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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.

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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.

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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.

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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).

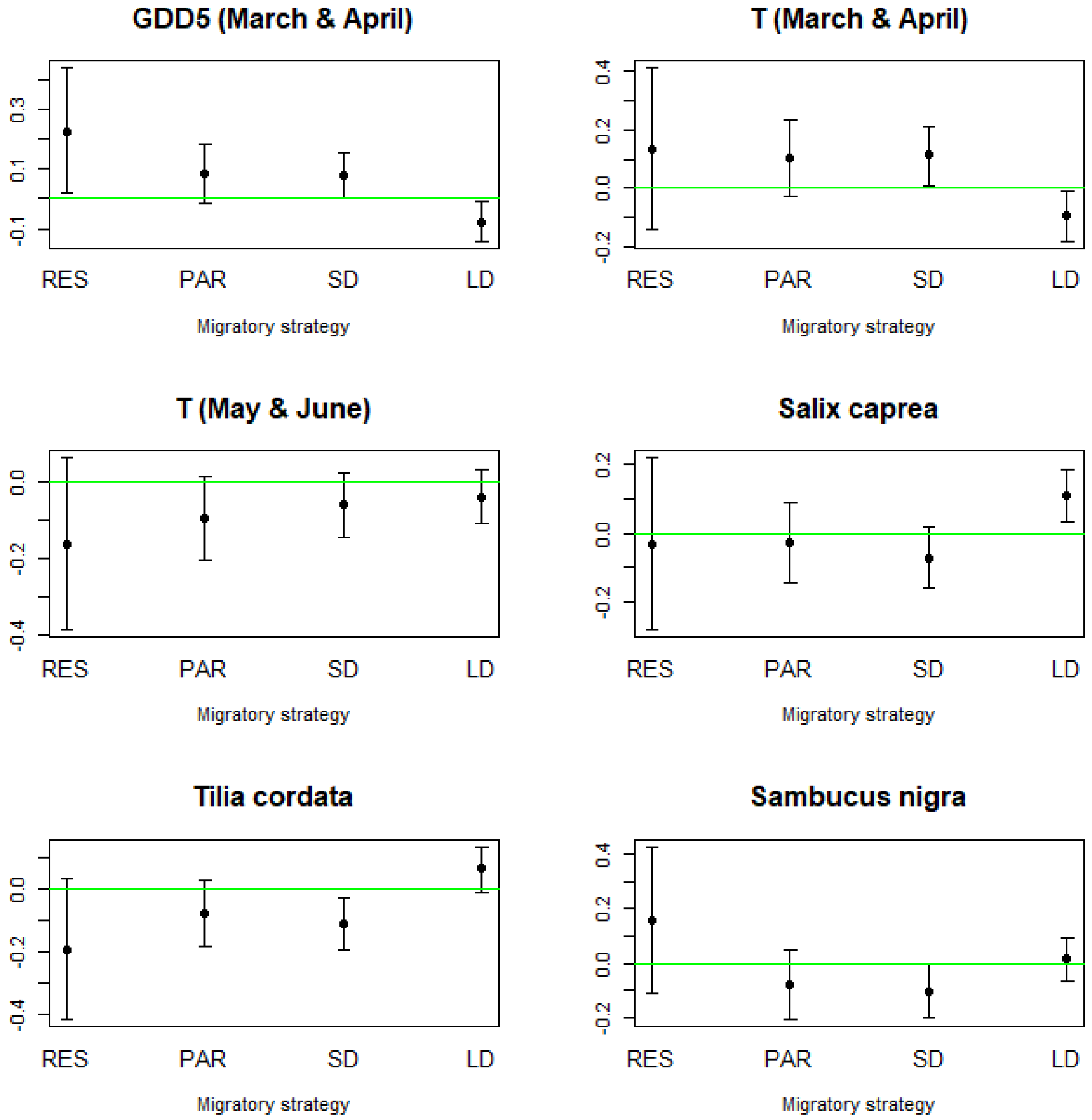

Fig. 1: Relationships between breeding productivity of bird groups defined by different migratory strategies and climatic variables reflecting spring phenology at breeding grounds. Each variable was tested in a single model taking also the potential effect of population density into account (see Table 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.

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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!

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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

Paper I

Srovnání změn početnosti hojných druhů ptáků zjištěných na základě síťového mapování s údaji z Jednotného programu sčítání ptáků v České republice

Population changes of common birds in the Czech Republic: comparison of atlas mapping with annual monitoring data

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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.*

Správné zachycení změn početnosti ptáků je důležité jak pro základní výzkum jejich ekologie, tak pro nastavení vhodných priorit pro jejich ochranu. Dva nejdůležitější zdroje dat v České republice poskytují (i) síťové mapování hnízdního rozšíření ptáků probíhající zhruba v 15letých periodách a (ii) každoroční monitoring hnízdních populací v rámci Jednotného programu sčítání ptáků (JPSP). Lze předpokládat, že u hojných ptačích druhů, jejichž rozšíření zahrnuje téměř celou ČR a nedoznává v čase výrazných změn, mohou být změny početnosti pomocí síťového mapování zachyceny pouze nedokonale. U 73 nejhojnějších druhů českých ptáků, pro něž existují kvalitní data z JPSP, jsme vyjádřili změnu početnosti mezi dvěma mapovacími obdobími (1985–1989 a 2001–2003) pomocí dat z kvadrátového mapování a zároveň pomocí dat z JPSP. U druhů, pro které nebyly při zpracování síťového mapování využity údaje z JPSP, se výsledky z obou zdrojů dat výrazně liší. Obecně hodnotí síťové mapování změny početnosti pozitivněji než JPSP – některé ubývající druhy jsou podle mapování hodnoceny jako stabilní či přibývající, některé druhy beze změny početnosti podle mapování přibývají. Jakékoliv hodnocení změn početnosti hojných druhů ptáků by tedy pro dosažení nezkresleného obrazu mělo zohlednit i výsledky JPSP. Dále doporučujeme využívat údaje z JPSP i pro kalkulaci odhadů početnosti ptáků na základě síťového mapování.

Good recording of population changes in birds is important for basic studies of their ecology as well as for setting conservation priorities. There are two main data sources used to estimate bird population changes in the Czech Republic: (i) atlas mapping of breeding bird distribution conducted in ca 15–year cycles and (ii) Breeding Bird Monitoring Programme (BBMP) based on annual counts. We expected that the atlas mapping data do not measure population changes accurately in abundant species with countrywide distribution. We calculated changes in abundance between the periods of 1985–1989 and 2001–2003 in 73 commonest bird *species using the atlas mapping data and using the BBMP data, respectively. Population changes calculated using the atlas mapping data differed from those based on the BBMP data in species, for which the results of BBMP were not available during the atlas mapping work. In general, atlas mapping revealed more positive population changes compared to BBMP. Some species declining according to BBMP were classified as stable or increasing using the atlas data and species with no population change according to BBMP were classified as increasing using the atlas data. Therefore, we recommend that any studies focusing on population changes in common species should take BBMP results into account, otherwise their conclusions could be flawed.*

Keywords: abundance, atlas mapping, distribution, monitoring scheme, population trend

ÚVOD

Početnost je významná biologická charakteristika každého ptačího druhu (Newton 1998). Má úzký vztah např. k nárokům na prostředí, životní strategii či sociálnímu chování, přičemž vzájemné působení je často obousměrné (např. určitá životní strategie ovlivňuje hojnost daného druhu a zároveň jeho abundance tuto životní strategii formuje – Tuljapurkar et al. 2009). Změny početnosti tedy mohou představovat zásadní zásah do biologie ptačích druhů, který může měnit jejich ekologické vlastnosti a vztahy. Z ochranářského hlediska změna početnosti ukazuje, jak je dobře existence zájmových druhů v různých lokalitách či oblastech zajištěna (Purvis et al. 2000). Při formální klasifikaci stupně ohrožení jde o nejdůležitější ukazatel, který rozhoduje o tom, do jaké kategorie je ten který druh zařazen, a tedy jaké ochranářské úsilí mu bude věnováno (Mace et al. 2008).

Ze všech těchto důvodů je změnám početnosti věnována v ornitologickém výzkumu značná pozornost (Gregory et al. 2008). Nicméně kvalitně odhadnout změnu početnosti je velmi obtížný úkol (Bibby et al. 2000, Voříšek et al. 2008a). Ptačí druhy mají řadu vlastností, které tento úkol znesnadňují (vysoká mobilita, aktivita po omezenou denní či roční dobu, skrytý způsob života – Veselovský 2001), a přes desítky let vývoje specializovaných metodik zůstává kvalifikovaný odhad změn početnosti u řady druhů předmětem odborných sporů (Donald et al. 2008, Rodriguez-Munoz et al. 2008). V České republice existují dva projekty, jejichž výstupy umožňují odhadovat změny početnosti jednotlivých druhů naší avifauny: Mapování hnízdního rozšíření ptáků v ČR a Jednotný program sčítání ptáků v ČR (JPSP).

Mapování hnízdního rozšíření probíhá opakovaně v intervalech okolo 15 let a jeho cílem je zachytit rozšíření všech druhů ptáků, které na území ČR v dané době hnízdí (Šťastný et al. 1987, 1996, 2006). Rozsahem pokrývá celé státní území, které je překryto sítí stejně velkých kvadrátů o rozměrech cca 11×12 km. V každém kvadrátu je pořízen soupis hnízdících druhů s oceněním průkaznosti hnízdění a hrubým odhadem početnosti každého druhu. Ze síťového mapování lze tedy získat informaci nejen o rozšíření jednotlivých druhů ptáků (Storch & Šizling 2002), nýbrž i o druhovém bohatství (Storch et al. 2003a,b) a ornitologické významnosti různých částí ČR (Šťastný et al. 2006). Početnost druhu je určena na základě údajů z jednotlivých mapovacích čtverců a výsledků lokálních studií zaměřených na abundanci ptáků, případně na základě specializovaných výzkumů (např. u dravců a sov či chřástala polního, *Crex crex*). Porovnáním odhadu početnosti provedeného mezi dvěma mapováními hnízdního rozšíření lze zjistit změnu početnosti daného druhu za dobu, která mezi mapovacími akcemi uplynula (Voříšek et al. 2008b).

Síťové mapování vypovídá o české avifauně jako o celku, neboť zachycuje všechny druhy ptáků (Šťastný et al. 2006). Zejména u vzácných a řídce rozšířených druhů, které mohou jinak snadno uniknout pozornosti, je možné díky rovnoměrnému pokrytí celého státního území zmapovat v podstatě všechna jejich hnízdiště. Údaje o změnách početnosti takových druhů jsou proto velmi přesné a z hlediska jejich ochrany neocenitelné (Donald et al. 2007). Určitý problém však při zjišťování změn početnosti pomocí síťového mapování mohou představovat běžné druhy, které bývají přítomny téměř ve všech mapovacích čtvercích. Z dat, která se pomocí mapování shromáždí, se o změnách jejich početnosti dá usuzovat velmi obtížně: abundance je v jednotlivých kvadrátech odhadována do hrubých kategorií a široké rozšíření běžných druhů nedoznává v čase příliš významných změn (Webb et al. 2007). Skutečná změna početnosti může být přitom velmi výrazná.

JPSP se zjišťováním změn početnosti zabývá coby svou hlavní výzkumnou náplní (Reif et al. 2005). Projekt probíhá každoročně zhruba na 100 lokalitách ve všech částech republiky, zvláštní důraz se klade na standardizovanou metodiku zjišťování početnosti a zachování dlouhodobého charakteru výzkumu (Šťastný et al. 2004, Reif et al. 2006). Kvalita odhadu změn početnosti pomocí každoročního monitoringu silně závisí na množství dat, které se o daném druhu v jednotlivých letech shromáždí. Nastává zde tedy opačný problém než u síťového mapování – změny početnosti jsou nejlépe odhadnuty u hojných druhů a vypovídací hodnota s rostoucí vzácností druhu klesá.

Při sestavování odhadů změn početnosti ptáků se tedy nabízí využití informací z obou datových zdrojů. Pro odhady celkové početnosti jednotlivých druhů ptáků v ČR při síťovém mapování v letech 2001–2003 byly údaje z JPSP k dispozici pouze pro 58 druhů, a to pro období 1982–2003 (Šťastný et al. 2006). V současné době je možné vyjádřit změny početnosti pro všechny druhy, které byly v JPSP zaznamenány, a to pro libovolně definované období z intervalu 1982–2008.

Cílem této studie je spočítat změny početnosti na základě odhadů ze síťového mapování pro ty hojné druhy, které mají velmi kvalitní podklady z JPSP, a porovnat je se změnami zjištěnými v JPSP. Dalším cílem je zjistit, jak dobře spolu oba zdroje dat souhlasí, a detailněji rozebrat případy, kdy jsou změny zjištěné z mapovacích dat výrazně odlišné od změn zjištěných na základě JPSP.

MATERIÁL A METODIKA

Odhad změn početnosti na základě síťového mapování rozšíření ptáků v ČR byl proveden pomocí dat z posledních dvou mapovacích akcí, které proběhly v letech 1985–1989 a 2001–2003 (Šťastný et al. 1996, 2006). Terénní metodiku mapování podrobně popisují např. Šťastný et al. (1996, 2006). Při každém z těchto mapování byla terénními spolupracovníky v jednotlivých mapovacích čtvercích odhadnuta početnost každého hnízdícího druhu do kategorií na logaritmické škále o základu 5 (tj. 1–5 párů, 6–25, 26–125 atd.). Koordinátoři mapování pak z těchto údajů a dále pak z denzit jednotlivých druhů v publikovaných lokálních studiích a z výsledků práce specializovaných skupin provedli odhad maximální a minimální početnosti každého druhu v ČR pro dané mapovací období. V této práci jsme pro každé období (tj. 1985–1989 a 2001–2003) spočítali u jednotlivých druhů geometrický průměr z odhadu maximální a minimální početnosti. Z těchto průměrů jsme změnu početnosti mezi obdobími vyjádřili jako procentuální podíl početnosti v druhém období ku početnosti v prvním období.

Odhad změn početnosti na základě JPSP jsme provedli pro časový úsek 1987–2002. Začátek časové řady tedy spadá do prostředního roku prvního z porovnávaných síťových mapování, konec spadá do prostředního roku druhého mapování. Terénní metodika práce na JPSP je popsána v publikacích Šťastný et al. (2004) a Reif et al. (2006). Ve zkoumaném období probíhalo sčítání na celkem 184 lokalitách; na každé lokalitě byly dobrovolnými spolupracovníky jednou až třikrát za hnízdní sezónu sčítáni všichni vidění a slyšení ptáci standardizovanou bodovou metodou. Každý dobrovolný spolupracovník si mohl umístění své sčítací lokality libovolně vybrat. Pro celý časový úsek 1987–2002 jsme u každého druhu spočítali změny početnosti pomocí log-lineárních modelů ve statistickém programu TRIM, kdy byl zohledněn vliv roku a vliv lokality na meziroční změnu početnosti (Pannekoek & van Strien 2001). Pro každý druh byl spočítán index početnosti (v procentech) v každém roce časové řady vzhledem k prvnímu roku (tj. 1987), pro který byla početnost stanovena jako 100 %. Důležitým ukazatelem je průměrná meziroční změna početnosti, tzv. trend početnosti.

Např. hodnota trendu 1,04 nám říká, že velikost populace z roku na rok v průměru vzroste o 4 %. Počítá se jako exponenciální funkce směrnice regresní přímky proložené logaritmy ročních indexů (Pannekoek & van Strien 2001). Jako nejvhodnější ukazatel změny početnosti mezi rokem 1987 a 2002 pro účely srovnání s hodnotami odhadnutými na základě síťového mapování jsme zvolili tento:

$$\text{změna podle JPSP} = t^{\,2002-1987}, \qquad (1)$$

kde t je trend početnosti. Jedná se tedy vlastně o relativní změnu početnosti mezi prvním a posledním rokem časové řady, odhadnutou na základě průměrné meziroční změny početnosti v celé časové řadě (tj. tak, jak předpovídá regresní přímka). Tento ukazatel zobrazuje celkovou změnu početnosti lépe než prostý index početnosti pro rok 2002, neboť není tak náchylný k fluktuacím jako jednotlivé indexy.

Pro srovnání hodnot změn početnosti mezi síťovým mapováním a JPSP jsme vybrali 73 druhy, které byly podle Šťastného et al. (2006) v ČR nejpočetnější a pro které zároveň existovaly spolehlivé údaje o změnách početnosti na základě JPSP. Do výběru se nedostal žádný druh, jehož trend spočítaný z dat JPSP byl pro období 1987–2002 vyhodnocen jako „nejistý“ (ve smyslu klasifikace uvedené v článku Reifa et al., 2006), dále byly vyloučeny druhy sčítané na malém počtu lokalit a druhy, jejichž indexy početnosti meziročně kolísaly o více než 300 %.

Změny početnosti zjištěné pomocí síťového mapování jsme ke změnám početnosti, které byly zjištěné pomocí JPSP, vztáhli lineární regresí, kdy údaje ze síťového mapování představovaly vysvětlovanou proměnnou a údaje z JPSP proměnnou vysvětlující. Další srovnání jsme provedli pomocí rozřazování druhů do následujících kategorií změn početnosti: (i) ubývající, (ii) stabilní, (iii) přibývající. Ubývající druh na základě síťového mapování měl změnu početnosti nižší než 100 %, stabilní rovnou 100 % a přibývající vyšší než 100 %. Na základě JPSP byla pro rozřazení druhů použita upravená klasifikace trendů založená na jejich hodnotách a středních chybách, uvedená v článku Reifa et al. (2006). Pro účely této studie jsme jako ubývající druhy považovali druhy s trendy „mírně klesajícími“ nebo „strmě klesajícími“, jako stabilní s trendy„stabilními“ a jako přibývající druhy s trendy „mírně stoupajícími“ nebo „strmě stoupajícími“.

Autoři atlasu shrnujícího výsledky síťového mapování v letech 2001–2003 měli pro 51 druhů, které jsou zkoumány v této studii, k dispozici údaje o změnách početnosti zaznamenané pomocí JPSP v letech 1982–2003. U některých druhů byly pro stanovení početnosti v ČR pro období 2001–2003 tyto údaje využity, což se promítlo i do hodnot námi spočítaných změn početnosti na základě síťového mapování. Výše popsaná srovnání změn početnosti jsme proto provedli (i) pro všech 73 druhů, (ii) pouze pro druhy, u nichž údaje z JPSP byly v době tvorby atlasu k dispozici (n = 51), (iii) pouze pro druhy, u nichž údaje z JPSP v době tvorby atlasu k dispozici nebyly (n = 22).

VÝSLEDKY

Změny početnosti zjištěné na základě síťového mapování byly poměrně silně korelovány se změnami početnosti zjištěnými na základě JPSP ($r = 0{,}45$, $n = 73$, $p < 0{,}001$, $R^2 = 20\,\%$, obr. 1a). Vyřazením druhů, pro které byly k dispozici údaje z JPSP v době tvorby odhadů početnosti pro síťové mapování 2001–2003, se síla vztahu podstatně snížila ($r = 0{,}17$, $n = 22$, $p = 0{,}457$, $R^2 = 3\,\%$, obr. 1b). Samostatná analýza těchto vyřazených druhů nepříliš překvapivě ukázala mezi změnami početnosti ze síťového mapování a z JPSP velmi úzký vztah ($r = 0{,}64$, $n = 51$, $p < 0{,}001$, $R^2 = 42\,\%$, obr. 1c).

