Caprio, E. & Rolando, A. (2013) Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biological Conservation*, **167**, 127–135.

Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S., Hill, J.K. & Thomas, C.D. (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences*, **106**, 1479–1483.

Clausen, K.K. & Clausen, P. (2013) Earlier Arctic springs cause phenological mismatch in long-distance migrants. *Oecologia*, **173**, 1101–1112.

Denwood, M.J. (2016) runjags: An R Package Providing Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS. *Journal of Statistical Software*, **71**, 1–25.

Donnelly, A., Yu, R. & Liu, L. (2014) Trophic level responses differ as climate warms in Ireland. *International Journal of Biometeorology*, **59**, 1007–1017.

Dunn, P.O., Winkler, D.W., Whittingham, L.A., Hannon, S.J. & Robertson, R.J. (2011) A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore? *Ecology*, **92**, 450–461.

Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015) Phenological plasticity will not help all species adapt to climate change. *Global Change Biology*, **21**, 3062–3073.

Finch, T., Pearce-Higgins, J.W., Leech, D.I. & Evans, K.L. (2014) Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. *Biodiversity and Conservation*, **23**, 2427–2444.

Fjeldsa, J., Bowie, R.C.K. & Rahbek, C. (2012) The Role of Mountain Ranges in the Diversification of Birds. *Annual Review of Ecology, Evolution, and Systematics, Vol 43* (ed D.J. Futuyma), pp. 249–265. Annual Reviews, Palo Alto.

Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P. & Shapiro, A.M. (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 2088–2092.

Gamero, A., Brotons, L., Brunner, A., Foppen, R., Fornasari, L., Gregory, R.D., Herrando, S., Hořák, D., Jiguet, F., Kmecl, P., Lehikoinen, A., Lindström, Å., Paquet, J.-Y., Reif, J., Sirkiä, P.M., Škorpilová, J., van Strien, A., Szép, T., Telenský, T., Teufelbauer, N., Trautmann, S., van Turnhout, C.A.M., Vermouzek, Z., Vikstrøm, T. & Voříšek, P. (2016) Tracking Progress Towards EU Biodiversity Strategy Targets: EU Policy Effects in Preserving its Common Farmland Birds. *Conservation Letters*, n/a-n/a.

Gordo, O. & Jose Sanz, J. (2008) The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *Journal of Ornithology*, **149**, 199–210.

Gordo, O. & Sanz, J.J. (2006) Climate change and bird phenology: a long-term study in the Iberian Peninsula. *Global Change Biology*, **12**, 1993–2004.

Gregory, R., Noble, D., Field, R., Marchant, J., Raven, M.J. & W. Gibbons, D. (2003) Using birds as indicators of biodiversity. *Ornis Hungarica*, **12**, 11–24.

Gregory, R.D., Vořišek, P., Noble, D.G., Strien, A.V., Klvaňová, A., Eaton, M., Meyling, A.W.G., Joys, A., Foppen, R.P.B. & Burfield, I.J. (2008) The generation and use of bird population indicators in Europe. *Bird Conservation International*, **18**, S223–S244.

Gregory, R.D., Vorisek, P., Van Strien, A., Meyling, A.W.G., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. & Burfield, I.J. (2007) Population trends of widespread woodland birds in Europe. *Ibis*, **149**, 78–97.

Gregory, R.D., Willis, S.G., Jiguet, F., Voříšek, P., Klvaňová, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. & Green, R.E. (2009) An Indicator of the Impact of Climatic Change on European Bird Populations. *PLoS ONE*, **4**.

Grytnes, J.-A., Kapfer, J., Jurasinski, G., Birks, H.H., Henriksen, H., Klanderud, K., Odland, A., Ohlson, M., Wipf, S. & Birks, H.J.B. Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology and Biogeography*, **23**, 876–884.

Hardesty-Moore, M., Deinet, S., Freeman, R., Titcomb, G.C., Dillon, E.M., Stears, K., Klope, M., Bui, A., Orr, D., Young, H.S., Miller-ter Kuile, A., Hughey, L.F. & McCauley, D.J. (2018) Migration in the Anthropocene: how collective navigation, environmental system and taxonomy shape the vulnerability of migratory species. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **373**, 20170017.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, Water, and Broad-Scale Geographic Patterns of Species Richness. *Ecology*, **84**, 3105–3117.

Heldbjerg, H. & Fox, T. (A D.). (2008) Long-term population declines in Danish trans-Saharan migrant birds: Capsule Long-distance migrant birds show less favourable trends than sedentary/short-distance species. *Bird Study*, **55**, 267–279.