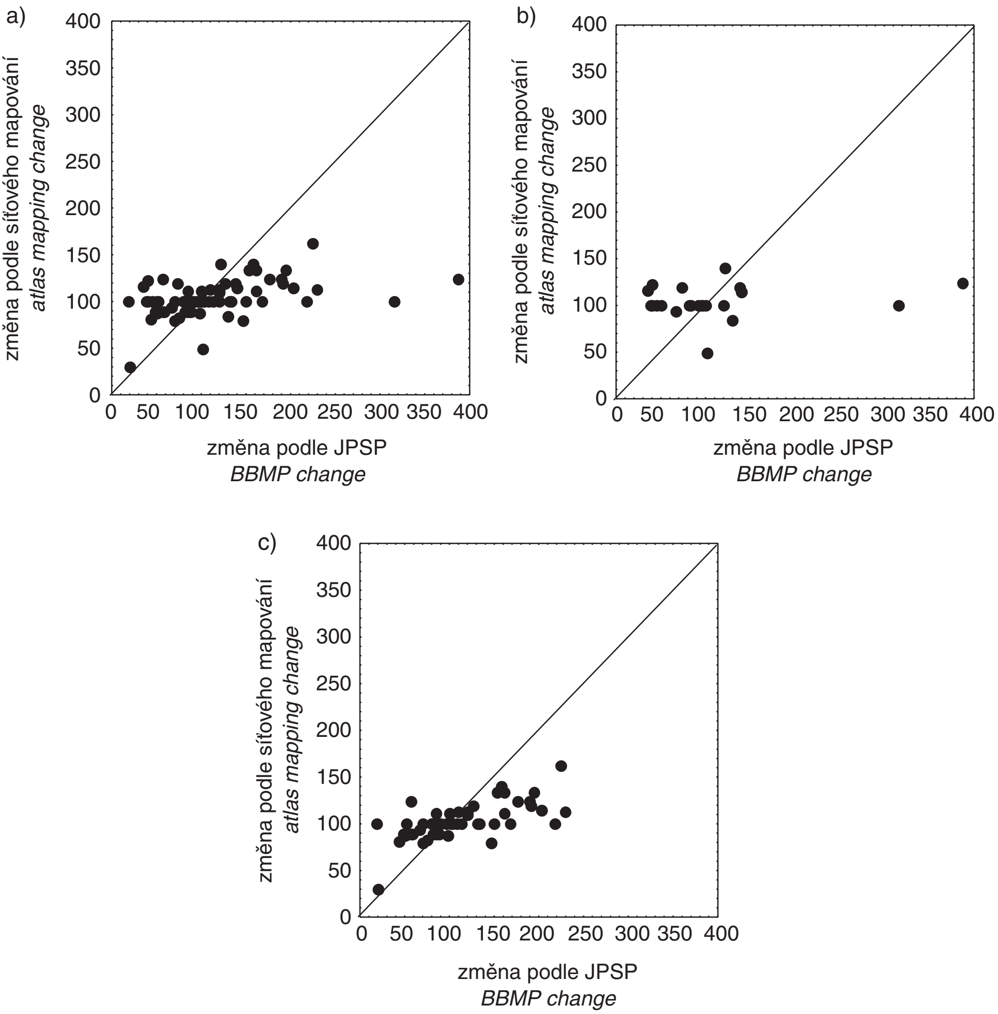
Kategorizace změn početnosti na základě síťového mapování souhlasila s kategorizací na základě JPSP u 62 % druhů (tab. 1a). Opět byla nižší míra shody (50 %) u druhů, pro které údaje z JPSP nebyly v období tvorby odhadů početnosti v letech 2001–2003 k dispozici (tab. 1b). Z těch druhů, u nichž se zdroje dat neshodovaly, byla ve 14 % případů kategorizace změn početnosti opačná, tj. síťové mapování signalizovalo úbytek, zatímco JPSP nárůst početnosti a naopak (tab. 1a).

Zaměříme-li se podrobněji na skupinu druhů, pro které údaje z JPSP nebyly v období tvorby odhadů početnosti v letech 2001–2003 k dispozici, je zajímavé, že u 11 druhů, na jejichž kategorizaci se porovnávané zdroje dat neshodovaly, data ze síťového mapování ukazovala výrazně častěji pozitivnější kategorie změny početnosti než data z JPSP – stalo se tak u 9 druhů (tab. 1b). Z těchto 9 druhů 7 podle JPSP ubývalo, zatímco síťové mapování signalizovalo nárůst početnosti či její stabilitu; zbývající dva druhy měly podle JPSP stabilní početnost, zatímco síťové mapování ukazovalo její nárůst (tab. 1b).

U druhů, pro které údaje z JPSP byly při síťovém mapování v letech 2001–2003 k dispozici, se obě klasifikace shodovaly ze dvou třetin (67 %, tab. 1c). Podíl druhů s opačně klasifikovanými změnami početnosti byl velmi nízký – pouze necelá 4 % (tab. 1c). Žádný ze zdrojů dat tentokrát neklasifikoval změny početnosti ptáků výrazně pozitivněji či negativněji než druhý zdroj dat (u 18 % bylo pozitivnější síťové mapování, u 16 % JPSP) (tab. 1c).

DISKUSE

Změny početnosti hojných druhů ptáků odhadnuté na základě síťových mapování v letech 1985–1989 a 2001–2003 poměrně dobře odpovídaly změnám početnosti spočítaným z JPSP pro období 1987–2002. Tato shoda však byla do značné míry způsobena tím, že u velké části druhů byly údaje z JPSP zohledněny již při oceňování početnosti v období druhého z pojednávaných síťových ma-



Obr. 1. Vztah změn početnosti (v %) 73 druhů ptáků spočítaných na základě Jednotného programu sčítání ptáků v ČR (změna podle JPSP) mezi roky 1987 a 2002 a na základě Mapování hnízdního rozšíření ptáků v ČR (změna podle síťového mapování) mezi obdobími 1985–1989 a 2001–2003. Zvlášť jsou uvedeny změny pro všechny zkoumané druhy ptáků (a), změny pro druhy, jejichž údaje z JPSP nebyly pro zpracování síťového mapování použity (b) a změny pro druhy, jejichž údaje z JPSP byly pro zpracování síťového mapování použity (c). Přímka v obrázku zobrazuje shodné hodnoty změn početnosti. Podrobnosti k výpočtu změny početnosti jsou uvedeny v oddíle Materiál a metodika.

Fig. 1. *Relationship between population changes (%) in 73 bird species calculated using data from the Breeding Bird Monitoring Programme in the Czech Republic (BBMP change) between 1987 and 2002 and using data from the mapping of breeding bird distribution in the Czech Republic (atlas mapping change) between 1985–1989 and 2001–2003. Separate figures are given (a) for all species, (b) for species in which the BBMP data did not exist at the time of atlas mapping, and (c) for species in which the BBMP data existed at the time of atlas mapping. Note the identity line in the figure. See Methods for more details on population change calculation.*

Tab. 1. Počty druhů ptáků jednotlivých kategoriích změny početnosti. Změna početnosti byla spočítána jednak na základě Jednotného programu sčítání ptáků v ČR (JPSP) mezi roky 1987 a 2002 a jednak na základě Mapování hnízdního rozšíření ptáků v ČR (síťové mapování) mezi obdobími 1985–1989 a 2001–2003. Podle zjištěné změny početnosti byly druhy klasifikovány jako ubývající, stabilní nebo přibývající. Zvlášť jsou uvedeny všechny zkoumané druhy ptáků (a), druhy, jejichž údaje z JPSP nebyly pro zpracování síťového mapování použity (b), druhy, jejichž údaje z JPSP byly pro zpracování síťového mapování použity (c). Počty druhů klasifikovaných stejně podle síťového mapování i JPSP jsou zvýrazněny. Podrobnosti k výpočtu změny početnosti a její klasifikaci jsou uvedeny v oddíle Materiál a metodika.
Table 1. *Numbers of bird species in particular categories of population change. Population change was calculated using data from the Breeding Bird Monitoring Programme in the Czech Republic (BBMP) between 1987 and 2002 and using data from the mapping of breeding bird distribution in the Czech Republic (atlas mapping) between 1985–1989 and 2001–2003. Species were classified as decreasing, stable or increasing, respectively, according to revealed population change. Separate tables are given (a) for all species, (b) for species in which the BBMP data did not exist at the time of atlas mapping, and (c) for species in which the BBMP data existed at the time of atlas mapping. Numbers of species classified into the same category according to both BBMP and atlas mapping data are in bold. See Methods for more details on population change calculation and species' classification.*

a)	ubývá podle JPSP *BBMP – declining*	stabilní podle JPSP *BBMP – stable*	přibývá podle JPSP *BBMP – increasing*
ubývá podle síťového mapování *Atlas mapping – declining*	**14**	2	2
stabilní podle síťového mapování *Atlas mapping – stable*	9	**17**	6
přibývá podle síťového mapování *Atlas mapping – increasing*	3	6	**14**

b)	ubývá podle JPSP *BBMP – declining*	stabilní podle JPSP *BBMP – stable*	přibývá podle JPSP *BBMP – increasing*
ubývá podle síťového mapování *Atlas mapping – declining*	**1**	0	1
stabilní podle síťového mapování *Atlas mapping – stable*	5	**7**	1
přibývá podle síťového mapování *Atlas mapping – increasing*	2	2	**3**

c)	ubývá podle JPSP *BBMP – declining*	stabilní podle JPSP *BBMP – stable*	přibývá podle JPSP *BBMP – increasing*
ubývá podle síťového mapování *Atlas mapping – declining*	**13**	2	1
stabilní podle síťového mapování *Atlas mapping – stable*	4	**10**	5
přibývá podle síťového mapování *Atlas mapping – increasing*	1	4	**11**

pování. Samostatná analýza druhů, pro které údaje z JPSP v době analýzy mapovacích dat nebyly autorům mapování k dispozici, ukázala, že oba zdroje dat hodnotí změny početnosti těchto druhů velmi rozdílně. Zatímco ocenění pomocí tří kategorií změn početnosti ukázalo 50%-ní míru shody, kvantitativní rozdíly byly podstatně větší – v lineární regresi spolu změny početnosti zjištěné na základě JPSP a změny početnosti ze síťového mapování v podstatě nesouvisely.

Vezmeme-li v úvahu, že jsme pro účely této studie vybrali 73 druhy, pro které jsou data JPSP nejspolehlivější, je pravděpodobné, že většina neshod bude způsobena spíše nedokonalostí odhadů velikosti ptačích populací na základě síťového mapování než špatnými údaji v JPSP. Proč tedy data ze síťového mapování poskytují nepřesný obraz o početnosti hojných ptačích druhů? Existuje několik možných vysvětlení. Terénní spolupracovníci údajům o početnosti jednotlivých druhů ve zpracovávaných kvadrátech věnují méně pozornosti než prokazování jejich hnízdění – zatímco údaje o průkaznosti hnízdění existují ze všech 628 mapovacích kvadrátů, údaje o početnosti u mnoha, zejména hojných druhů, ve velké části kvadrátů chybějí. I když je početnost daného druhu v kvadrátu spolupracovníkem odhadnuta a údaj je zaslán koordinátorům mapování, nemusí uvedená hodnota početnosti zachytit její změnu ve srovnání s minulým mapováním. To může být způsobeno jednak hrubostí stupnice sloužící pro odhad počtu párů (např. změna početnosti o 20 % se nemusí v údaji na mapovací kartě vůbec projevit), ale i lidským faktorem. Řada oblastí byla v různých obdobích síťového mapování zpracovávána různými spolupracovníky (srov. Šťastný et al. 1996 a Šťastný et al. 2006). Ovšem i stejný pozorovatel si při mapovací práci nemusí změny početnosti hojného druhu, který je téměř všudypřítomný, vůbec povšimnout: druhy jako kos černý (*Turdus merula*) či pěnkava obecná (*Fringilla coelebs*) jsou stále extrémně hojné, přitom se podle JPSP početnost každého z nich velmi výrazně změnila. Tento fenomén může být varující z ochranářského hlediska, kdy snížení početnosti bývá zaznamenáno až při drastickém úbytku dříve hojného druhu, kdy může být na přijetí účinných ochranných opatření již pozdě (Gaston & Fuller 2008): známý je případ holuba stěhovavého (*Ectopistes migratorius*) – Halliday (1980), v našich podmínkách byl téměř podobně postižen chocholouš obecný (*Galerida cristata*) – Línek (1999), v dnešní době k tomu má blízko např. čejka chocholatá (*Vanellus vanellus*) – Šálek (2000), Reif et al. (2008).

Je zajímavé, že JPSP zaznamenal u řady druhů úbytek početnosti, přičemž síťové mapování odhadovalo stabilní nebo rostoucí populace, případně JPSP signalizoval stabilní početnost, zatímco síťové mapování odhadovalo její nárůst. Opačných případů, kdy síťové mapování ukazovalo negativnější změny početnosti než JPSP, bylo přitom podstatně méně. Zdá se tedy, že síťové mapování může poskytovat optimističtější obraz o vývoji početnosti hojných druhů ptáků než k jakému ve skutečnosti dochází. Z našeho souboru druhů toto bylo zjištěno např. u koroptve polní (*Perdix perdix*), pěvušky modré (*Prunella modularis*), pěnice slavíkové (*Sylvia borin*), králíčka obecného (*Regulus regulus*), sýkory parukářky (*Lophophanes cristatus*), zvonohlíka zahradního (*Serinus serinus*) nebo kavky obecné (*Corvus monedula*). Poslední jmenovaný případ, coby koloniální druh bez výrazné zpěvní aktivity, je nutné brát s jistou rezervou, protože JPSP nemusí jeho početnost zachytit zcela dostatečně. O možném vysvětlení tohoto jevu je těžké spekulovat, nicméně samotná jeho existence je minimálně u některých ze zmíněných druhů zásadní z hlediska ochrany přírody. Kavka obecná a koroptev polní jsou zvláště chráněné druhy a hodnocení změn jejich početnosti může mít vliv na oceňování účinnosti zákonné ochrany (Voříšek et al. 2008b). Naše výsledky ukazují, že v případě použití dat ze síťového mapování bez zohlednění dalších dostupných zdrojů může být takové hodnocení příliš optimistické. Pozitivnější odhad změn početnosti, než k jakým ve skutečnosti došlo, může také vyústit v nedostatečnou pozornost ze strany badatelů, která by odhalila příčiny úbytku zájmových druhů (Mace et al. 2008). Z námi hodnocených druhů se toto může týkat např. pěvušky modré, sýkory parukářky a zvonohlíka zahradního.

Data z JPSP ovšem nemusí být zcela přesná ani u námi zkoumaného souboru druhů. Vývoj početnosti lindušky luční (*Anthus pratensis*) – úbytek podle JPSP, nárůst podle síťového mapování – nebo křivky obecné (*Loxia curvirostra*) – úbytek podle JPSP, nárůst podle síťového mapování – může být lépe podchycen síťovým mapováním než každoročním monitoringem. První druh je rozšířen zejména ve vyšších polohách v pohraničních oblastech (Šťastný et al. 2006), které transekty JPSP nepokrývají tak kvalitně jako zbytek území ČR (viz http://jpsp.birds.cz/vysledky.php?menu=loc_map). Početnost druhého druhu zase doznává značných meziročních výkyvů (Förschler et al. 2006) a termíny sčítání v rámci JPSP vůbec nemusí jeho hnízdní populace zachytit. Kromě těchto výjimek jsou však údaje z JPSP velmi pravděpodobně spolehlivé.

Jako optimální řešení pro určení změn početnosti našich ptáků se nám jeví kombinace obou zdrojů dat. Při konstrukci celkových odhadů početnosti pomocí síťového mapování lze zohlednit změny početnosti spočítané na základě JPSP. Tento přístup byl již při tvorbě odhadů pro mapovací období 2001–2003 využit, ovšem k dispozici byly údaje pouze pro 58 druhů (Šťastný et al. l.c.). Krom toho období 1982–2003, pro které byly změny početnosti z dat JPSP vyjádřeny, neodpovídalo úplně mapovacím periodám (1985–1989 a 2001–2003). Celkový trend početnosti pro roky 1982–2003 tedy mohl být z pohledu síťových mapování mírně zavádějící, každoroční indexy početnosti mohou být zase často velmi rozkolísané. Tyto faktory by mohly vysvětlovat námi zjištěný mírný nesouhlas mezi síťovým mapováním a údaji JPSP u druhů, kde data z JPSP byla v době tvorby odhadů početnosti pro roky 2001–2003 jejich autorům k dispozici. Doporučujeme tedy při využití dat JPSP vždy znovu spočítat změny početnosti z primárních údajů přesně pro zájmovou periodu a nepoužívat publikované výsledky s údaji pro jiné období.

Závěrem lze říci, že podle výsledků naší studie jsou u hojných druhů ptáků údaje z JPSP pouze obtížně nahraditelné a odhady změn početnosti, které data JPSP nezohlední, mohou být zavádějící. Kvalita dat JPSP je přímo úměrná počtu sčítaných transeptů; je proto velmi žádoucí, aby tento počet byl co nejvyšší a do práce na projektu se zapojila co největší část odborné ornitologické veřejnosti. Jenom tímto způsobem bude možné dostatečně věrohodně zjistit, jak se mění početnost našich ptáků a z těchto zjištění vycházet při jejich dalším studiu či ochraně.

PODĚKOVÁNÍ

Děkujeme tisícům ornitologů, kteří se zúčastnili Mapování hnízdního rozšíření ptáků v ČR a Jednotného programu sčítání ptáků v ČR. Bez jejich nezištného úsilí by tato studie nemohla být zpracována. Dva anonymní recenzenti naznačili zajímavé možnosti vylepšení rukopisu. Výzkum byl podporován granty GAČR (206/97/0771 a 206/04/1254) a GAAV ČR (KJB601110919).

SUMMARY

Accurate estimates of bird population changes are important for basic research of avian ecology as well as for setting priorities in bird conservation. For instance, abundance of the species is in interaction with its life-history strategy, and the rate of population change is the most important criterion in assessment of the species' threat status. Rates of population change can be estimated using mapping of breeding bird distribution if the data on the species' abundance in particular mapping squares are collected simultaneously with the information about their breeding status. Results of such mapping are often published in distribution atlases. However, it is very difficult to estimate population changes in common species with countrywide distribution when based on atlas mapping only. We expected that data from annual monitoring of breeding bird populations produce more accurate estimates in such common species.

We expressed population changes between the last two periods of atlas mapping in the Czech Republic (i.e. 1985–1989 and 2001–2003) in 73 species (i) using population size estimates published in the distribution atlases corresponding to these mapping periods, and (ii) using data from the annual Breeding Bird Monitoring Programme (BBMP). They are the most abundant species for which good quality BBMP data are available at the same time. Population changes from the BBMP data were calculated using log-linear models in the TRIM software for the time series of 1987–2002. Together with quantitative estimates of population changes we classified all species into three categories of population change recognizing increasing species, stable species and decreasing species, respectively. The categorisation was performed independently for each data source. The species were further sorted into two groups: (i) species for which BBMP data were available during the atlas work (n = 51), and (ii) species for which BBMP data were not available during the atlas work (n = 22).

Population changes calculated from atlas mapping well corresponded to population changes calculated from BBMP (Fig. 1a). However, such good fit was caused by the species for which BBMP data were available during the atlas work (Fig. 1c). We did not reveal any relationship between atlas-based population changes and BBMP-based population changes in the species for which BBMP data were not available during the atlas work (Fig. 1b). Moreover, in the latter species the classification into the categories of population change was more positive when based on atlas mapping than on BBMP (Table 1b). Specifically, some species declining according to BBMP were classified as stable or increasing using atlas data and species with no population change according to BBMP were classified as increasing using atlas data (Table 1b). Examples include species of conservation concern such as Grey Partridge (Perdix perdix) *or Eurasian Jackdaw* (Corvus monedula*) as well as very common species such as Chaffinch* (Fringilla coelebs)*, Hedge Accentor* (Prunella modularis)*, Crested Tit* (Parus cristatus) *or European Serin* (Serinus serinus).

Based on these results, we recommend that BBMP data should be taken in account in studies dealing with long-term

population changes of common birds. Neglecting BBMP data may result in flawed assessment of population status in a substantial part of the Czech bird fauna. From the conservation perspective, it is very important to track the first signs of decline even in very common species as their decline rate may be accelerating in the future. It might be too late for conservation actions when such species become rare. We also recommend that BBMP results should be included into procedures of population size estimates based on atlas data. For this purpose, it is important to calculate population trends from BBMP for appropriate time intervals.

LITERATURA

Bibby C. J., Burgess N. D., Hill D. A. & Mustoe S. H. 2000: Bird census techniques. *Academic Press, London.*

Donald P. F., Sanderson F. J., Burfield I. J., Bierman S. M., Gregory R. D. & Waliczky Z. 2007: International conservation policy delivers benefits for birds in Europe. *Science 317: 810–813.*

Donald P. F., Sanderson F. J., Burfield I. J., Bierman S. M., Gregory R. D. & Waliczky Z. 2008: Response to Comment on International conservation policy delivers benefits for birds in Europe. *Science 319: doi 10.1126/science.1151939.*

Förschler M. I., Förschler L. & Dorka U. 2006: Population fluctuations of siskins *Carduelis spinus*, common crossbills *Loxia curvirostra*, and citril finches *Carduelis citrinella* in relationship to flowering intensity of spruce *Picea abies*. *Ornis Fennica 83: 91–96.*

Gaston K. J. & Fuller R. A. 2008: Commonness, population depletion and conservation biology. *Trends Ecol. Evol. 23: 14–19.*

Gregory R. D., Voříšek P., Noble D. G., van Strien A., Klvaňová A., Eaton M., Gmelig Meyling A. W., Joys A., Foppen R. P. B. & Burfield I. J. 2008: The generation and use of bird population indicators in Europe. *Bird Conserv. Int. 18: S223–S244.*

Halliday T. R. 1980: Extinction of the Passenger Pigeon *Ectopistes migratorius* and its relevance to contemporary conservation. *Biol. Conser. 17: 157–162.*

Línek V. 1999: Rozšíření a početnost chocholouše obecného v Praze. *Sylvia 35: 69–81.*

Mace G.M., Collar N.J., Gaston K.J., Hilton-Taylor C., Akcakaya H. R., Leader-Williams N., Milner-Gulland E.J. & Stuart S. N. 2008: Quantification of extinction risk: IUCN's system for classifying threaned species. *Conserv. Biol. 22: 1424–1442.*

Newton I. 1998: Population limitation in birds. *Academic Press, London.*

Pannekoek J. & van Strien A. 2001: TRIM 3 manual. *Statistics Netherlands, Voorburg.*

Purvis A., Mace G. M. & Jones K. E. 2000: Extinction. *BioEssays 22: 1123–1133.*

Reif J., Šťastný K., Bejček V. & Voříšek P. 2005: Jednotný program sčítání ptáků v České republice: současný stav a perspektivy. *Zprávy ČSO 60: 56–61.*

Reif J., Voříšek P., Šťastný K. & Bejček V. 2006: Trendy početnosti ptáků v České republice v letech 1982–2005. *Sylvia 42: 22–37.*

Reif J., Voříšek P., Šťastný K., Bejček V. & Petr J. 2008: Agricultural intensification and farmland birds: new insights from a central European country. *Ibis 150: 596–605.*

Rodriguez-Munoz R., Ojanguren A. F. & Tregenza T. 2008: Comment on International conservation policy delivers benefits for birds in Europe. *Science 319: doi 10.1126/science.1151810.*

Storch D., Konvička M., Beneš J., Martinková J. & Gaston K. J. 2003a: Distribution patterns in butterflies and birds of the Czech Republic: separating effects of habitat and geographical position. *J. Biogeogr. 30: 1195–1205.*

Storch D. & Šizling A. L. 2002: Patterns of commonness and rarity in central European birds: reliability of the core-satellite hypothesis within a large scale. *Ecography 25: 405–416.*

Storch D., Šizling A. L. & Gaston K. J. 2003b: Geometry of the species-area relationship in central European birds: testing the mechanism. *J. Anim. Ecol. 72: 509–519.*

Šálek M. 2000: Čejka chocholatá (*Vanellus vanellus*). *Sylvia 36: 51–52.*

Šťastný K., Bejček V. & Hudec K. 1996: Atlas hnízdního rozšíření ptáků v České republice 1985–1989. *H & H, Jinočany.*

Šťastný K., Bejček V. & Hudec K. 2006: Atlas hnízdního rozšíření ptáků v České republice. *Aventinum, Praha.*

Šťastný K., Bejček V., Voříšek P. & Flousek J. 2004: Populační trendy ptáků lesní a zemědělské krajiny v České republice v letech 1982–2001 a jejich využití jako indikátorů. *Sylvia 40: 27–48.*

Šťastný K., Randík A. & Hudec K. 1987: Atlas hnízdního rozšíření ptáků v ČSSR 1973/77. *Academia, Praha.*

Tuljapurkar S., Steiner U. K. & Orzak S. H. 2009: Dynamic heterogeneity in life histories. *Ecol. Lett. 12: 93–106.*

Veselovský Z. 2001: Obecná ornitologie. *Academia, Praha.*

Voříšek, P., Klvaňová A., Wotton S. & Gregory R. D. (eds) 2008a: A best practice guide for wild bird monitoring schemes. *RSPB, Cambridge.*

Voříšek P., Reif J., Šťastný K. & Bejček V. 2008b: How effective can be the national law in protecting birds? A case study from the Czech Republic. *Folia Zool. 57: 221–230.*

Webb T. J., Noble D & Freckleton R. P. 2007: Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *J. Anim. Ecol. 76: 123–134.*

Apendix: Změny početnosti (v %, zaokrouhleno na celá čísla) u 73 druhů ptáků spočítané na základě Jednotného programu sčítání ptáků v ČR (Změna podle JPSP) mezi roky 1987 a 2002 a na základě Mapování hnízdního rozšíření ptáků v ČR (Změna podle atlasu) mezi obdobími 1985–1989 a 2001–2003. Podle zjištěné změny početnosti byly druhy klasifikovány jako ubývající, stabilní nebo přibývající. U 51 druhu byly údaje z JPSP koordinátorům síťového mapování k dispozici (JPSP k dispozici – ano), u 22 druhu nikoliv (JPSP k dispozici – ne). Podrobnosti k výpočtu změny početnosti a její klasifikaci jsou uvedeny v oddíle Materiál a metodika.
Appendix: *Population changes (%, rounded to integer) in 73 bird species in the Czech Republic. Population change was calculated using data from the Breeding Bird Monitoring Programme in the Czech Republic (BBMP change) between 1987 and 2002 and using data from the mapping of breeding bird distribution in the Czech Republic (Atlas mapping change) between 1985–1989 and 2001–2003. The species were classified as decreasing (ubývající), stable (stabilní) or increasing (přibývající), respectively, according to revealed population change. For 51 species the BBMP data existed at the time of atlas mapping (BBMP existed – ano), for 22 did not (BBMP existed – ne). See Methods for more details on population change calculation and species' classification.*

druh	JPSP k dispozici	změna podle JPSP	kategorie podle JPSP	změna podle atlasu	kategorie podle atlasu
species	*BBMP existed*	*BBMP change*	*BBMP category*	*Atlas mapping change*	*Atlas mapping category*
Buteo buteo	ano	161	přibývající	112	přibývající
Falco tinnunculus	ano	133	stabilní	100	stabilní
Perdix perdix	ne	40	ubývající	122	přibývající
Phasianus colchicus	ne	102	stabilní	50	ubývající
Vanellus vanelllus	ano	20	ubývající	30	ubývající
Columba oenas	ne	386	přibývající	125	přibývající
Columba palumbus	ano	176	přibývající	125	přibývající
Streptopelia decaocto	ne	129	přibývající	85	ubývající
Streptopelia turtur	ano	75	ubývající	83	ubývající
Cuculus canorus	ano	96	stabilní	100	stabilní
Apus apus	ne	94	stabilní	100	stabilní

druh *species*	JPSP k dispozici *BBMP existed*	změna podle JPSP *BBMP change*	kategorie podle JPSP *BBMP category*	změna podle atlasu *Atlas mapping change*	kategorie podle atlasu *Atlas mapping category*
Picus viridis	ano	217	přibývající	100	stabilní
Dryocopus martius	ano	195	přibývající	133	přibývající
Dendrocopos major	ano	119	přibývající	110	přibývající
Alauda arvensis	ano	98	stabilní	88	ubývající
Hirundo rustica	ano	69	ubývající	80	ubývající
Delichon urbica	ne	119	stabilní	100	stabilní
Anthus trivialis	ano	56	ubývající	90	ubývající
Anthus pratensis	ne	34	ubývající	117	přibývající
Motacilla cinerea	ne	81	stabilní	100	stabilní
Motacilla alba	ano	58	ubývající	90	ubývající
Troglodytes troglodytes	ano	125	přibývající	120	přibývající
Prunella modularis	ano	56	ubývající	125	přibývající
Erithacus rubecula	ano	101	stabilní	100	stabilní
Phoenicurus ochruros	ne	91	stabilní	100	stabilní
Phoenicurus phoenicurus	ano	224	přibývající	163	přibývající
Turdus merula	ano	133	přibývající	100	stabilní
Turdus pilaris	ne	140	přibývající	114	přibývající
Turdus philomelos	ano	109	stabilní	100	stabilní
Turdus viscivorus	ano	202	přibývající	114	přibývající
Locustella naevia	ne	73	stabilní	120	přibývající
Locustella fluviatilis	ne	96	stabilní	100	stabilní
Acrocephalus palustris	ne	99	stabilní	100	stabilní
Acrocephalus scirpaceus	ne	40	ubývající	100	stabilní
Hippolais icterina	ano	84	stabilní	90	ubývající
Sylvia curruca	ne	138	přibývající	120	přibývající
Sylvia communis	ano	85	stabilní	111	přibývající
Sylvia borin	ne	83	ubývající	100	stabilní
Sylvia atricapilla	ano	160	přibývající	133	přibývající
Phylloscopus sibilatrix	ano	50	ubývající	88	ubývající
Phylloscopus collybita	ano	109	stabilní	113	přibývající
Phylloscopus trochilus	ano	48	ubývající	90	ubývající
Regulus regulus	ano	52	ubývající	100	stabilní
Regulus ignicapillus	ne	121	stabilní	140	přibývající
Muscicapa striata	ano	152	přibývající	133	přibývající
Ficedula albicollis	ano	157	přibývající	140	přibývající
Aegithalos caudatus	ano	43	ubývající	82	ubývající
Poecile montanus	ano	80	stabilní	100	stabilní
Lophophanes cristatus	ne	38	ubývající	100	stabilní
Periparus ater	ano	100	stabilní	111	přibývající
Cyanistes caeruleus	ano	114	stabilní	100	stabilní
Parus major	ano	102	stabilní	100	stabilní
Sitta europaea	ano	130	přibývající	100	stabilní
Certhia familiaris	ano	167	přibývající	100	stabilní

druh *species*	JPSP k dispozici *BBMP existed*	změna podle JPSP *BBMP change*	kategorie podle JPSP *BBMP category*	změna podle atlasu *Atlas mapping change*	kategorie podle atlasu *Atlas mapping category*
Oriolus oriolus	ano	149	přibývající	100	stabilní
Lanius collurio	ano	192	přibývající	120	přibývající
Garrulus glandarius	ano	229	přibývající	113	přibývající
Pica pica	ano	189	přibývající	125	přibývající
Corvus monedula	ano	18	ubývající	100	stabilní
Corvus corone	ano	70	ubývající	100	stabilní
Sturnus vulgaris	ano	119	stabilní	113	přibývající
Passer domesticus	ne	67	ubývající	93	ubývající
Passer montanus	ano	147	přibývající	80	ubývající
Fringilla coelebs	ano	84	ubývající	100	stabilní
Serinus serinus	ne	50	ubývající	100	stabilní
Carduelis chloris	ano	81	ubývající	90	ubývající
Carduelis carduelis	ano	89	stabilní	100	stabilní
Carduelis cannabina	ano	82	stabilní	100	stabilní
Carduelis flammea	ne	316	přibývající	100	stabilní
Loxia curvirostra	ne	45	ubývající	100	stabilní
C. coccothraustes	ano	67	ubývající	93	ubývající
Emberiza citrinella	ano	89	ubývající	90	ubývající
Emberiza schoeniclus	ano	80	stabilní	100	stabilní

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Paper II

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Relationships between winter temperature and breeding bird abundance on community level: importance of interspecific differences in diet

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Abstract. Winter weather limits populations of resident bird species. Although many small-scale or species-specific studies illustrated this fact, our knowledge of interspecific differences in population responses to winter temperatures is incomplete due to lack of community-level studies. For this purpose, we have used long-term monitoring data on breeding bird populations of 37 common bird species wintering in the Czech Republic. We predicted that species will differ in their relationship between winter temperature and abundance with respect to their body mass and dietary niche. Smaller species having relatively higher energy expenditure should show closer relationship between breeding abundance and winter temperature than larger species. Concerning dietary niche, abundance of species feeding on animals should be more affected by temperature than abundance of species feeding on plants or omnivorous species. Our results confirmed the second prediction: populations of species preying on animals followed winter temperatures more closely than populations of species feeding on both animals and plants. Food-mediated mortality is probably more important than direct effects of low temperatures. In general, relationships between abundance and temperature were relatively weak in most species and we suggest that possible changes in winter temperatures may not seriously affect populations of common breeding birds in the Czech Republic.

Key words: climate, food type, body size, abundance, bird assemblage, population regulation

Introduction

Harsh winter weather strongly affects populations of resident bird species and there are several ways to such density regulation (Newton 1998). First, low temperatures can directly kill individuals that are not able to adjust their thermal regulation to conditions of higher energetic demands (Bakken et al. 1991). Second, birds' food requirements increase in colder periods to cover higher energy expenditure needed to keep body temperature constant. Under conditions of food shortage, some bird individuals are not able to satisfy their energy demands and they die due to lack of food (Lahti et al. 1998, Robison et al. 2007). Food accessibility might be lower in winter either due to low temperatures when the prey is hidden in refuges to prevent freezing or due to snow or ice cover (Rolstad & Rolstad 2000). Therefore, breeding abundance of many resident bird species is dependent to large extent on weather conditions in the preceding winter (Newton 1998). For this reason, temperature in winter months became an integral part of models predicting species' responses to global climatic changes in terms of distributional shifts (Huntley et al. 2007, Doswald et al. 2009).

Although these models do not discriminate among species-specific ecological characteristics (but see Doswald et al. 2009), we suggest that population

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response to winter climate does need not to be universal within resident bird species.

Empirical studies of the relationships between population abundance and climatic conditions are not very common on community level (Jones et al. 2003). Most of the current knowledge is based on studies performed on species level in local scale (e.g. Holmes et al. 1986, Virkkala 2004) showing adverse effects of harsh winters on selected resident species due to lower food supply or temperature-mediated mortality (Lahti et al. 1998, Newton et al. 1998, Sæther et al. 2000, Robinson et al. 2007, Siriwardena et al. 2007). Climatic conditions in the Czech Republic, a central European country situated in transition zone between oceanic and continental climate (Tolasz et al. 2007), offer good opportunity to explore the effects of winter temperature variation on bird populations. Due to occurrence of both harsh and mild winters we can expect remarkable variation in bird populations caused by annual fluctuations of climatic conditions. Moreover, long tradition of annual monitoring of bird populations in this country (Janda & Šťastný 1984) provided high quality data on breeding abundance for number of species enabling a community level analysis (Reif et al. 2006).

For such an analysis, we have selected species with high proportion of individuals staying on breeding grounds during winter (Cepák et al. 2008). We have related breeding abundance of each species to average temperature of the preceding winter to express its dependence on winter weather. We have predicted that the species would differ in responses of their populations to winter weather due to the influence of ecological differences among species. First, efficiency of thermal regulation increases with body mass (Aschoff 1981, Meehan et al. 2004). Therefore, we expected that abundance of larger species would follow changes in temperature less closely than abundance of smaller species. Second, the effects of temperature might act through food supply (Lahti et al. 1998, Robinson et al. 2007). We can expect that species with different dietary niches would differ in dependence of their abundance on winter temperature. Accessibility of seeds and other plant tissues should be less dependent on temperature compared to the food of animal predators because their prey can actively hide in places enabling survival during the period of low temperatures (Avery & Krebs 1984, Carrascal et al. 2001, Zmihorski & Rejt 2007). Therefore, we can predict that abundance of species feeding on animals (carnivores and insectivores) should be more affected by temperature than abundance of species feeding on plants (e.g. seed-eaters) or omnivorous species. The aim of this paper was to test these two predictions using Czech bird monitoring data.

Material and Methods

Data

We used data from the Breeding Bird Monitoring Programme (BBMP) for the assessment of breeding bird population changes between 1982 and 2007 in the Czech Republic. BBMP is a large-scale generic bird monitoring scheme based on fieldwork of skilled volunteers (Janda & Šťastný 1984, Reif et al. 2006). 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). Standardized point counts are used as a field method with 20 points visited two times per breeding season (to detect both early and late breeding species) at each census site. During one visit, all birds seen or heard were recorded for five minutes on each census point. In each year, abundance of a species at a given census site was calculated as the mean number of individuals from both visits (see Reif et al. 2007, 2008a for more details on field methods).

Wintering of bird species in the Czech Republic was assessed using information from the Atlas of bird migration in the Czech Republic and Slovakia (Cepák et al. 2008) based on all known ringing recoveries until 2002. For purposes of this study, we have selected 37 species with more than 75% of Czech breeding population wintering on the territory of the country (Cepák et al. 2008) and having good record in BBMP data at the same time (see Reif et al. 2008b). For these species (Table 1), we have obtained information about their body mass from local ornithological monographs (Hudec 1983, 1994, Hudec & Šťastný 2005) and about their winter diet from Bejček et al. (1995). We have recognized following categories of species' dietary niche: species feeding on animals (n = 9, three carnivorous species and six insectivorous), species feeding on both animals and plants (n = 15, including four omnivorous corvids), species feeding on plants only (n = 13, all but one were seed-eaters).

Winter temperatures were supplied by the Czech Hydrometeorological Institute as monthly means for December, January and February in each year from 1982 to 2007 (Table 1). Temperatures were positively correlated across years among all months but the correlation coefficients were relatively low and only one relationship was significant ($r_{\mathrm{December–January}} = 0.46$, $P = 0.018$, $r_{\mathrm{December–February}} = 0.22$, $P = 0.286$, $r_{\mathrm{January–February}} = 0.28$, $P = 0.166$, $N = 26$ in all cases). Therefore, particular months were treated separately in following analyses.

Table 1. *Mean temperatures in particular winter months (December, January, February) in the Czech Republic measured from 1982 to 2007. Note that December temperatures were measured in the preceding calendar year (i.e. in December 1981 for the winter 1982 etc).*

Winter	December	January	February
1982	-3.1	-5.3	-2.1
1983	0.8	2.4	-3.2
1984	-1.2	-1.0	-1.7
1985	-0.8	-7.8	-5.6
1986	1.8	-1.6	-7.4
1987	-0.6	-7.9	-1.8
1988	0.5	1.3	0.9
1989	1.0	-0.2	2.5
1990	0.2	-0.3	3.6
1991	-1.0	-0.2	-4.5
1992	-2.0	-0.1	1.4
1993	-1.4	-0.1	-2.9
1994	1.6	1.7	-1.2
1995	1.0	-1.8	3.4
1996	-2.6	-4.6	-4.6
1997	-4.9	-4.5	1.5
1998	0.8	0.2	2.8
1999	-1.7	-0.4	-1.5
2000	-0.2	-2.2	2.3
2001	0.6	-1.5	0.4
2002	-3.4	-1.2	3.4
2003	-2.9	-2.3	-4.1
2004	-0.5	-3.7	0.7
2005	-0.6	-0.2	-3.4
2006	-1.1	-5.9	-2.8
2007	2.3	3.0	2.7

Statistical analyses

We have transformed abundance of each bird species into annual indices using log-linear models in TRIM 3.51 with the effects of individual census sites and years included into the model formula (Pannekoek & van Strien 2001). Log-linear models are standard tools for analysis of bird monitoring data based on counts and having Poisson distribution of errors. Serial correlation and over-dispersion from Poisson distributions were taken into account. The value of the index was set at 100% in 1982 as the first year.