Holmes, R.T. (2007) Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis*, **149**, 2–13.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2008) *A Climatic Atlas Of European Breeding Birds*. Lynx Edicions, Barcelona.

Illan, J.G., Thomas, C.D., Jones, J.A., Wong, W.-K., Shirley, S.M. & Betts, M.G. (2014) Precipitation and winter temperature predict long-term range-scale abundance changes in Western North American birds. *Global Change Biology*, **20**, 3351–3364.

Johnston, A., Robinson, R.A., Gargallo, G., Julliard, R., van der Jeugd, H. & Baillie, S.R. (2016) Survival of Afro-Palaearctic passerine migrants in western Europe and the impacts of seasonal weather variables. *Ibis*, **158**, 465–480.

Joint Institute for the Study of the Atmosphere and Ocean (JISAO). University of Washington, Seattle, WA, USA (http://jisao.washington. edu/data_sets/sahel/).

Kery, M. & Royle, J.A. (2016) *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS: Volume 1: Prelude and Static Models*, 1 edition. Academic Press.

Kéry, M. & Schaub, M. (2012) *Bayesian Population Analysis Using WinBUGS*. Elsevier.

King, D.A. (2004) Climate Change Science: Adapt, Mitigate, or Ignore? *Science*, **303**, 176–177.

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P.P., Møller, A.P., Nilsson, A.L.K., Péron, G., Ranta, E., Rubolini, D., Sparks, T.H., Spina, F., Studds, C.E., Sæther, S.A., Tryjanowski, P. & Stenseth, N.C. (2011) Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, **86**, 928–946.

Kolarova, E. & Adamik, P. (2015) Bird arrival dates in Central Europe based on one of the earliest phenological networks. *Climate Research*, **63**, 91–98.

Laake, J.L. (2013) *RMark: An R Interface for Analysis of Capture-Recapture Data with MARK*. AFSC Processed Rep., Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA.

Laaksonen, T., Ahola, M., Eeva, T., Vaisanen, R.A. & Lehikoinen, E. (2006) Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos*, **114**, 277–290.

Laaksonen, T. & Lehikoinen, A. (2013) Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. *Biological Conservation*, **168**, 99–107.

Lamb, E.G., Bayne, E., Holloway, G., Schieck, J., Boutin, S., Herbers, J. & Haughland, D.L. (2009) Indices for monitoring biodiversity change: Are some more effective than others? *Ecological Indicators*, **9**, 432–444.

Laurance, W.F., Useche, D.C., Shoo, L.P., Herzog, S.K., Kessler, M., Escobar, F., Brehm, G., Axmacher, J.C., Chen, I.-C., Arellano Gamez, L., Hietz, P., Fiedler, K., Pyrcz, T., Wolf, J., Merkord, C.L., Cardelus, C., Marshall, A.R., Ah-Peng, C., Aplet, G.H., del Coro Arizmendi, M., Baker, W.J., Barone, J., Bruehl, C.A., Bussmann, R.W., Cicuzza, D., Eilu, G., Favila, M.E., Hemp, A., Hemp, C., Homeier, J., Hurtado, J., Jankowski, J., Kattan, G., Kluge, J., Kroemer, T., Lees, D.C., Lehnert, M., Longino, J.T., Lovett, J., Martin, P.H., Patterson, B.D., Pearson, R.G., Peh, K.S.-H., Richardson, B., Richardson, M., Samways, M.J., Senbeta, F., Smith, T.B., Utteridge, T.M.A., Watkins, J.E., Wilson, R., Williams, S.E. & Thomas, C.D. (2011) Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation*, **144**, 548–557.

Lehikoinen, A., Green, M., Husby, M., Kålås, J.A. & Lindström, Å. (2014) Common montane birds are declining in northern Europe. *Journal of Avian Biology*, **45**, 3–14.

Lemoine, N., Bauer, H.-G., Peintinger, M. & Boehning-Gaese, K. (2007) Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology*, **21**, 495–503.

Lenoir, J., Gégout, J.C., Marquet, P.A., Ruffray, P. de & Brisse, H. (2008) A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. *Science*, **320**, 1768–1771.

Louchart, A. (2008) Emergence of long distance bird migrations: a new model integrating global climate changes. *Naturwissenschaften*, **95**, 1109–1119.

Mácha, K.H. (1836) *Máj*.

Møller, A.P., Rubolini, D. & Lehikoinen, E. (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences*, **105**, 16195–16200.

Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K. & Gill, J.A. (2013) Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. *Diversity and Distributions*, **19**, 1051–1058.