As breeding bird abundance often shows density dependence it is impossible to relate abundance to environmental variables directly over time (Piha et al. 2007). We have adopted approach introduced by Sæther et al. (2003) expressing annual growth rate (r) of population of each species:

$$r = N_{t+1}/N_t \quad (1)$$

where N_t is the index of population abundance (computed using log-linear models, see above) in the year t. In the next step, we have related the logarithm of annual growth rate of the breeding population of a given species to winter temperature controlling for the effect of N_t:

$$\log(r) = a + bZ + cN_t \quad (2)$$

where Z is a vector of environmental variables (mean temperature in a given winter month in our case) and a, b and c are model parameters. Parameter b indicates the effect of winter temperature, parameter c indicates the effect of density dependence. As Z and N_t were not correlated, multicollinearity was not a problem in this regression model. To assess the strength of the effect of winter temperature on population of each species we used partial correlation coefficient calculated in the model. The more positive correlation, the higher dependence of species' breeding abundance on temperature in the preceding winter. We ran separate models for each of the winter months (i.e. December, January and February, respectively). As a result, each bird species obtained three different partial correlation coefficients, corresponding to respective months, quantifying the effects of winter weather of its population.

In the next step, we have modelled partial correlation coefficients as functions of body mass and dietary niche and their interaction across species. Partial correlation coefficients corresponding to different months were included together into a common model with the effect of "month" as an additional explanatory variable. This approach enabled us to test whether the partial correlation coefficients were more positive in one month compared to the others and thus to judge which part of winter has the strongest limiting effect on bird populations. Moreover, it was possible to focus on the interactions between different variables, testing, for instance, whether the effect of body mass is different in December compared to January. This approach also did not elevate the probability of Type I error.

Finally, we have performed linear mixed-effects models with random effects of species, genera, families and orders to control for the effects of phylogenetic relatedness of the focal species (expressed by taxonomy). Mixed-effects models were fitted using lme function in R package nlme (R development core team 2005) using maximum likelihood method recommended for comparison of models with different fixed effects structures (Crawley 2007). We have also used mixed-effects models to examine the within- and between-taxon-variability of partial correlation coefficients from the relationships between abundance and winter temperature. For this purpose, we used restricted maximum likelihood method which is independent on fixed effects (Crawley 2007). Classification of species to orders and families was based on information from Sibley & Monroe (1990) and to genera on information from Dudley et al. (2006). Body mass was log-transformed for statistical analyses to achieve normality. Partial correlation coefficients showed normal distribution among species (Kolmogorov-Smirnov tests: $d_{December} = 0.09$, $d_{January} = 0.11$, $d_{Febraury} = 0.09$, all $P > 0.20$).

Results

Temperature in winter months explained small part of annual variation in breeding abundance of particular bird species (Table 2). Generally, partial correlation coefficients indicating the strength of dependence of annual growth rates of species' populations on winter

Table 2. *Characteristics of 37 resident bird species with breeding populations monitored between 1982 and 2007 in the Czech Republic. Species are sorted with respect to their winter diet to: plant-eating species (P), animal-eating species (A), and species feeding on both animals and plants (A+P). Partial correlation coefficients (partial r) with corresponding significance levels (p) revealed by linear models show the effects of temperature (Temperature) in particular winter months (separate set of models were run for December, January and February) and species' abundance in previous breeding season (Abundance), respectively, on annual population growth rates of particular species. Species showing signifficant effect of temperature (at least in one month) are in bold.*

Species	Diet	Body mass (g)	December				January				February			
			Temperature		Abundance		Temperature		Abundance		Temperature		Abundance	
			partial r	*p*	partial r	*p*	partial r	*p*	partial r	*p*	partial r	*p*	partial r	*p*
Cygnus olor	P	10250	-0.26	0.212	-0.54	0.007	-0.11	0.624	-0.58	0.003	-0.10	0.626	-0.59	0.002
Anas platyrhynchos	A+P	1063	-0.01	0.974	-0.28	0.193	0.01	0.980	-0.27	0.200	0.41	0.047	-0.31	0.141
Buteo buteo	A	848	-0.12	0.563	-0.59	0.002	0.21	0.330	-0.60	0.002	0.51	0.011	-0.61	0.001
Falco tinnunculus	A	220	-0.02	0.938	-0.66	0.000	0.19	0.385	-0.68	0.000	0.29	0.176	-0.64	0.001
Perdix perdix	P	365	0.37	0.075	-0.43	0.034	0.18	0.406	-0.38	0.069	0.12	0.565	-0.33	0.110
Phasianus colchicus	P	1163	0.20	0.355	-0.56	0.004	0.09	0.661	-0.54	0.006	0.00	0.993	-0.53	0.007
Streptopelia decaocto	P	198	0.33	0.112	-0.20	0.355	0.60	0.002	-0.25	0.245	0.28	0.183	-0.29	0.168
Alcedo atthis	A	41	0.20	0.347	-0.44	0.030	0.48	0.019	-0.50	0.012	0.45	0.026	-0.58	0.003
Picus viridis	A	191	-0.08	0.717	-0.42	0.040	0.26	0.222	-0.39	0.057	-0.08	0.721	-0.41	0.045
Dryocopus martius	A	310	0.09	0.659	-0.35	0.092	0.07	0.008	-0.37	0.531	-0.07	0.731	-0.37	0.076
Dendrocopos major	A+P	81	0.27	0.206	-0.61	0.001	0.29	0.170	-0.52	0.009	0.00	0.996	-0.64	0.001
Dendrocopos minor	A+P	21	-0.21	0.322	-0.81	0.000	-0.26	0.228	-0.80	0.000	0.17	0.440	-0.80	0.000
Troglodytes troglodytes	A	10	0.54	0.007	-0.44	0.032	0.80	0.000	-0.74	0.000	0.49	0.015	-0.65	0.001
Turdus merula	A+P	93	0.56	0.005	-0.20	0.349	0.74	0.000	-0.40	0.056	0.35	0.095	-0.41	0.046
Aegithalos caudatus	A	8	0.00	0.987	-0.39	0.062	-0.22	0.292	-0.34	0.101	0.05	0.815	-0.38	0.068
Poecile palustris	A+P	11	-0.02	0.941	-0.39	0.061	-0.31	0.139	-0.40	0.052	-0.29	0.173	-0.46	0.025
Poecile montanus	A+P	11	0.16	0.442	-0.65	0.001	-0.10	0.648	-0.61	0.002	0.19	0.382	-0.67	0.000
Lophophanes cristatus	A+P	11	0.03	0.546	-0.44	0.130	-0.19	0.363	-0.41	0.047	-0.31	0.142	-0.41	0.046
Periparus ater	A+P	10	-0.29	0.172	-0.51	0.011	-0.26	0.224	-0.48	0.018	0.12	0.587	-0.51	0.012
Cyanistes caeruleus	A+P	10	0.17	0.437	-0.62	0.001	-0.03	0.873	-0.65	0.001	-0.10	0.632	-0.66	0.000
Parus major	A+P	12	-0.01	0.973	-0.56	0.005	-0.32	0.127	-0.54	0.006	-0.21	0.329	-0.59	0.003
Sitta europaea	A+P	19	0.02	0.935	-0.50	0.014	0.06	0.781	-0.52	0.010	0.36	0.086	-0.56	0.004
Certhia familiaris	A+P	23	0.34	0.101	-0.62	0.001	0.02	0.933	-0.63	0.001	0.28	0.189	-0.62	0.001
Certhia brachydactyla	A	9	0.15	0.498	-0.58	0.003	0.10	0.637	-0.60	0.002	0.02	0.923	-0.58	0.003
Garrulus glandarius	A+P	161	-0.10	0.652	-0.46	0.023	0.30	0.159	-0.37	0.073	0.12	0.577	-0.46	0.025
Pica pica	A+P	200	-0.22	0.300	-0.54	0.006	0.05	0.806	-0.55	0.005	-0.42	0.042	-0.54	0.006
Corvus monedula	A+P	230	0.22	0.311	-0.43	0.037	-0.01	0.973	-0.42	0.040	-0.06	0.796	-0.42	0.038
Corvus corone	A+P	506	0.00	0.983	-0.40	0.053	-0.08	0.714	-0.44	0.032	-0.08	0.696	-0.44	0.031
Passer domesticus	P	32	0.13	0.531	-0.28	0.182	0.28	0.190	-0.21	0.322	-0.12	0.582	-0.28	0.181
Passer montanus	P	23	0.29	0.173	-0.53	0.008	0.28	0.179	-0.52	0.009	0.14	0.506	-0.50	0.013
Fringilla coelebs	P	23	0.04	0.838	-0.22	0.301	0.05	0.827	-0.21	0.316	-0.03	0.893	-0.21	0.320
Carduelis chloris	P	28	-0.03	0.893	-0.32	0.134	-0.15	0.497	-0.34	0.104	0.39	0.061	-0.09	0.693
Carduelis carduelis	P	17	0.08	0.712	-0.54	0.007	0.09	0.674	-0.55	0.005	0.36	0.083	-0.53	0.008
Carduelis flammea	P	11	-0.35	0.097	-0.33	0.114	-0.18	0.400	-0.40	0.052	-0.15	0.497	-0.39	0.059
Loxia curvirostra	P	41	0.10	0.646	-0.64	0.001	0.23	0.277	-0.64	0.001	0.05	0.832	-0.64	0.001
Pyrrhula pyrrhula	P	28	0.35	0.095	-0.64	0.001	-0.08	0.704	-0.58	0.003	-0.02	0.916	-0.57	0.003
Emberiza citrinella	P	29	-0.01	0.959	-0.22	0.294	-0.23	0.272	-0.25	0.238	-0.44	0.030	-0.32	0.127

temperature were positive (mean$_{\text{December}}$ = 0.08 ± 0.04 (standard error), mean$_{\text{January}}$ = 0.08 ± 0.05, mean$_{\text{February}}$ = 0.07 ± 0.04) indicating that winter weather affects breeding population of Czech birds to some extent. The values of partial correlation coefficients did not differ among months ($F_{2,\,108}$ = 0.01, P = 0.992) suggesting no indication of higher importance of some months compared to others for limiting of bird populations.

Only one species, winter wren (*Troglodytes troglodytes*), was significantly affected by temperatures in all three focal months. Five species were significantly affected by temperatures in one or two months: blackbird *Turdus merula* (December and January), kingfisher *Alcedo atthis* (January and February), buzzard *Buteo buteo* (February), mallard *Anas platyrhynchos* (February), collared dove *Streptopelia decaocto* (January). Majority of the focal species (63–78%, depending on the month used for the analysis) showed significant negative dependence of population growth rate on abundance in the previous breeding season, none showed positive dependence (Table 2).

Species' dietary niche was a significant predictor of the interspecific variation in the strength of the relationship between breeding abundance and temperature in particular winter months (month: $F_{2,\,106}$ = 0.01, P = 0.991; dietary niche: $F_{2,\,106}$ = 4.08, P = 0.020). Abundance of species feeding on animals followed winter temperatures more closely than abundance of species feeding on both animals and plants (post-hoc contrasts: difference between feeding on animals and feeding on both animals and plants P = 0.013, difference between feeding on animals and feeding on plants P = 0.151, difference between feeding and plants and feeding on both animals and plants P = 0.540, Fig. 1). The effect of dietary niche did not differ among particular winter months as indicated by non-significant interaction between month and dietary niche (month: $F_{2,\,102}$ = 0.01, P = 0.991; dietary niche: $F_{2,\,102}$ = 3.99, P = 0.022; month x dietary niche: $F_{4,\,102}$ = 0.37, P = 0.829). In contrast to the significant effect of dietary niche on the relationship between breeding abundance and temperature, this relationship was not affected by body mass (month: $F_{2,\,107}$ = 0.01, P = 0.992; body mass: $F_{1,\,107}$ = 0.26, P = 0.609). The effect of body mass did not differ among months (month: $F_{2,\,105}$ = 0.01, P = 0.992; body mass: $F_{1,\,105}$ = 0.26, P = 0.609; month x body mass: $F_{2,\,105}$ = 0.92, P = 0.400).

The significant effect of dietary niche and no effect of body mass remained consistent over various designs of linear models: after simultaneous testing the effects of dietary niche and body mass (month: $F_{2,\,105}$ = 0.01, P = 0.991; dietary niche: $F_{2,\,106}$ = 4.06, P = 0.020; body mass: $F_{1,\,106}$ = 0.28, P = 0.595), after including the interaction between dietary niche and body mass (month: $F_{2,\,103}$ = 0.01, P = 0.991; dietary niche: $F_{2,\,103}$ = 4.12, P = 0.019; body mass: $F_{1,\,103}$ = 0.29, P = 0.592; dietary niche x body mass: $F_{2,\,103}$ = 1.81, P = 0.169), after including interaction between month and dietary niche and interaction between month and body mass, respectively (month: $F_{2,\,97}$ = 0.01, P = 0.991; dietary niche: $F_{2,\,97}$ = 4.02, P = 0.021; body mass: $F_{1,\,97}$ = 0.28, P = 0.597; dietary niche x body mass: $F_{2,\,97}$ = 1.77, P = 0.176; month x dietary niche: $F_{4,\,97}$ = 0.37, P = 0.827; month x body mass: $F_{2,\,97}$ = 0.99, P = 0.373). Reversed order of explanatory variables in the linear models showed the same significant terms (results not shown).

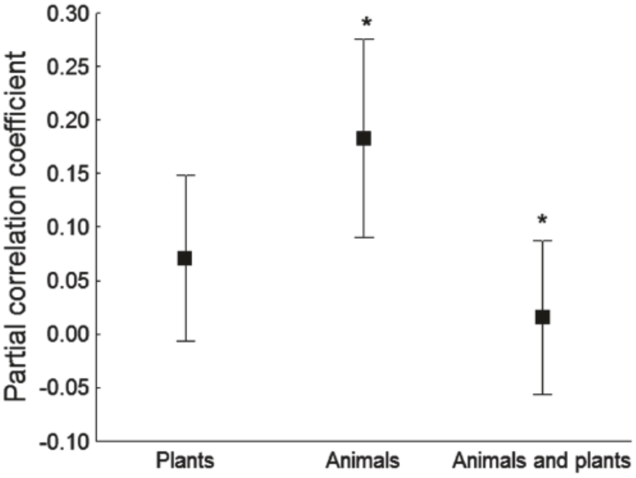

Fig. 1. *Mean (±95% confidence interval) strengths of relationships between species' breeding abundance and winter temperature (quantified by partial correlation coefficients) in the Czech Republic in three groups of resident bird species defined by species' winter diet (i.e. species feeding on animals, plants, or both animals and plants). Groups significantly different from each other according to results of post-hoc contrasts are marked with asterisks. See Methods section for more details on computation of relationship between breeding abundance and winter temperature.*

Linear mixed-effects models examined the fixed effects of month, diet and body mass given the random effects of species relatedness expressed by their species, genus, family and order status. These analyses did not reveal any significant results implying strong effect of phylogeny on ability of the explanatory variables to explain interspecific variability in the relationships between breeding bird abundance and winter temperature: model with dietary niche (month: $F_{2,72} = 0.02$, $P = 0.984$; dietary niche: $F_{2,13} = 0.43$, $P = 0.658$), model with body mass (month: $F_{2,72} = 0.02$, $P = 0.984$; body mass: $F_{1,6} = 0.00$, $P = 0.999$), model with interaction between dietary niche and month (month: $F_{2,68} = 0.02$, $P = 0.984$; dietary niche: $F_{2,13} = 0.42$, $P = 0.668$; dietary niche x month: $F_{4,68} = 0.70$, $P = 0.596$), model with interaction between body mass and month (month: $F_{2,70} = 0.02$, $P = 0.983$; body mass: $F_{1,6} = 0.00$, $P = 0.999$; body mass x month: $F_{2,70} = 1.89$, $P = 0.159$), model with interaction between dietary niche and body mass (month: $F_{2,72} = 0.02$, $P = 0.984$; dietary niche: $F_{2,13} = 0.43$, $P = 0.657$; body mass: $F_{1,4} = 0.00$, $P = 0.968$; dietary niche x body mass: $F_{2,4} = 0.79$, $P = 0.513$), the most complex model (month: $F_{2,66} = 0.02$, $P = 0.984$; dietary niche: $F_{2,13} = 0.41$, $P = 0.673$; body mass: $F_{1,4} = 0.00$, $P = 0.969$; dietary niche x body mass: $F_{2,4} = 0.75$, $P = 0.530$; month x dietary niche: $F_{4,66} = 0.70$, $P = 0.593$; month x body mass: $F_{2,66} = 1.87$, $P = 0.162$). All results were robust to different orderings of explanatory variables in the models (results not shown).

Finally, we have examined the random effects of species' taxonomonic categorization alone on the variability in partial correlation coefficients between breeding abundance and temperatures in particular winter months. Variability at the species level was highest for December (75%) and February (79%), respectively, and second highest for January (40%). Variability at the family level was the second highest for two months (December 25%, February 13%). For January, the variability explained at the family level was even the highest among all taxonomic levels (49%). The order level contributed to substantial part of variation for February (8%), and the genus level for January (12%). For the remaining months, order and genus levels had negligible contributions to variability in partial correlation coefficients (less than 1% in all cases).

Discussion

Our examination of relationships between breeding abundance and winter temperature in 37 common bird species wintering in the Czech Republic revealed four main patterns: (i) relationships were generally weak in most species, only six species showed significant partial correlation between population growth rate and temperature in at least one of the three winter months (December, January or February); (ii) the strength of these relationships was affected by diet: species preying on animals had stronger relationship between abundance and winter temperature than species feeding on both animals and plants; this pattern was consistent across all winter months; (iii) body mass did not affect the strength of the relationship between abundance and temperature; (iv) populations of more than two thirds of species showed density dependence (negative in all cases).

The first and fourth patterns imply that winter severity is not a very important component of population regulation of resident bird species in the Czech Republic. Intrinsic population processes seem much more important as most of the species showed significant negative density dependence. It means that annual change in breeding abundance of a species depends more on its abundance in the previous year than on temperature in winter. This finding is in contrast with the strong effect of climate on spring arrival dates. In central Europe, several studies described dependence of mean arrival dates of migrants on temperatures in spring or on the Northern Atlantic Oscillation index (Hubálek 2003, Tryjanowski et al. 2005, Hubálek & Čapek 2008). Climatically-induced shift in arrival date might translate into change in breeding abundance resulting in population decline of species not able to adjust their arrival on breeding grounds to warmer climate (Tryjanowski et al. 2005, Møller et al. 2008). Putting these findings together with the results of our study, we suggest that abundance of central European birds in the breeding season is strongly affected by spring temperature (Tryjanowski et al. 2005, Reif et al. 2008b) but the effect of winter temperature is weak (this study). However, we should bear in mind that winter weather was expressed as monthly temperate means. Although mean temperature is frequently used to test the effects of winter conditions on animal populations (e.g. Jones et al. 2003, Huntley et al. 2007, Link & Sauer 2007), use of such mean can mask the effects of temperature anomalies such as short periods of deep frost that may limit bird abundance more directly. Future studies can focus on performance of various measures of winter severity in bird population models.

The second and third patterns indicate that winter climate in the Czech Republic impacts upon bird populations indirectly through food supply rather than directly in which case the effect of body mass would be expected. Dietary niche thus seems to determine the effect of winter temperature on breeding bird populations: species feeding on both animals and plants (including omnivorous species) showed weaker relationships to temperature than species feeding on animals. This effect of dietary niche was consistent over particular winter months implying that none of the months have stronger limiting effect on bird food supply compared to the others. Results of our study expand on initial findings of Robinson et al. (2007) reporting high importance of dietary differences for relationships between abundance and winter temperature in 10 passerine species.

Low temperatures may reduce the activity of potential prey (especially invertebrates) and/or the prey might be less accessible (Avery & Krebs 1984, Rolstad & Rolstad 2000). The first factor might explain relatively close relationship between abundance and temperature in winter wren. Abundance of this species showed the tightest relationships to temperature, significant in all winter months. Indeed, Cannell et al. (1999) included the index of winter wren breeding abundance among indicators of climatic change in Great Britain as its abundance signalised impacts of winter severity on animals very clearly. Our data confirm indicative potential of this species. Reduced prey accessibility was probably important for limitation of populations of carnivorous species in our data because all species with this dietary specialisation were among those with the strongest abundance-temperature relationships. Ice cover on rivers and water bodies probably restricted accessibility of food for kingfisher (Keller et al. 1989, Kelly & Van Horne 1997), snow cover hid movements of small rodents (Solonen 2006), the main component of diet of kestrel (*Falco tinnunculus*) and buzzard (Zmihorski & Rejt 2007, Riegert et al. 2009). In contrast, species with wider dietary niche may switch to the food type temporary available to prevent starving during unfavourable weather conditions (Brandle et al. 2002). This explanation, however, is conditional on broad dietary niche on the level of particular individuals (Colles et al. 2009) and this assumption remains to be tested in species in our data.

Most of the species showed negative density dependence in population growth rate. This result corresponds to findings of Greenwood & Baillie (1991) and Newton et al. (1998), who reported poor breeding performance of common birds following the years of high abundance. Presence of density dependence confounds the effects of environmental factors on abundance and the studies searching for determinants of population changes need to separate the effects of extrinsic and intrinsic factors (Link & Sauer 2007, Piha et al. 2007). However, even recent studies apply direct correlations between species' abundance and the factor of interest (Wesołowski et al. 2009), although such analyses might produce substantially flawed results. As the recent mathematical tools enable to include a simple population model into statistical tests (Sæther et al. 2003) we urge to use this approach.

Our mixed-effects models showed that the effects of dietary niche on the strength of the relationship between abundance and winter temperature were insignificant if the taxonomic relatedness of the focal species was taken into account. Although the strength of abundance-temperature relationships varied considerably among species, about one fourth (or even more, depending on which of the winter months was used in the models) of the variability was found at the family level. Moreover, bird diet is specific for higher taxa (Bennett & Owens 2002) and closely related species within families or genera often feed on similar food (Price 2008). As a result, the effect of dietary niche was weaker if the phylogenetic component of variability (expressed in taxonomic categories) was highlighted. Nevertheless, significant phylogenetic effects do not preclude use of the results for conservation praxis (Thomas 2008). For instance, from the effect of winter temperatures on populations of species feeding on animals we can infer that these species may be particularly sensitive to human disturbance on wintering sites. Such disturbance could reduce the amount of time needed by the birds to search for their animal food. Therefore, such disturbance should be limited at least in the species of conservation concern like kingfisher.

Our results might be useful for considerations about results of modelling of species' potential responses to climatic change (Diniz-Filho et al. 2009). Such predictions often use models with only a few climatic variables including winter temperature (e.g. Huntley et al. 2007). We have found that the effect of winter temperature on breeding bird abundance is relatively weak at least in the conditions of the Czech Republic and its strength is modified by species' dietary niche. Therefore, predictive models with sole climatic variables might be too simplistic and the patterns of species' diversity and abundance predicted by these models not realistic. Inclusion of some ecological characteristics of the focal species such as dietary niche might result in improvement of predictive power of such models.

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Literature

Aschoff J. 1981: Thermal conductance in mammals and birds – its dependence on body size and circadian phase. *Comp. Biochem. Physiol. 69: 611–619.*

Avery M.I. & Krebs J.R. 1984: Temperature and foraging success of great tits *Parus major* hunting for spiders. *Ibis 126: 33–38.*

Bakken G.S., Murphy M.T. & Erskine D.J. 1991: The effect of wind and air temperature on metabolism and evaporative water-loss rates of dark-eyed juncos *Junco heymalis* – a standard operative temperature scale. *Physiol. Zool. 64: 1023–1049.*

Bejček V., Šťastný K. & Hudec K. 1995: Atlas of winter distribution of birds in the Czech Republic 1982–1985. *H & H, Jinočany. (in Czech)*

Bennett P. & Owens I. 2002: Evolutionary ecology of birds. *Oxford University Press, Oxford.*

Brandle M., Prinzing A., Pfeifer R. & Brändl R. 2002: Dietary niche breadth for Central European birds: Correlations with species-specific traits. *Evol. Ecol. Res. 4: 643–657.*

Cannell M.G.R., Palutikof J.P. & Sparks T.H. 1999: Indicators of climate change in the UK. *The Stationery Office, London.*

Carrascal L.M., Diaz J.A., Huertas D.L. & Mozetich I. 2001: Behavioral thermoregulation by treecreepers: Trade-off between saving energy and reducing crypsis. *Ecology 82: 1642–1654.*

Cepák J., Klvaňa P., Škopek J., Schröpfer L., Jelínek M., Hořák D., Formánek J. & Zárybnický J. (eds.) 2008: Bird migration atlas of the Czech Republic and Slovakia. *Aventinum, Praha. (in Czech with English summary)*

Colles A., Liow L.H. & Prinzing A. 2009: Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecol. Lett. 12: 849–863.*

Crawley M.J. 2007: The R book. *Wiley, London.*

Diniz-Filho J.A.F., Bini L.M., Rangel T.F., Loyola R.D., Hof C., Nogues-Bravo D. & Araujo M.B. 2009: Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography 32: 897–906.*

Doswald N., Willis S.G., Collingham Y.C., Pain D.J., Green R.E. & Huntley B. 2009: Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers. *J. Biogeogr. 36: 1194–1208.*

Dudley S.P., Gee M., Kehoe C. & Melling T.M. 2006: The British List: A checklist of birds of Britain (7th edition). *Ibis 148: 526–563.*

Greenwood J.J.D. & Baillie S.R. 1991: Effects of density-dependence and weather on population changes of English passerines using a nonexperimental paradigm. *Ibis 133: 121–133.*

Holmes R.T., Sherry T.W. & Sturges F.W. 1986: Bird community dynamics in a temperate deciduous forest: Long-term study at Hubbard Brook. *Ecol. Monogr. 56: 201–220.*

Hubálek Z. 2003: Spring migration of birds in relation to North Atlantic Oscillation. *Folia Zool. 52: 287–289.*

Hubálek Z. & Čapek M. 2008: Migration distance and the effect of North Atlantic Oscillation on the spring arrival of birds in Central Europe. *Folia Zool. 57: 212–220.*

Hudec K. (ed.) 1983: Fauna of the Czech Republic. Birds 3. *Academia, Praha. (in Czech with German summary)*

Hudec K. (ed.) 1994: Fauna of the Czech Republic. Birds 1. *Academia, Praha. (in Czech with German summary)*

Hudec K. & Šťastný K. (eds.) 2005: Fauna of the Czech Republic. Birds 2. *Academia, Praha. (in Czech with German summary)*

Huntley B., Green R.E., Collingham Y.C. & Willis S.G. 2007: A climatic atlas of European breeding birds. *Lynx Editions, Barcelona.*

Janda J. & Šťastný K. 1984: Breeding bird monitoring programme in the Czech Republic. *Zprávy ČSO 26: 25–33. (in Czech)*

Jones J., Doran P.J. & Holmes R.T. 2003: Climate and food synchronize regional forest bird abundances. *Ecology 84: 3024–3032.*

Keller M., Jedrzejewska B. & Jedrzejewski W. 1989: Wintering tactics of the kingfisher *Alcedo atthis*. *Ornis Fennica 66: 157–160.*

Kelly J.F. & Van Horne B. 1997: Effects of scale-dependent variation in ice cover on the distribution of wintering belted kingfishers *Ceryle alcyon*. *Ecography 20: 506–512.*

Lahti K., Orell M., Rytkonen S. & Koivula K. 1998: Time and food dependence in willow tit winter survival. *Ecology 79: 2904–2916.*

Link W.A. & Sauer J.R. 2007: Seasonal components of avian population change: Joint analysis of two large-scale monitoring programs. *Ecology 88: 49–55.*

Meehan T.D., Jetz W. & Brown J.H. 2004: Energetic determinants of abundance in winter landbird communities. *Ecol. Lett. 7: 532–537.*

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. *Proc. Natl. Acad. Sci. USA 105: 16195–16200.*

Newton I. 1998: Population limitation in birds. *Academic Press, London.*

Newton I., Rothery P. & Dale L.C. 1998: Density-dependence in the bird populations of an oak wood over 22 years. *Ibis 140: 131–136.*

Pannekoek J. & Van Strien A. 2001: TRIM 3 Manual. *Statistics Netherlands, Vootburg.*

Piha M., Lindén A., Pakkala T. & Tiainen J. 2007: Linking weather and habitat to population dynamics of a migratory farmland songbird. *Ann. Zool. Fenn. 44: 20–34.*

Price T. 2008: Speciation in birds. *Roberts & Co. Publishers, Greenwood Village.*

R Development Core Team 2005: R: A language for statistical computing, reference index version 2.2.1. *R Foundation for Statistical Computing, Vienna.*

Reif J., Voříšek P., Šťastný K. & Bejček V. 2006: Population trends of birds in the Czech Republic during 1982–2005. *Sylvia 42: 22–37. (in Czech with English summary)*

Reif J., Voříšek P., Šťastný K., Bejček V. & Petr J. 2007: Population increase of forest birds in the Czech Republic between 1982 and 2003. *Bird Study 54: 248–255.*

Reif J., Voříšek P., Šťastný K., Bejček V. & Petr J. 2008a: Agricultural intensification and farmland birds: New insights from a central European country. *Ibis 150: 569–605.*

Reif J., Voříšek P., Šťastný K., Koschová M. & Bejček V. 2008b: The impact of climate change on long-term population trends of birds in a central European country. *Anim. Conserv. 11: 412–421.*

Riegert J., Lövy M. & Fainová D. 2009: Diet composition of common kestrels *Falco tinnunculus* and long-eared owls *Asio otus* coexisting in an urban environment. *Ornis Fennica 86: 123–130.*

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.*

Rolstad J. & Rolstad E. 2000: Influence of large snow depths on black woodpecker *Dryocopus martius* foraging behavior. *Ornis Fennica 77: 65–70.*

Sæther B.-E., Engen S., Møller A.P., Matthysen E., Adriaensen F., Fiedler W., Leivits A., Lambrechts M.M., Visser M.E., Anker-Nilssen T., Both C., Dhondt A.A., McCleery R.H., McMeeking J., Potti J., Rostad O.W. & Thomson D. 2003: Climate variation and regional gradients in population dynamics of two hole-nesting passerines. *Proc. Roy. Soc. Lond. B 270: 2397–2404.*

Sæther B.-E., Tufto J., Engen S., Jerstad K., Rostad O.W. & Skatan J.E. 2000: Population dynamical consequences of climate change for a small temperate songbird. *Science 287: 854–856.*

Sibley C.G. & Monroe B.L. 1990: Distribution and taxonomy of birds of the world. *Yale University Press, New Haven.*

Siriwardena G.M., Stevens D.K., Anderson G.Q.A., Vickery J.A., Calbrade N.A. & Dodd S. 2007: The effect of supplementary winter seed food on breeding populations of farmland birds: Evidence from two large-scale experiments. *J. Appl. Ecol. 44: 920–932.*

Solonen T. 2006: Overwinter population change of small mammals in southern Finland. *Ann. Zool. Fenn. 43: 295–302.*

Thomas G.H. 2008: Phylogenetic distributions of British birds of conservation concern. *Proc. R. Soc. Lond. B 275: 2077–2083.*

Tolasz R., Míková T., Valeriánová A. & Voženílek V. (eds.) 2007: Climatic atlas of Czechia. *Czech Hydrometeorological Institute & Palacký University, Praha & Olomouc.*

Tryjanowski P., Kuzniak S. & Sparks T.H. 2005: What affects the magnitude of change in first arrival dates of migrant birds? *J. Ornithol. 146: 200–205.*

Virkkala R. 2004: Bird species dynamics in a managed southern boreal forest in Finland. *Forest Ecol. Manag. 195: 151–163.*

Wesołowski T., Rowiński P. & Maziarz M. 2009: Wood warbler *Phylloscopus sibilatrix*: A nomadic insectivore in search of safe breeding grounds? *Bird Study 56: 26–33.*

Zmihorski M. & Rejt L. 2007: Weather-dependent variation in the cold-season diet of urban kestrels *Falco tinnunculus*. *Acta Ornithol. 42: 107–113.*

Paper III

RESEARCH ARTICLE

Population Trends of Central European Montane Birds Provide Evidence for Adverse Impacts of Climate Change on High-Altitude Species

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Abstract

Climate change is among the most important global threats to biodiversity and mountain areas are supposed to be under especially high pressure. Although recent modelling studies suggest considerable future range contractions of montane species accompanied with increased extinction risk, data allowing to test actual population consequences of the observed climate changes and identifying traits associated to their adverse impacts are very scarce. To fill this knowledge gap, we estimated long-term population trends of montane birds from 1984 to 2011 in a central European mountain range, the Giant Mountains (Krkonoše), where significant warming occurred over this period. We then related the population trends to several species' traits related to the climate change effects. We found that the species breeding in various habitats at higher altitudes had more negative trends than species breeding at lower altitudes. We also found that the species moved upwards as a response to warming climate, and these altitudinal range shifts were associated with more positive population trends at lower altitudes than at higher altitudes. Moreover, long-distance migrants declined more than residents or species migrating for shorter distances. Taken together, these results indicate that the climate change, besides other possible environmental changes, already influences populations of montane birds with particularly adverse impacts on high-altitude species such as water pipit (*Anthus spinoletta*). It is evident that the alpine species, predicted to undergo serious climatically induced range contractions due to warming climate in the future, already started moving along this trajectory.

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Introduction

Climate change ranks among the top drivers of biodiversity changes worldwide [1]. However, severity of its impacts varies over the Earth's surface with mountain areas being among those under extraordinarily high pressure [2, 3]. To better understand potential consequences of climate change in these areas, it is important to quantify the magnitude of this impact on species' populations and to determine the species being under the highest risk [4].

Under the circumstances of climate change, montane species typically shift their ranges towards higher altitudes tracking their climatic optima [5–8], although some other drivers might be also involved in such shifts [9]. This pattern of shift was found in vast majority of cases because it is consistent with globally warming temperatures and a gradient of decreasing temperature with altitude [10]. However, space limitations at high altitudes constrain possibilities of montane species to cope with climatic changes and make them particularly vulnerable: in an extreme case, the climatic niche of some of these species can move beyond the mountain tops driving such species ultimately to extinction [11]. Although various studies modelled and predicted such threats for the future conditions [2, 12, 13], empirical evidence for these impacts of the current climate change on montane species remains limited due to the lack of long-term data on species' distribution and abundance at high altitudes [14].

Here we focused on the impacts of climate change on long-term population trends of birds in a central European mountain range, the Giant (Krkonoše) Mountains, Czech Republic. The Giant Mts. cover an altitudinal range of 1200 m from the low-altitude forests and cultural landscape to high-altitude alpine grasslands above timberline [15]. Quantification of long-term population trends was enabled by the existence of a unique long-term data set collected using a standardized technique by a single observer since 1984 and covering the entire altitudinal gradient in these mountains. We studied the effects of climate change on populations of montane bird species by means of interspecific comparative analysis relating population trends to species-specific traits [16] testing following predictions.

(i) Population trends of species breeding at higher altitudes should be more negative than the trends of species breeding at lower altitudes. Distribution of the species breeding at high altitudes is constrained by mountain tops and thus their populations are more likely to decline under the conditions of warming climate [11]. (ii) Long-distance migrants should have more negative trends than the short-distance migrants and residents because they are more adversely affected by climatic changes on breeding grounds [17] and also adversely affected by habitat deterioration at the wintering and stopover sites [18]. (iii) Species with slow life history strategies should have more negative trends than the species with fast strategies. The fast life history is characterized by potentially high population growth rate [19] enabling a quick recovery of species' population after an impact of environmental change [20], which is more problematic for the slow life history species making them more sensitive to the impacts of global changes [21]. On the other hand, slow life history species may be more resistant to environmental pertubations making their populations more stable [22, 23]. In addition, the climate change was found to affect central European populations of birds according to the mean temperature in their European breeding ranges, when regional abundance of species breeding in warmer (southern or lowland) regions increase, while species of colder (northern or montane) regions decline [21, 24, 25, 26]. Therefore, (iv) species with lower temperature of European breeding range should have more negative population trends than the species breeding in warmer temperatures.

Population trends of particular species may also be related to upward shifts of their altitudinal ranges caused by warming climate [27]. By shifting to higher altitudes species compensate the adverse impacts of climate change on their populations [28]. Therefore, depending on the altitude of species' breeding occurrence, we could expect differences in population trends between long- and short-shifting species. Specifically, population trends of species experiencing longer altitudinal range shifts should be less negative than the trends of species showing shorter shifts in the case of species breeding at lower altitudes, but the reverse will be true at higher altitudes. We thus tested this hypothesis as a (v) final prediction.

The aims of this study were (i) to calculate the long-term population trends of particular bird species breeding in the Giant Mts., (ii) to describe the climate change in this mountain range, (iii) to test the predictions formulated above.

Materials and Methods

Study area

The study was conducted in the Giant Mts. (Krkonoše), the highest mountain range in the Czech Republic spanning an altitudinal range of more than 1200 m and with the highest peak of 1603 m a.s.l. The range spreads over four altitudinal vegetation belts: submontane, montane, subalpine and alpine [29, 30]. The two lower belts are covered by forests with a timber line at about 1300 m a.s.l.: more or less close-to-nature and autochthonous beech-spruce and mountain spruce forests prevail at higher elevations, whereas most forests at lower elevations are managed mixed and spruce stands [31]. The two upper belts are covered by open habitats of artic-alpine tundra [32]: glacial corries, rocks, alpine and subalpine grasslands, subarctic peatbogs and stands of *Pinus mugo*. Meadows and pastures are also present at lower elevations replacing original forest vegetation in some areas below and around the timber line [33]. Most of the Giant Mts. is protected as a national park and the intensity of human impact decreases from the foothills and valleys with permanent human population towards higher altitudes [31]. See [7] for more details on the study area.

Climate data

To describe patterns in climate change during the bird breeding season (May-July; note that the breeding starts later in montane environment) in the Giant Mts. over the study period we used data collected at three meteorological stations (S1 Table): Labska bouda (1315 m a.s.l.), Pec pod Snezkou (816 m a.s.l.) and Janske Lazne (650 m a.s.l.). The stations were located in different parts of the national park providing meaningful information about the climatic conditions in the Giant Mts. The data are the mean temperatures over the focal months (May-July) supplied by the Czech Hydrometeorological Institute.

Bird census

Bird census was approved by the Krkonoše National Park Administration. Since it was based just on observation and hearing of bird individuals without any disturbance, there was no need for approval of animal welfare committee. Birds were counted by JF along ten transects scattered throughout the mountain range covering all altitudinal vegetation belts (see Fig A1 in [7]) annually from 1984 to 2011. Transects contained 6–27 points located in ca 400 m intervals. Each point was visited two times per breeding season (May-July) early in the morning under favourable weather conditions (no rain or fog, no strong wind). During one visit, all birds seen or heard were recorded within 100 m radius around each census point for five minutes. Locations of the points and transects did not change over the course of the study and the dates of the visits varied less than ±7 days between years. Maximum count from both visits was taken as the abundance of a given species at one point in a given year. Such maximum counts are frequently used in studies inferring population trends from annual monitoring data because they are most likely closer to real abundances than, for example, mean counts [21, 34]. These point-abundances were summed to calculate the abundance of every species at each transect in a given year. These annual abundances at the transect level were used for further analysis to estimate the species' population trends.