Newton, I. (2004) Population limitation in migrants. *Ibis*, **146**, 197–226.

Norman, D. & Peach, W.J. (2013) Density-dependent survival and recruitment in a long-distance Palaearctic migrant, the Sand Martin Riparia riparia. *Ibis*, **155**, 284–296.

Norris, D.R. & Marra, P.P. (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor*, **109**, 535–547.

Nussey, D.H., Postma, E., Gienapp, P. & Visser, M.E. (2005) Selection on Heritable Phenotypic Plasticity in a Wild Bird Population. *Science*, **310**, 304–306.

Ockendon, N., Johnston, A. & Baillie, S.R. (2014) Rainfall on wintering grounds affects population change in many species of Afro-Palaearctic migrants. *Journal of Ornithology*, **155**, 905–917.

Ockendon, N., Leech, D. & Pearce-Higgins, J.W. (2013) Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. *Biology Letters*, **9**, 20130669.

Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E. & Delgado, M. del M. (2013) Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences*, **110**, 13434–13439.

Peach, W., Baillie, S. & Underhill, L. (1991) Survival of British Sedge Warblers Acrocephalus schoenobaenus in relation to west African rainfall. *Ibis*, **133**, 300–305.

Pearce-Higgins, J.W., Eglington, S.M., Martay, B. & Chamberlain, D.E. (2015) Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, **84**, 943–954.

Pearce-Higgins, J.W., Yalden, D.W., Dougall, T.W. & Beale, C.M. (2008) Does climate change explain the decline of a trans-Saharan Afro-Palaearctic migrant? *Oecologia*, **159**, 649–659.

Pedersen, L., Fraser, K.C., Kyser, T.K. & Tottrup, A.P. (2016) Combining direct and indirect tracking techniques to assess the impact of sub-Saharan conditions on cross-continental songbird migration. *Journal of Ornithology*, **157**, 1037–1047.

Pe’er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Baldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbe, A., Wulf, F. & Scott, A.V. (2014) AGRICULTURE POLICY EU agricultural reform fails on biodiversity. *Science*, **344**, 1090–1092.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**, 1246752.

Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C. & Bonenfant, C. (2014) Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. *Plos Biology*, **12**, e1001828.

Plummer, M. (2003) *JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling*.

Pöysä, H. & Väänänen, V.-M. (2014) Drivers of breeding numbers in a long-distance migrant, the Garganey (Anas querquedula): effects of climate and hunting pressure. *Journal of Ornithology*, **155**, 679–687.

R Core Team. (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reif, J. & Hanzelka, J. (2016) Grassland winners and arable land losers: The effects of post-totalitarian land use changes on long-term population trends of farmland birdse. *Agriculture Ecosystems & Environment*, **232**, 208–217.

Reif, J., Prylová, K., Šizling, A., Vermouzek, Z., Šťastný, K. & Bejček, V. (2013) Changes in bird community composition in the Czech Republic from 1982 to 2004: increasing biotic homogenization, impacts of warming climate, but no trend in species richness. *Journal of Ornithology*, **154**, 359–370.

Risely, A., Blackburn, E. & Cresswell, W. (2015) Patterns in departure phenology and mass gain on African non-breeding territories prior to the Sahara crossing in a long-distance migrant. *Ibis*, **157**, 808–822.

Robinson, R.A., Baillie, S.R. & Crick, H.Q.P. (2007) Weather-dependent survival: implications of climate change for passerine population processes. *Ibis*, **149**, 357–364.

Robson, D. & Barriocanal, C. (2011) Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. *Journal of Animal Ecology*, **80**, 320–331.

Rockwell, S.M., Bocetti, C.I. & Marra, P.P. (2012) Carry-Over Effects of Winter Climate on Spring Arrival Date and Reproductive Success in an Endangered Migratory Bird, Kirtland's Warbler (setophaga Kirtlandii). *Auk*, **129**, 744–752.

Rolstad, J. & Rolstad, E. (2000) Influence of large snow depths on Black Woodpecker Dryocopus martius foraging behavior. *Ornis Fennica*, **77**, 65–70.

Rubolini, D., Moller, A.P., Rainio, K. & Lehikoinen, E. (2007) Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research*, **35**, 135–146.

Rubolini, D., Saino, N. & Moller, A.P. (2010) Migratory behaviour constrains the phenological response of birds to climate change. *Climate Research*, **42**, 45–55.

Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hueppop, K., Hueppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M. & Sokolov, L. (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 835–842.