Bird population trends

Population trends were estimated for all but one 51 common bird species whose altitudinal range shifts in the Giant Mts. were investigated in our earlier study [7]. The only exception was black grouse (*Tetrao tetrix*) whose counts were too low (five observations per year on average) and we thus excluded this species from the analysis of trends. Our final dataset thus contained 50 species. Trends were computed in TRIM, a statistical software developed specifically for the analysis of long-term time series data from animal monitoring programmes [35], which is currently among the most frequently used frameworks to infer bird population trends (see e.g. [24, 25, 36–38]). For the analysis we employed log-linear models with Poisson error structure where species' abundance at particular transects was a response variable (see above) and years (1984–2011) and transects were respective explanatory variables. Moreover, serial correlation and overdispersion were taken into account. As a result, we obtained yearly population indices of particular species and the population trend of a given species was estimated as a slope (with its standard error) of the regression line through the logarithms of the yearly indices. The trend can thus be translated as a logarithm of mean annual population growth rate. Negative values of trends signify population decline, and positive values population increase. These species' trends and standard errors (S2 Table) were taken for further analysis.

Species' traits

For each bird species, we defined following ecological traits (S2 Table):

Mean altitude of the breeding occurrence is the mean altitude (m) of the census points in the Giant Mts. where a given species was detected during the breeding season in the time period 1986–1988. These data were taken from our earlier study [7] and provide information about the mean altitude of species' distribution in the Giant Mts. early after the bird monitoring had started.

Altitudinal range shift is the mean annual shift of breeding altitudinal range of a given species between 1986 and 2011. Although altitudinal range shifts of birds in the Giant Mts. were already quantified in our earlier study [7], they had data only from three shorter periods available. Therefore, we decided to use bird census data collected at the annual basis for the purpose of the current study. We adopted the approach described in [39] focusing on shifts in the mean altitude of species' occurrence. To take the information from each year of the time series into account, we first calculated the mean altitude of occurrence in Giant Mts. for each species in a given year as a weighted mean of altitudes of points occupied by a species with its abundance on these points taken as a weight. These mean altitudes we regressed across years revealing species-specific slopes quantifying the magnitude of mean annual shift of each species over the focal time period. These species-specific slopes were taken as a response variable in further analysis.

Migration strategy is based on the information about migratory habits of particular species inferred from ringing recoveries collected over 20th century and published in the Czech Bird Migration Atlas [40]. According to the information in [40] species are classified as (1) residents (wintering in central Europe), (2) short-distance migrants (wintering in Western Europe or Mediterranean region) and (3) long-distance migrants (wintering in sub-Saharan Africa or Asia).

Life history strategy was expressed as a first ordination axis from a principal component analysis on species' values of six life history traits (body mass, egg mass, number of broods per year, laying date, clutch size and incubation length) performed by [41]. This axis ordinated species along a fast-slow life history gradient from "r-selected" to "K-selected" species.

European climatic niche was taken from [42] as a mean temperature within species' European breeding ranges. It was calculated by crossing maps of species' breeding distribution in Europe [43] with maps of mean temperatures in species-specific breeding season in particular mapping squares. See [42] for more details on its calculation.

Statistical analysis

We first calculated pairwise correlations among the trait variables (S3 Table). Pearson correlation coefficients were considerably lower than the level indicating that multicollinearity among predictors would be an issue [44]. Therefore, we used all traits for further analysis.

We related bird population trends to species' traits using linear models with the trend as a response variable, particular traits as explanatory variables and the inverse standard error of trend as a weight to give more weight to species with more accurate trend estimates, which is often used in such studies (see e.g. [24–25]). To test our hypotheses, we first composed a model containing the main effects of all traits as well as the interaction between the mean altitude of breeding occurrence and the altitudinal range shift (full model). To obtain the parameter estimates for the main effects of interacting variables not affected by their interactions, we also fitted the model without interaction term (main effects model).

All explanatory variables were standardized prior to statistical analysis to obtain comparable parameter estimates [45].

Bird species are phylogenetically related to various extent due to common evolutionary history [46]. Therefore, it is necessary to test whether this effect could influence the results of statistical modelling [47]. For this purpose, we tested for the presence of phylogenetic autocorrelation in residuals of the tested models using Moran's I in the R-package 'ape' [48]. Phylogeny of the focal species was extracted from [49].

Annual data on temperatures in the breeding season from particular meteorological stations were regressed across years to reveal the trends over time.

Results

Climate change

Temperatures in the bird breeding season increased from 1980 to 2009 according to data from all three stations located in the Giant Mts. ($F_{1,84} = 24.27$, $P < 0.001$; Fig 1). Interestingly, the rate of increase was slightly higher at the station located in the highest elevation (Labska bouda: intercept = 7.8, slope = 0.08°C/year, $R^2 = 0.33$) than at the two other stations in lower elevations of the Giant Mts. (Pec pod Snezkou: intercept = 11.4, slope = 0.05°C/year, $R^2 = 0.19$; Janske Lazne: intercept = 12.7, slope = 0.04°C/year, $R^2 = 0.13$) suggesting the climate change is progressing somewhat quicker at higher altitudes, but not significantly so ($F_{2,84} = 1.19$, $P = 0.309$).

Bird population changes

More species had positive (n = 31) than negative trends (n = 19) in our sample. Within the species showing the strongest declines dominated those breeding at the highest altitudes of the Giant Mts.: specialists strictly confined to the alpine habitats near mountaintops such as water pipit (*Anthus spinoletta*) or bluethroat (*Luscinia svecica svecica*), species of alpine grasslands

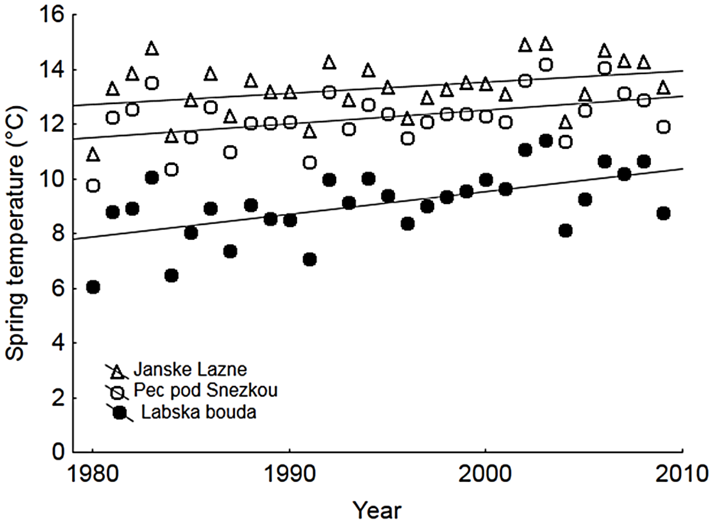

Fig 1. Annual changes of mean temperatures in the Giant Mountains. The temperatures refer to the local breeding season of birds (May-July) and were measured at three meteorological stations (Labska bouda: 1315 m a.s.l.—black circles, Pec pod Snezkou: 816 m a.s.l.—open circles, Janske Lazne: 650 m a.s.l.—open triangles). Solid lines are linear fits depicted for respective data sets.

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and montane meadows such as skylark (*Alauda arvensis*) or meadow pipit (*Anthus pratensis*), species of rocky outcrops and human buildings such as black redstart (*Phoenicurus ochruros*) or white wagtail (*Motacilla alba*) and species most abundant in shrubby habitats along timberline such as whinchat (*Saxicola rubetra*) or tree pipit (*Anthus trivialis*).

In the interspecific comparative analysis, the full model explained 28.53% of variability in long-term population trends of montane birds ($F_{6,43} = 4.26$, $P = 0.002$) and showed that the traits with the significant main effects were the mean altitude of the breeding occurrence and migration strategy, while the altitudinal range shift, life history strategy and European climatic niche were unrelated to the trends (Table 1). However, the mean altitude of the breeding occurrence × altitudinal range shift was significant (Table 1). By deleting the interaction term we obtained the main effects model. It showed the same significant main effects as the previous

Table 1. Relationships between long-term population trends of birds breeding in the Giant Mountains (Czech Republic), estimated for the time period 1984–2011, and particular species' traits as revealed by linear models.

Model term	Full model				Main effects model			
	Estimate	SE	t	P	Estimate	SE	t	P
mean altitude of breeding occurrence	**-0.40**	**0.12**	**-3.40**	**0.001**	**-0.38**	**0.12**	**-3.09**	**0.003**
altitudinal range shift	0.29	0.16	1.85	0.071	0.21	0.16	1.34	0.187
migration strategy	**-0.26**	**0.11**	**-2.39**	**0.021**	**-0.24**	**0.11**	**-2.18**	**0.035**
life history strategy	-0.01	0.12	-0.12	0.905	0.03	0.12	0.27	0.788
European climatic niche	0.01	0.10	0.11	0.914	0.05	0.11	0.43	0.670
mean altitude of breeding occurrence × altitudinal range shift	**-0.35**	**0.16**	**-2.15**	**0.037**	-	-	-	-

Significant results are printed in bold.

See text for definitions of particular trait variables and for more details on the models.

The explanatory variables were standardized to zero mean and unit variance before analysis.

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model (Table 1) but the amount of variability explained by this model was lower—22.65% ($F_{5,44} = 3.87$, $P = 0.005$).

The parameter estimates from the main effects model (Table 1) confirmed the observation of population declines in the high-altitude species when the effect of the mean altitude of the breeding occurrence was strongly negative with more negative population trends having the species breeding at higher altitudes (Fig 2A). Concerning the effect of migration strategy, the longer migratory route was associated with more negative trends (Fig 2B). We also found a significantly negative interaction between the altitudinal range shift and the mean altitude of the breeding occurrence (Table 1). It means that the long altitudinal range shift is beneficial for species breeding at lower altitudes, but it is associated with population declines at higher altitudes.

The residuals of both models did not indicate any significant phylogenetic autocorrelation in data (full model: Moran's I = -0.02, SD = 0.01, p = 0.752; main effects model: Moran's I = -0.02, SD = 0.01, p = 0.986). Therefore, the results can be treated as not affected by a common evolutionary history of the focal species.

Discussion

Population trends of birds in the Giant Mts. clearly demonstrate the adverse effect of the climate change on high-altitude species in the past 30 years. It seems that the increasing temperatures, which were observed in the Giant Mts. over the same time period as the bird monitoring was performed, accompanied with the space limitation at high altitudes most likely have detrimental effect on populations of these species. Our results thus provide one of the first robust evidence that the alpine species, which are predicted to undergo serious climatically-induced range contractions in the future due to warming climate [2, 12], already started to move along this trajectory. For example, several studies recognized water pipit, specialist to alpine grasslands, as one of the species being at the highest risk of extinction due to future climatic warming in alpine environments [12, 50], possibly as a consequence of adverse impacts of higher temperatures on species' physiology, competitive interactions or nest predation rate [50]. Indeed, this species ranks among those with the steepest declines over the study period according to our data providing support for these predictions.

Possible mechanisms of the adverse impacts of warming climate on population of high-altitude species are insufficiently known [51]. Although the habitat composition does not seem to be altered at the highest altitudes in the Giant Mts., warmer climate can cause reduction of food supply for breeding birds, as was observed in the case of red grouse (*Lagopus scoticus*) in the Scottish Highlands [52], or alteration of species interactions, such as increased predation risk on hole-nesting birds due to earlier termination of hibernation in edible dormouse (*Glis glis*) in Moravia [53] or more intensive competition from the side of lower-altitude species [54]. Other factors might include direct detrimental effects of more frequent weather anomalies caused by higher temperatures such as strong storms [55] and physiological stress [56], or complex interactions between climate and local habitat conditions [57]. For example, particularly high temperatures at the start of the spring, which occur since 1990s also in the Giant Mts. [58], can cause rapid melting of snow followed by drought later during the vegetation season, which can constrain food supply in the time of rearing of chicks.

The relationship between migration strategy and bird population trends, when species migrating for longer distances had more negative trends in the Giant Mts. than species migrating for shorter distances, may be also caused by the climate change, although its effect is less clear in this case. Various studies found long-distance migrants to be more sensitive to the climate change impacts due to phenological mismatch [59]. The mismatch occurs when the

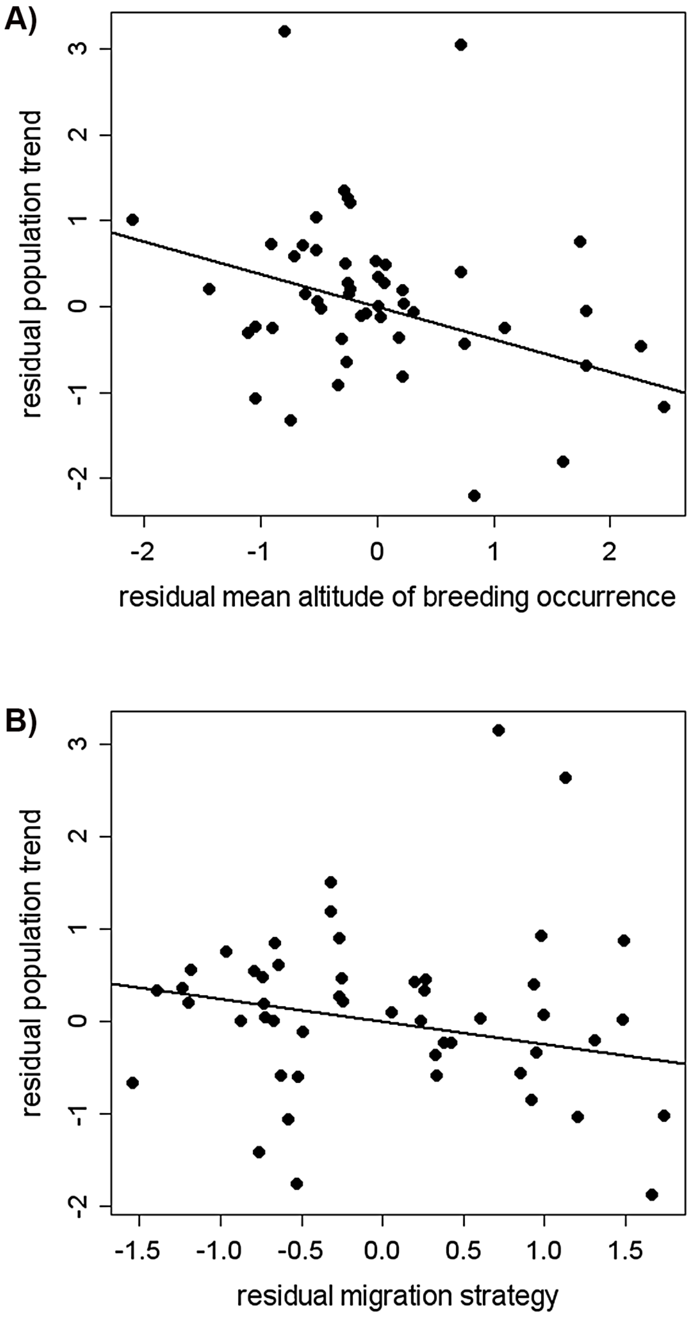

Fig 2. Relationships between long-term population trends of birds breeding in the Giant Mountains and their predictors. The trends were estimated for the time period 1984–2011 and are significantly related to (a) mean altitude of breeding occurrence at beginning of the monitoring period (the higher the value, the higher altitude a given species uses for breeding) and (b) migration strategy (the higher the value, the longer migration route a given species takes) as revealed by the linear main effects model (see text for more details on particular variables and the model). The plots show pure effects of the focal variables after controlling for the effects of all other traits.

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timing of maximum food supply does not correspond to the time of the highest demands for food during birds' breeding cycle leading to reduced survival of nestlings and ultimately to population decline [17, 60]. Alternatively, phenological changes in nest cover development can also play a role [61]. However, population consequences of the phenological mismatch need not to be always negative [62]. Moreover, populations of long-distance migrants may also decline due to various other factors such as habitat change at stopover sites and wintering grounds or droughts in Sahel zone [18].

Another possible consequence of climate change impacts on montane species are altitudinal range shifts. By these shifts the species most likely track their climatic optima that moved upward due to the climate change and thus escape the negative population consequences of warming climate [63]. These climatically-induced altitudinal range shifts were observed in montane species throughout the world [5, 6, 8, 64, 65] and birds in the Giant Mts. are among these examples [7]. Therefore, in species breeding at low altitudes, we expected less negative population trends for those showing the longer shifts than for those showing the shorter shifts as a consequence of climatic impacts, and the reverse pattern was our expectation in the case of species breeding at high altitudes. The significant interaction altitudinal range shift × mean altitude of breeding occurrence confirmed these expectations. The mechanism is most likely connected to space limitations near the mountain tops, when the observed shifts are inevitably resulting in range contractions and thus decline in abundance. In contrast, species breeding at lower altitudes have more space to shift upwards. As a consequence, the lower-altitude species with long altitudinal range shifts have less negative trends than long-shifting high-altitude species. They can indeed benefit from milder climate, perhaps due to extended breeding period providing time for more breeding attempts [66], which is hardly possible at high altitudes. These altitudinal differences in the effects of climate change may be accentuated by slightly higher rate of warming at higher altitudes in the Giant Mts., which produces a high pressure on high-altitude birds to shift upwards, but these shifts are not sufficient to track the rapid climate change contributing to population decline [67].

The other traits which were important predictors of interspecific variability in bird population trends in Europe (including the Czech Republic), i.e. life history strategy and European climatic niche [21, 23–25], did not show any significant effects on breeding bird populations in the Giant Mts. We suggest this difference can be explained by specificity of montane conditions differing to some extent from an “average” central European landscape where the data on these traits were collected (see [41] and references therein). As a consequence, the mechanisms which are specific to montane environment probably override the influence of the other drivers which are generally connected with the climate change.

We have to note that the climate change may be not the only driver of the trends in bird populations we detected [68]. Although the land use changes observed in other European mountain ranges such as abandonment of mountain meadows and pastures [69, 70] does not occur in the Giant Mts. [31], we cannot exclude the other factors could limit populations of some species together with climate. Specifically, forest regeneration on sites previously affected by industrial emissions [15] can contribute to the decline of whinchat or tree and meadow pipit [71]. However, land-cover data collected by Corine Land Cover database [72, 73] do not indicate that the proportions of main habitats at the large-scale changed in that direction (expansion of pastures by 14% and reduction of forest cover by 2% between 1990 and 2006). Therefore, we argue that the climate change is the most principal driving force responsible for the patterns in bird populations observed in the Giant Mts. Finally, the climate change *per se* can produce patterns in bird counts due to altered detectability of particular species [74]. Specifically, advancement of species’ arrival due to milder spring temperatures could result in higher counts earlier in the breeding season resulting in overestimates of bird abundance [75]. Although, we cannot exclude that such improved detectability may have contributed to the observed increases in lower-altitude species, this effect acts contra the pattern of declines in high-altitude species over the course of our study.

Conclusions and Conservation Implications

Our study provides evidence for adverse impacts of current climate change on populations of high-altitude species, here exemplified by birds in the Giant Mts., a central European mountain range. Since recent modelling work predicts for the future more intensive warming on mountains with potentially detrimental impacts on species adapted to the life at mountain tops [2, 12], their negative population trends already found over the last decades are alarming. The fact that the altitudinal range shift further magnifies the differences in trends between the species breeding at lower-altitudes from the trends of the species breeding at high-altitudes, calls for a need of more detailed further studies focusing on causal mechanisms of the impacts of warming climate on particular species. Although knowledge of such mechanisms is crucial for formulating the future conservation strategies, we suggest that it is possible to perform some conservation actions right now focusing on other possible human-induced threats to populations of high-altitude species such as building development, massive tourism and expansion of ski pistes and lifts [76–79]. These threats might contribute to the declines of high-altitude species together with (most likely dominant) climatic changes, but they are easier to mitigate by enforcement of local conservation legislation, especially in protected areas such as the Giant Mts. Along with these options for local actions, we suggest that global scale measures targeted to slow down or even reverse recent climate warming trends are necessary to guarantee the future for the montane species living at the highest altitudes.

Supporting Information

S1 Table. Mean temperatures in the Giant Mountains. The temperatures were measured at three meteorological stations (Labska bouda: 1315 m a.s.l., Pec pod Snezkou: 816 m a.s.l., Janske Lazne: 650 m a.s.l.) from 1980 to 2009.
(DOCX)

S2 Table. Population trends and traits of 50 bird species used in the present study. *Trend*–logarithm of mean annual population growth rate with standard error (SE) in the Giant Mountains between 1984 and 2011 computed using log-linear models in TRIM software. *Altitude*–mean altitude of breeding occurrence in the Giant Mts. in 1986–1988 calculated by Reif & Flousek (2012). *Altitudinal range shift*–mean annual shift of breeding occurrence in the Giant Mts. between 1984 and 2011 estimated as a slope of the regression line fitted through mean altitudes of occurrence of a given species in particular years. *Migration strategy*–classification of species according to their migratory behaviour as residents (1), short-distance migrants (2) and long-distance migrants (3) taken from Koleček & Reif (2011). *Life history strategy*–positions of species along a fast-slow life history gradient from “r-selected” to “K-selected” species calculated by Koleček & Reif (2011). *European climatic niche*–mean temperature within species’ European breeding ranges taken from Reif et al. (2013).
(DOCX)

S3 Table. Relationships among predictor variables used for the analysis. The relationships were expressed using Pearson correlation coefficient.
(DOCX)

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Author Contributions

Conceived and designed the experiments: JF JR. Performed the experiments: JF. Analyzed the data: TT JR JH JF. Wrote the paper: JR JF TT JH.

References

1. Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, et al. The biodiversity of species and their rates of extinction, distribution, and protection. Science. 2014; 344: 1246752. doi: 10.1126/science.1246752 PMID: 24876501
2. La Sorte FA, Jetz W. Projected range contractions of montane biodiversity under global warming. Proc R Soc B. 2010; 277: 3401–3410. doi: 10.1098/rspb.2010.0612 PMID: 20534610
3. Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, et al. Attributing physical and biological impacts to anthropogenic climate change. Nature 2008; 453: 353–357. doi: 10.1038/nature06937 PMID: 18480817
4. Lehikoinen A, Green M, Husby M, Kålås JA, Lindström A. Common montane birds are declining in northern Europe. J Avian Biol. 2014; 45: 3–14.
5. Popy S, Bordignon L, Prodon R. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. J Biogeogr. 2010; 37: 57–67.
6. Maggini R, Lehmann A, Kéry M, Schmid H, Beniston M, Jenni L, et al. Are Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes. Ecol Model. 2011; 222: 21–32.
7. Reif J, Flousek J. The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. Oikos. 2012; 121: 1053–1060.
8. Auer SK, King DI. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. Global Ecol Biogeogr. 2014; 23: 867–875.
9. Tryjanowski P, Sparks TH, Profus P. Uphill shifts in the distribution of the white stork Ciconia ciconia in southern Poland: the importance of nest quality. Divers Distrib. 2005; 11: 219–223.
10. Pautasso M. Observed impacts of climate change on terrestrial birds in Europe: an overview. Ital J Zool. 2012; 79: 296–314.
11. Sekercioglu CH, Schneider SH, Fay JP, Loarie SR Climate change, elevational range shifts, and bird extinctions. Conserv Biol. 2008; 22: 140–150. doi: 10.1111/j.1523-1739.2007.00852.x PMID: 18254859
12. Chamberlain DE, Negro M, Caprio E, Rolando A. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biol Conserv. 2013; 167: 127–135.
13. Harris J, Berton C, Putra DD, Gregory SD, Brook BW, Prawiradilaga DM, et al. Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Divers Distrib. 2014; 20: 773–785.
14. Chamberlain D, Arlettaz R, Caprio E, Maggini R, Pedrini P, Rolando A, et al. The altitudinal frontier in avian climate impact research. Ibis. 2012; 154: 205–209.
15. Flousek J. Impact of industrial emissions on bird populations breeding in mountain spruce forests in central Europe. Ann Zool Fenn. 1989; 26: 255–263.
16. Webb CT, Hoeting JA, Ames GM, Pyne MI, Poff NL. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecol Lett. 2010; 13: 267–283. doi: 10.1111/j.1461-0248.2010.01444.x PMID: 20455917
17. Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc R Soc B. 2010; 277: 1259–1266. doi: 10.1098/rspb.2009.1525 PMID: 20018784
18. Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Škorpilová J, et al. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis. 2014; 156: 1–22.
19. Sæther BE, Lande R, Engen S, Weimerskirch H, Lillegard L, Altwegg R, et al. Generation time and temporal scaling of bird population dynamics. Nature. 2005; 436: 99–102. PMID: 16001068
20. Owens IPF, Bennett PM. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proc Natl Acad Sci USA. 2000; 97: 12144–12148. PMID: 11005835
21. Jiguet F, Gadot AS, Julliard R, Newson SE, Couvet D. Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biol. 2007; 13: 1672–1684.

22. Sol D, Maspons J, Vall-llosera M, Bartomeus I, García-Peña GE, Piñol J, Freckleton RP. Unraveling the life history of successful invaders. Science 2012; 337: 580–583. doi: 10.1126/science.1221523 PMID: 22859488
23. Koleček J, Schleuning M, Burfield IJ, Báldi A, Böhning-Gaese K, Devictor V, et al. Birds protected by national legislation show improved population trends in Eastern Europe. Biol Conserv 2014; 172: 109–116.
24. Gregory RD, Willis SG, Jiguet F, Voříšek P, Klvaňová A, van Strien A, et al. An ndicator of the impact of climatic change on European bird populations. PLoS ONE. 2009; 4: e4678. doi: 10.1371/journal.pone.0004678 PMID: 19259270
25. Reif J, Böhning-Gaese K, Flade M, Schwarz J, Schwager M. Population trends of birds across the iron curtain: brain matters. Biol Conserv. 2011; 144: 2524–2533.
26. Devictor V, van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliola J, et al. Differences in the climatic debts of birds and butterflies at a continental scale. Nature Clim. Change. 2012; 2: 121–124.
27. Parmesan C. Ecological and evolutionary responses to recent climate change. Annual Rev Ecol Evol Syst. 2006; 37: 637–669.
28. Bellard C, Bertelsmeier C, Leadley C, Thuiller W, Courchamp S. Impacts of climate change on future of biodiversity. Ecol Lett. 2012; 15: 365–377. doi: 10.1111/j.1461-0248.2011.01736.x PMID: 22257223
29. Flousek J. Krkonoše/Karkonosze Bilateral Biosphere Reserve. In: Jeník J, Price M, editors. Biosphere Reserves on the Crossroads of Central Europe. Czech Republic—Slovak Republic. Praha: Unesco MAB; 1994. pp. 17–32.
30. Štursa J. The development of opinions on the geo-biodiversity of the Giant Mountains' arctic-alpine tundra and its conservation. Opera Corcontica. 2013; 50/S: 55–74.
31. Flousek J, Hartmanová O, Štursa J, Potocki J, editors. Giant Mountains—Nature, History, Life. Praha: Nakladatelstvi Milos Uhlir—Baset; 2007.
32. Soukupová L, Kociánová M, Jeník J, Sekyra J. Arctic-alpine tundra in the Krkonoše, the Sudetes. Opera Corcontica. 1995; 32: 5–88.
33. Krahulec F, Blažková D, Balátová-Tuláčková E, Štursa J, Pecháčková S, Fabšičová M. Grasslands of the Krkonoše Mountains: plant communities and their dynamics. Opera Corcontica. 1996; 33: 3–250.
34. Newson SE, Massimino D, Johnston A, Baillie SR, Pearce-Higgins JW. Should we account for detectability in population trends? Bird Study. 2013; 60: 384–390.
35. Pannekoek J, van Strien AJ. TRIM 3 Manual. Voorburg: Statistics Netherlands; 2005.
36. Salido L, Purse BV, Marrs R, Chamberlain DE, Schultz S. Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. Ecography. 2012; 35: 604–613.
37. Laaksonen T, Lehikoinen A. Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. Biol. Conserv. 2013; 168: 99–107.
38. Herrando S, Anton M, Sardà -Palomera F, Bota G, Gregory RD, Brotons L. Indicators of the impact of land use changes using large-scale bird surveys: Land abandonment in a Mediterranean region. Ecol Indic. 2014; 45: 235–244.
39. Virkkala R, Lehikoinen A. Patterns of climate-induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. Global Change Biol. 2014; 20: 2995–3003.
40. Cepák J, Klvaňa P, Škopek J, Schröpfer L, Jelínek M, Hořák D et al. Bird Migration Atlas of the Czech Republic and Slovakia. Praha: Aventinum; 2008.
41. Koleček J, Reif J. Differences between the predictors of abundance, trend and distribution as three measures of avian population change. Acta Ornit. 2011; 46: 143–153.
42. Reif J, Prylová K, Šizling AL, Vermouzek Z, Šťastný K, Bejček V. 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. J Ornithol. 2013; 154: 359–370.
43. Hagemeijer WJM, Blair MJ, editors. The EBCC atlas of European breeding birds. Their distribution and abundance. London: T and AD Poyser; 1997.
44. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, et al. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 2013; 36: 27–46.
45. Schielzeth H. Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol. 2010; 1: 103–113.
46. Harvey PH, Purvis A. Comparative methods for explaining adaptations. Nature. 1991; 351: 619–624. PMID: 2052088
47. Paradis E. Analysis of phylogenetics and evolution with R. New York: Springer; 2006.

48. Paradis E, Bolker B, Claude J, Cuong HS, Desper R, Durand B, et al. Package 'ape'. Analyses of phylogenetics and evolution, version 2.4–1. Vienna: R Foundation for Statistical Computing; 2009.
49. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. The global diversity of birds in space and time. Nature. 2012; 491: 444–448. doi: 10.1038/nature11631 PMID: 23123857
50. Melendez L, Laiolo P. The role of climate in constraining the elevational range of the Water Pipit *Anthus spinoletta* in an alpine environment. Ibis. 2014; 156: 276–287.
51. Jenouvrier S. Impacts of climate change on avian populations. Global Change Biol. 2013; 19: 2036–2057.
52. Fletcher K, Howarth D, Kirby A, Dunn R, Smith A. Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. Ibis. 2013; 155: 456–463.
53. Adamík P, Král M. Climate and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds. J Zool. 2008; 275: 209–215.
54. Jankowski JE, Robinson SK, Levey DJ. Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. Ecology. 2010; 91: 1877–1884. PMID: 20715605
55. Robinson RA, Baillie SR, Crick HQP. Weather-dependent survival: implications of climate change for passerine population processes. Ibis. 2007; 149: 357–364.
56. Barbosa A, Merino S, Benzal J, Martınez J, Garcıa-Fraile S. Population variability in heat shock proteins among three Antarctic penguin species. Polar Biol. 2007; 30: 1239–1244.
57. Mantyka-Pringle CS, Martin TG, Rhodes JR. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biol. 2012; 18: 1239–1252.
58. Metelka L, Kliegrová S. Systematic changes of basic climatic characteristics in the Giant Mountains between 1961 and 2005. Hradec Kralove: Czech Hydrometeorological Institute; 2006.
59. Both C, Visser ME. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature. 2001; 411: 296–298. PMID: 11357129
60. Both C, Bouwhuis S, Lessells CM, Visser ME. Climate change and population declines in a long-distance migratory bird. Nature. 2006; 441: 81–83. PMID: 16672969
61. Tryjanowski P, Sparks TH, KuŹniak S, Czechowski P, Jerzak L. Bird migration advances more strongly in urban environments. PLoS ONE. 2013; 8: e63482. doi: 10.1371/journal.pone.0063482 PMID: 23667625
62. Reed TE, Jenouvrier S, Visser ME. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. J Anim Ecol. 2013; 82: 131–144. doi: 10.1111/j.1365-2656.2012.02020.x PMID: 22862682
63. Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H. A significant upward shift in plant species optimum elevation during the 20th century. Science. 2008; 320: 1768–1771. doi: 10.1126/science.1156831 PMID: 18583610
64. Chen I. Elevation increases in moth assemblages over 42 years on a tropical mountain. Proc. Natl. Acad. Sci. USA. 2009; 106: 1479–1483. doi: 10.1073/pnas.0809320106 PMID: 19164573
65. Grytnes J-A, Kapfer J, Jurasinski G, Birks HH, Henriksen H, Klanderud K, et al. Identifying the driving factors behind observed elevational range shifts on European mountains. Global Ecol Biogeogr. 2014; 23: 876–884.
66. Schaefer H-C, Jetz W, Böhning-Gaese K. Impact of climate change on migratory birds: community reassembly versus adaptation. Global Ecol. Biogeogr. 2008; 17: 38–49.
67. Devictor V, Julliard R, Couvet D, Jiguet F. Birds are tracking climate warming, but not fast enough. Proc. R. Soc B. 2008; 275: 2743–2748. doi: 10.1098/rspb.2008.0878 PMID: 18713715
68. Clavero M, Villero D, Brotons L 2011. Climate change or land use dynamics: Do we know what climate change indicators indicate? PLoS ONE. 2011; 6: e18581. doi: 10.1371/journal.pone.0018581 PMID: 21533025
69. Laiolo P, Dondero F, Ciliento E, Rolando A. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. J Appl Ecol. 2004; 41: 294–304.
70. Álvarez-Martínez JM, Suárez-Seoane S, Stoorvogel JJ, Calabuig ED. Influence of land use and climate on recent forest expansion: a case study in the Eurosiberian-Mediterranean limit of north-west Spain. J Ecol. 2014; 102: 905–919.
71. Flousek J, Gramsz B. Atlas of breeding bird distribution in the Giant Mountains (1991–1994). Vrchlabi: Sprava KRNAP; 1999.
72. Büttner G, Feranec G, Jaffrain G. Corine land cover update 2000. Technical guidelines. Copenhagen: European Environment Agency; 2002.

73. European Environment Agency. CLC2006 technical guidelines. Copenhagen: European Environment Agency; 2007.

74. Tryjanowski P, Sparks TH. Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. Int J Biometeor. 2001; 45: 217–219.

75. Lehikoinen A. Climate change, phenology and species detectability in a monitoring scheme. 2013;55: 315–323.

76. Arlettaz R, Patthey P, Baltic M, Leu T, Schaub M, Palme R, et al. Spreading free-riding snow sports represent a novel serious threat for wildlife. Proc R Soc B. 2007; 274: 1219–1224. PMID: 17341459

77. Patthey P, Wirthner S, Signorell N, Arlettaz R. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. J Appl Ecol. 2008; 45: 1704–1711.

78. Caprio E, Chamberlain DE, Isaia M, Rolando A. Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. Biol Conserv. 2011; 144: 2958–2967.

79. Sato CF, Wood JT, Lindenmayer DB. The effect of winter recreation on alpine and subalpine fauna: a systematic review and meta-analysis. PLoS ONE. 2013; 8: e64282. doi: 10.1371/journal.pone.0064282 PMID: 23691190

Paper IV

Impacts of climate change on long-distance migrants: a demographic framework

Running head: Climate change impacts on avian demography

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Abstract

Climate change causes marked changes of current biota from genes to ecosystems. Various mechanisms of climatic impacts on animal populations have been described, but studies linking their influence on demography to population dynamics are almost absent. Here we took long-distance migratory birds wintering in sub-Saharan Africa, a species group suffering from particularly steep population declines, to disentangle the contribution of particular demographic mechanisms underlying their population changes. Using data from a long-term mist-netting programme in the Czech Republic, we built population models assessing: (i) the influence of spring advancement on species' breeding productivity, (ii) the influence of water availability in species' non-breeding grounds on adult survival, together with (iii) the carry-over effect of these non-breeding climatic conditions on species' breeding productivity; finally, (iv) we quantified relative contribution of these demographic mechanisms to bird population changes. We found a strong support for the phenological mismatch hypothesis because migrants' breeding productivity was lowest in years with the most advanced spring phenology and vice versa. Adult survival was higher in years with higher water availability in non-breeding grounds and the relationship was significant when considering the Sahel zone, and not for the species' entire non-breeding ranges. The carry-over effect of non-breeding climatic conditions on breeding productivity was weak. Quantifying the contributions of breeding productivity and adult survival to long-distance migrants' population changes showed important influence of both mechanisms, although the former one seems to be stronger. Therefore, both breeding and non-breeding climatic conditions shape the widespread population declines of long-distance migrants but the key more likely lies in the non-breeding grounds.

Introduction

Climate change ranks among the top drivers of the current biodiversity crisis (Urban, 2015). It causes shifts in species' geographic ranges (Pecl et al., 2017), alters interspecific interactions (Devictor et al., 2012) and changes the timing of the main events within species' annual cycles (Lavergne et al., 2010). Despite its widespread influence on animal populations detectable at the scale of entire continents (Stevens et al., 2016), causal mechanisms underlying the population-level impacts of climatic conditions are still poorly understood (Bellard et al., 2012).

Here we focused on elucidation of the mechanisms underpinning the climatic impacts on animal populations using long-distance migratory birds as model organisms. Species migrating over long distances are exposed to various adverse impacts in different regions (Wilcove & Wikelski, 2008), resulting in steeper declines of their populations compared to other species (Reif, 2013; Gilroy et al., 2016). Various anthropogenic pressures were suggested as drivers of these declines (Sanderson et al., 2006; Heldbjerg & Fox, 2008). However, recent evidence indicates that the climate-induced impact, especially in the context of the recent climate change, is the most important factor (Newton, 2004; Calvert, Walde & Taylor, 2009; Vickery et al., 2014).

The climate affects long-distance migrants on both breeding and non-breeding grounds. The most important pressure related to climate change on the breeding grounds is the phenologic mismatch. Changing climate manifesting by raising spring temperatures (Schwartz, Ahas & Aasa, 2006) results in phenology shifts, but these shifts differ among trophic levels (Devictor et al., 2012). Higher trophic levels usually shift at slower pace than lower trophic levels, which yields fitness consequences (Winder & Schindler, 2004; Thackeray et al., 2010; Donnelly, Yu & Liu, 2014). In the case of birds, mismatch occurs between the phenology of their food and their breeding. Earlier timing of budburst and leaf unfolding is accompanied with earlier hatching of caterpillars, the most important avian food source in breeding period (Cramp, 1977). Bird phenology advances as well, however, long-distance migrants are not able to adjust their phenology to track these changes adequately (Rubolini, Saino & Moller, 2010; Saino et al., 2011; Kolarova & Adamik ,2015), possibly due to innate constraints of their annual cycle (Rubolini, Saino & Moller, 2010). This trophic mismatch results in lower breeding productivity of long-distance migratory birds (Both & Visser, 2005; Clausen & Clausen, 2013) and subsequent population decline (Both et al., 2006; Møller, Rubolini & Lehikoinen, 2008).

Climate also affects long-distance migrants in non-breeding grounds. For example, the relationship between precipitation in the Sahel and annual survival was described for several European bird species wintering in sub-Saharan Africa (Winstanley, Spencer & Williamson, 1974; Peach, Baillie & Underhill, 1991) and a similar pattern was observed at the American continent (Studds & Marra, 2007). Climatic conditions in non-breeding season may not only affect migrants' survival, but may also carry-over to affect the breeding performance (Newton, 2004; Norris & Marra, 2007). For instance, lower water availability in Africa may delay migrants' arrival to the breeding grounds (Saino *et al.* 2004, 2007; Gordo & Sanz, 2006, 2008), reduce body condition after arrival (Smith & Moore, 2003), and affect breeding performance (Schaub, Jakober & Stauber, 2011; Rockwell, Bocetti & Marra, 2012; Norman & Peach, 2013; Finch et al., 2014). The influence of carry-over effect on population dynamics is complicated, since the apparent negative effect of non-breeding grounds' conditions on survival might be also affecting the population positively via reducing intensity of intraspecific competition at the breeding grounds (Calvert, Walde & Taylor, 2009).