Saino, N., Rubolini, D., Jonzen, N., Ergon, T., Montemaggiori, A., Stenseth, N.C. & Spina, F. (2007) Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. *Climate Research*, **35**, 123–134.

Saino, N., Szep, T., Romano, M., Rubolini, D., Spina, F. & Moller, A.P. (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters*, **7**, 21–25.

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, **131**, 93–105.

Schaub, M., Jakober, H. & Stauber, W. (2011) Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. *Oecologia*, **167**, 445.

Schwartz, M.D., Ahas, R. & Aasa, A. (2006) Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology*, **12**, 343–351.

Şekercioğlu, Ç.H., Primack, R.B. & Wormworth, J. (2012) The effects of climate change on tropical birds. *Biological Conservation*, **148**, 1–18.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, **22**, 140–150.

Shakespeare, W. (1597) *Romeo and Juliet*.

Simmons, R.E., Kolberg, H., Braby, R. & Erni, B. (2015) Declines in migrant shorebird populations from a winter-quarter perspective. *Conservation Biology: The Journal of the Society for Conservation Biology*, **29**, 877–887.

Smith, R.J. & Moore, F.R. (2003) Arrival Fat and Reproductive Performance in a Long-Distance Passerine Migrant. *Oecologia*, **134**, 325–331.

Sorte, F.A.L. & Iii, F.R.T. (2007) Poleward Shifts in Winter Ranges of North American Birds. *Ecology*, **88**, 1803–1812.

Studds, C.E. & Marra, P.P. (2007) Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, Setophaga ruticilla. *Climate Research*, **35**, 115–122.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J. & Wanless, S. (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313.

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B. & Araujo, M.B. (2011) Consequences of climate change on the tree of life in Europe. *Nature*, **470**, 531–534.

Tøttrup, A.P., Klaassen, R.H.G., Strandberg, R., Thorup, K., Kristensen, M.W., Jørgensen, P.S., Fox, J., Afanasyev, V., Rahbek, C. & Alerstam, T. (2012) The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 1008–1016.

Van Turnhout, C.A.M., Foppen, R.P.B., Leuven, R.S.E.W., Van Strien, A. & Siepel, H. (2010) Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation*, **143**, 173–181.

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D. (2014) The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, **156**, 1–22.

Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2561–2569.

Wilcove, D.S. & Wikelski, M. (2008) Going, Going, Gone: Is Animal Migration Disappearing. *PLOS Biol*, **6**, e188.

Winder, M. & Schindler, D.E. (2004) Climate Change Uncouples Trophic Interactions in an Aquatic Ecosystem. *Ecology*, **85**, 2100–2106.

Winstanley, D., Spencer, R. & Williamson, K. (1974) Where Have All the Whitethroats Gone? *Bird Study*, **21**, 1–14.

Wright, L.J., Hoblyn, R.A., Green, R.E., Bowden, C.G.R., Mallord, J.W., Sutherland, W.J. & Dolman, P.M. (2009) Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark Lullula arborea. *Journal of Animal Ecology*, **78**, 1191–1202.

Zwarts, L., bijlsma, rob, van der kamp, jan & Wymenga, E. (2009) *Zwarts L., Bijlsma R.G., van Der Kamp J. & Wymenga E. 2009. Living on the Edge: Wetlands and Birds in a Changing Sahel. KNNV Publishing, Zeist, The Netherlands.*

Attached publications

Publications (Paper I, II, III and IV) could not be uploaded as part of this file (due to the rules set in the Student Information System) and were submitted in a separate attachment file.

Also, here are their full references:

Paper I: Reif J., Šťastný K., **Telenský T.** & Bejček V. (2009): Srovnání změn početnosti hojných druhů ptáků zjištěných na základě síťového mapování s údaji z Jednotného programu sčítání ptáků v České republice. *Sylvia* 45: 137–150

Paper II: Reif, J., **Telenský, T.**, Stastný, K., Bejcek, V. & Klvana, P. (2010) Relationships between winter temperature and breeding bird abundance on community level: importance of interspecific differences in diet. Folia Zoologica, 59, 313–322.

Paper III: Flousek, J., **Telenský, T.**, Hanzelka, J. & Reif, J. (2015) Population Trends of Central European Montane Birds Provide Evidence for Adverse Impacts of Climate Change on High-Altitude Species. PLOS ONE, 10, e0139465.

Paper IV: Telenský, T., Cepák, J., Klvaňa, P., Jelínek, M. & Reif, J.: Impacts of climate change on long-distance migrants: a demographic framework. Global Change Biology (resubmitted manuscript).