However, while the studies cited above described particular mechanisms how climate might affect bird populations via factors acting specifically at breeding or non-breeding grounds, there has not been so far, to our knowledge, performed a comprehensive assessment of their relative importance and contribution to the population dynamics of long-distance migrants. Previous attempts in this respect were of limited importance due to neglecting some key demographic parameters (e.g. the absence of contrast between breeding productivity and annual survival), focusing on a single species or covering only a few sites (see Knudsen et al., 2011 and Vickery et al., 2014 for reviews). At the same time, general, multi-species studies focusing on the comparison of relative contribution of particular mechanisms in shaping species' populations over their whole annual cycle 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 (Thingstad, Hogstad & Speed, 2015).

For this purpose, we dismantle the whole population dynamics of long-distance migratory birds using a conceptual demographic framework recognizing the key population limitations within the birds' annual cycle (Fig. 1). Based on this framework, we test the hypotheses about the most important climatic effects on demographic parameters of long-distance migratory birds (summarized in Table 1) using unique data from a national long-term constant effort mist-netting programme. Finally, we relate particular demographic parameters to population growth rates of birds and assess the relative importance of these factors as drivers of population dynamics in long-distance migrants.

Fig. 1: Decomposition of mechanisms acting in population dynamics of long-distance migrants.

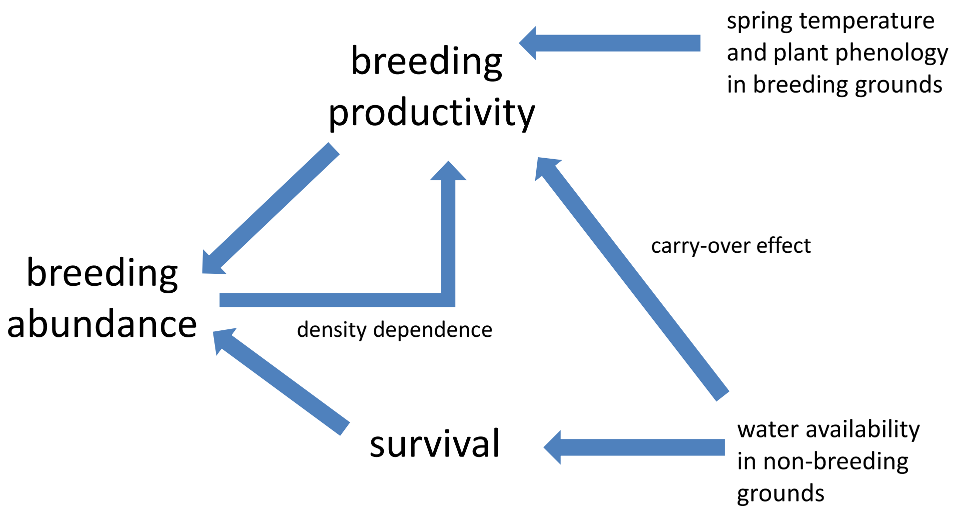


Table 1: Hypotheses about the influence of climatic factors on demographic parameters of long-distance migratory birds.

Hypothesis	Driver	Mechanism	Prediction
Phenological mismatch	Advancement of spring phenology (higher spring temperatures, earlier leaf unfolding).	Peak in food supply occurs earlier than optimum for rearing birds' offspring.	Lower breeding productivity of birds with rigid migration strategies (i.e. long-distance migrants) in years with warmer springs.
Negative density dependence	High abundance of breeding population.	Increased intraspecific competition limits resource availability for breeding.	Lower breeding productivity in years with higher breeding abundance.
Survival limitation	Drought in non-breeding grounds.	Reduced water availability causes habitat deterioration and food shortage.	Lower survival in years with lower water availability in non-breeding grounds.
Carry-over effect	Drought in non-breeding grounds.	Reduced water availability causes habitat deterioration and food shortage.	Lower breeding productivity in years with lower water availability in non-breeding grounds.

Materials and Methods

Data

Birds

Bird population data were collected within 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 (Cepák & Škopek, 2005). 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 (Baillie et al., 1986, Baillie, 1990). Since the sampling effort is constant at each site across years, these data enable modelling estimates reasonable 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).

At each of 43 sites scattered throughout the Czech Republic, birds were mist-netted during 9 visits in ca 10-day intervals covering the advanced breeding season (May - July) every year. During each visit of a given site, the ringer opened at least 70 m of mist nets (mean across all sites = 111.7 m; range 70-168 m) for six hours and sampled the birds. The exact location, total length and operation time of mist nets were kept constant at each site across all visits in a given year, as well as across all years. The sites occurred mostly in wet and shrubby habitats (e.g. reedbeds, willow carrs, scrubland) and at forest edges. Forest interior habitats and human settlements were not sampled. Each trapped bird was aged to discriminate adults (i.e. birds born earlier than in the current calendar year) and juveniles (i.e.

birds born during the breeding season of the current calendar year) of a given species. These data allowed to estimate population changes (see section “Population changes”), as well as breeding productivity (see section “Breeding productivity”). Capture histories of individual birds allowed for estimation of adult survival (see section “Adult survival”).

For further analysis, we excluded species recorded at low proportion of sites (less than one sixth) in any of the years. Moreover, we excluded *Hirundo rustica* due to its irruptive occurrence at CES sites which do not sample its breeding sites. Captures of this species thus cannot be used to estimate demographic parameters. As a result, we considered 11 long-distance migratory species for further analysis, along with 13 other species of different migratory strategies according to the classification of Cepák et al. (2008): one resident species, four partial migrants and eight short-distance migrants (Table S1). For the survival analysis (see below), we excluded three species of long-distance migrants with less than 30 inter-annual recaptures (Table S1), thus analysing eight long-distance migrants for this purpose.

To study the adult survival, it is important to identify the non-breeding grounds of the focal species (Kéry & Royale 2016). Non-breeding grounds of Czech populations of long-distance migrants were identified by Cepák et al. (2008). Cepák et al. (2008) divided sub-Saharan Africa into four regions (Fig. S1) and, according to ringing recoveries originating from breeding populations from the Czech Republic and neighbouring countries, they defined the sub-Saharan non-breeding ground of each species as one or more of these regions (Table S1). Therefore we used the regions indicated by Cepák et al. (2008) for a given species as its non-breeding range for further analysis. The division is quite coarse since the ringing recovery data from sub-Saharan Africa are scarce for most of the species (Cepák et al., 2008). However, it is comparable to divisions used in other studies considering sub-Saharan non-breeding grounds for an analysis of population dynamics of European breeding bird populations (e.g. Thaxter et al., 2010; Jørgensen et al., 2016).

Using available information from geolocators (Adamik et al., 2016; Koleček et al., 2016), ring recoveries of Czech birds (Cepák et al., 2008; Cepák, unpublished data), and complemented with faunistic observations from Africa (eBird.org), we found that Czech populations of most of the focal species arrive to sub-Saharan Africa at the end of August or in September, and stay until April. For the purposes of our study, we thus defined the non-breeding period in sub-Saharan Africa as August-April and considered these months for calculations of climatic conditions in non-breeding grounds in further analysis.

Climate

We focused on two sets of climatic parameters: (i) measures of spring progress at breeding grounds where we expect relationships to advancement of spring phenology having thus impact on birds' breeding productivity and (ii) water availability at non-breeding grounds where we expect relationships to birds' annual survival (see Table 1).

To describe spring phenology on breeding grounds, we used following variables supplied on annual basis from 2004 to 2014 by Czech Hydrometeorological Institute. First, mean temperature in early spring (March and April) shapes environmental conditions preceding or during arrival of long-distance migrants and controls bud burst and invertebrates phenology (Finch et al., 2014). Second, mean temperature in late spring (May and June) reflects conditions during breeding of long-distance migrants (Pearce-Higgins et al., 2015). Third, we used growing degree-days (GDD5), i.e. sum of mean daily temperatures above 5°C since first day of spring onset, defined as the first period of 6 consecutive days with mean temperature >= 5°C in a given year, in March and April. Growing degree-days should mirror the influence of temperature on plant and invertebrate phenology in a biologically more relevant way than the mean temperature (Ambrosini et al., 2011; Saino et al., 2011; Cayton et al., 2015). Fourth, we used data on woody plant phenology – the Julian date of 10% leaf unfolding of *Salix capria*, *Tilia cordata* and *Sambucus nigra*. This phenophase means that 10% of the plant leaves started to unfold, having the whole midrib visible already, but the leaf is still partially folded (Czech Hydrometeorological Institute, 2009). Temperature and GDD5 were taken as an average from 30 meteorological stations scattered throughout the area of the Czech Republic; plant phenology was taken as a median date from 26-27 stations where these data were available.

To measure water availability in non-breeding grounds in sub-Saharan Africa, we used the ratio of actual to potential evapotranspiration (AET/PET). Unlike commonly used measures like rainfall, which is a measure of water income, or indirect measures like NDVI, AET/PET much more directly quantifies the amount of water available in the ecosystem (Šímová & Storch, 2017). The monthly data on AET/PET were obtained from MODIS MOD 16 (Mu, Zhao & Running, 2011), in particular MOD16A2 monthly data in the GeoTIFF raster format with 0.5 degree resolution. For each of the four regions where the Czech long-distance migrants occur in sub-Saharan Africa, we extracted average AET/PET for each month. Water availability is highly variable in space and thus averaging across large areas covering both extremely wet and arid sites (such as our focal non-breeding regions) can result in mean values that are biologically irrelevant. Therefore, following the idea of Hawkins et al. (2003), we assume that the water limitation occurs in the most arid sites and we set the upper limit for AET/PET to 0.2 corresponding to the highest value in Sahel region at the beginning of the dry season. As a consequence, grid cells with AET/PET higher than 0.2 in a given month count as 0.2. Next, we averaged the monthly values across each winter season (August to April) from 2004/2005 to 2013/2014. Finally, we computed area-weighted average across the combination of the four regions where a given species spends its non-breeding season in sub-Saharan

Africa (see above). Together with the discrimination of these four regions, we divided sub-Saharan Africa on the Sahelian part (defined as north of the 13° latitude), and the southern part (south of the 13° latitude). Sahel zone has extraordinary importance for long-distance migrants compared to other regions because nearly every bird migrating across Sahara desert stops and refuels in this area (Risely, Blackburn & Cresswell, 2015). We thus expected particularly strong effects of water availability in Sahel on survival of long-distance migrants.

Statistical analyses

Population changes

For each species, we produced yearly relative abundance index using generalized estimating equations (GEE) with Poisson error distribution and log link function in program TRIM applying the "effects for each time point" model (Pannekoek & Van Strien, 2005). In this model, the total count of adult individuals captured in a given year and site is taken as a response variable, and year and site as independent categorical variables. The GEE procedure took into account first-order serial correlation of the counts in time series (AR(1)), as well as overdispersion of the counts. The abundance index (on the log scale) then consists of the resultant year coefficients (and their standard errors).

Breeding productivity

To assess the impact of climate on breeding productivity, we proceeded in several steps. First, for each species separately, we produced yearly relative productivity index using quasibinomial generalised linear model (GLM) in R environment (R Core Team, 2016). For each year and site, the proportion of the total count of juvenile individuals captured to total count of all individuals captured is modelled as a function of year and site as independent categorical variables. Logarithm of productivity index then consists of the resultant year coefficients (and their standard errors). To avoid problems with zero standard error for the reference year in the next step, we took the year 2013, which was indeed excluded from further analysis due to unusual weather conditions, see below, as a reference level.

In the next step, we computed the impact of particular climatic variables on species' productivity indices. In this analysis, we ran separate models for each species and climatic variable. We excluded year 2013 because of extreme weather conditions during late spring with heavy rain and floods in May and June resulting in extraordinary low breeding productivity obviously unrelated to our focal effect of spring phenology. For the analysis, we used a variant of linear regression based on meta-analytic Bayesian approach which takes into account the uncertainty of response variable. Rather than taking the response variable as a firm given number, it is taken as a normal distribution with given standard error (Kéry & Royle, 2016). Each model contained logarithm of yearly productivity index as a response variable with a normal distribution with a given standard error, and a single, normalized climate variable as a predictor. Moreover, we included logarithm of relative abundance index in a given year (calculated as described above) into each model to account for possible confounding effects of density dependence. These linear regression models were fitted using MCMC procedure in Bayesian environment in JAGS (Plummer, 2003), with 3 chains, 100 000 iterations, first half disposed as a burn-in.

Further, we compared the impacts of particular climate variables in the analysis across all species of long-distance migrants. For each climate variable, we ran a model in JAGS, with 3 chains, 400 000 iterations, thinning factor 20 and disposing first half as a burn-in. To assess the proportion of variance explained by the climate variable (after filtering out the effect of density dependence), we used Bayesian measure of the proportion of explained variance (R^2_var), computed as $(\sigma^2_{\text{total}} - \sigma^2)/\sigma^2_{\text{total}}$, where σ^2 is model residual variance and

σ^2_{total} is residual variance of a so called 'constant model' (Kéry & Royle, 2016, their chapter 5.7). In our case, the constant model is the equivalent model without the climatic covariate but still with the density dependence and species as a random intercept effect and a random slope effect. We also computed a variant of these models with the random intercept only (i.e. without the random slope) because such an approach is used in the vast majority of studies. However, although this variant brings more significant results, it underestimates R^2_var.

Finally, we used the same model as in the previous step, but we added the interaction of a given climatic variable with the migratory strategy after supplementing the set of the long-distance migrants by data on 13 bird species with other migratory strategies (see section "Bird data" above). The species was taken as a random intercept and a random slope effect. The contrast between long-distance migrants and other migratory strategies was evaluated on the posterior distribution of the coefficients, comparing the coefficient of long-distance migrants with the weighted average (weighted by the number of species) of the coefficients of the remaining migratory strategies.

All climatic variables were normalized to zero mean and unit variance before the analysis.

Carry-over effect

The impact of carry-over effect of climatic conditions at sub-Saharan non-breeding grounds on breeding productivity was tested in the same way as the impact of spring advancement (see above), considering only long-distance migrant species and replacing spring climate variables with a single AET/PET variable in the non-breeding grounds. We considered three variants of non-breeding ranges: (i) the whole non-breeding range, (ii) its Sahelian part north of 13° latitude and (iii) in its southern part south of 13° latitude (see section "Climate data" for more details on definitions of these parts) in separate models. To estimate the relationships across all long-distance migrants, we run the models with species coded as random slope and random intercept effects, as well as the models containing the species as the random intercept only (see above).

Adult survival

To assess the impact of water availability in sub-Saharan Africa on survival of adult birds of each long-distance migrant species, we used Cormack-Jolly-Seber (CJS) survival model (White & Burnham, 1999). Inter-annual survival between two consecutive years was modelled as a linear function (after logit transformation) of AET/PET in a given non-breeding season (August-April, see section "Climatic data") in the non-breeding range of a given species. Similarly to the modelling of the carry-over effects, we considered three variants of non-breeding areas in separate models (see above). Models were computed in program MARK (White & Burnham, 1999) ran within the R-package RMark (Laake, 2013).

The estimates of adult survival are often biased due to the presence of transient individuals in the focal population (Pradel et al., 1997). We accounted for the presence of transients using the method described by Johnston et al. (2016). The transience, i.e. the probability that an individual is transient, was modelled as a constant over years. We expected that the proportion of transients may differ according to the habitat type for some species. Numerous CES sites were dominated by reedbeds, while the others were not. Therefore, we initially modelled transience as specific per two types of sites when one type was recognized as sites with more than 50% coverage of reedbeds and the second type were the remaining sites. We found that there were significantly more transients in the sites dominated by reeds in all three *Sylvia* species, while in the other species no significant effect of habitat was observed so we did not further discriminate the two types of sites in their case. There was no significant temporal trend in transience for any of the species.

Next, we computed the percentage of deviance explained by the climate variable (R^2_dev) using the ANODEV method (Grosbois et al., 2008, their p. 378, eqn 6). Then, to assess the overall impact across species, we computed the mean of all AET/PET coefficients across all species, taking their standard errors into account using the meta-analytic Bayesian approach in the same way as described in the "Breeding productivity" section above. This model was fit in JAGS, with 3 chains, 200 000 iterations and disposing first half as a burn-in.

We also produced yearly relative survival index of adult birds for each species to investigate its relationship to annual population changes (see the next section). For this purpose, we employed the CJS survival model, where the inter-annual survival was modelled as a function of year as categorical explanatory variable.

Linking demographic parameters with population dynamics

In this analysis, we tested whether breeding productivity or adult survival limits population growth of long-distance migrants.

First, for each species, we performed linear regression with logarithm of inter-annual population growth between two consecutive years (i.e. $\log I_{t+1}/I_t$, where I_t is a population index in year t) as a dependent variable and the logarithm of yearly relative productivity index as an explanatory variable. Second, we applied the same model but replaced the logarithm of productivity index with logit of the survival index. Each value of productivity and survival index entered the analysis as a normal distribution (on log and logit scale, respectively) with a given standard error, again using meta-analytic Bayesian approach as described above. Here we excluded the inter-annual change between years 2013/2014 due to extreme weather conditions and thus very low productivity in 2013 unrelated to factors tested here (see above). Models were fit in JAGS, with 3 chains, 100 000 iterations, first half disposed as a burn-in. Percentage of explained variance (R^2_var) was computed the same way as in the Breeding productivity (see section “Breeding productivity”), where the “constant” model is an equivalent model with the intercept only.

Next, we performed this analysis across species (note that three species not entering the survival analysis due to their small sample size, see above, were not included). Once again, we tested the effects of productivity index and survival index in two separate models. Logarithm of population growth was modelled as a linear function of productivity and survival indices, with species as a random intercept and random slope effect. As in the previous analyses, the covariates were taken as normal distributions (on log scale) with given standard error. Models were fitted in JAGS, with 3 chains, 400 000 iterations, thinning factor 20, and disposing first half as a burn-in. Percentage of explained variance (R^2_var) was computed the same way as in the case of breeding productivity (see section “Breeding productivity”), where the “constant” model is an equivalent model with intercept only and species as random intercept effect to keep the interspecific component of variance out of the equation.

Additional information on the modelling techniques

For model comparison, we used Deviance Information Criterion (DIC) and Penalized Expected Deviance (PED) recommended for these purposes (Plummer, 2008). Convergence was tested using potential scale reduction factor (Gelman & Rubin, 1992) using *gelman.diag* function from R package ‘coda’ (Plummer et al., 2016). Since we were interested in responses of present-day species to environmental changes within a time period considerably shorter than the time scales of evolutionary processes, we did not apply so called phylogenetic “correction” in cross-species analyses (see Westoby, Leishman & Lord, 1995 and Bello et al., 2015 for more arguments on this topic).

Results

Breeding productivity

After factoring out density-dependence, breeding productivity of long-distance migrants was negatively related to more advanced spring phenology (Table 2a). The relationship was significant for the GDD5 (Table 2a), but the models for the phenology of *Salix caprea*, *Tilia cordata* and for the early spring temperature also explained considerably high amount variability in breeding productivity being close to significance (Table 2a) and indeed turned to significance in the model variant with species as the random intercept, i.e. without the random slope effect (Table S2a). Focusing on particular species, breeding productivity was negatively affected by the advancement of spring phenology in *Acrocephalus palustris* (Table S3).

The pattern found in long-distance migrants markedly contrasted with the relationships found for species of other migratory strategies: breeding productivity of resident species, partial and short-distance migrants was not negatively affected by more advanced spring phenology and even increased in warmer springs in short-distance migrants as shown by their relationships to the phenology of *Salix caprea* and *Tilia cordata* and to the early spring temperatures (Fig. 2, Table S4).

Density of breeding populations had always strongly negative effect on breeding productivity of birds irrespective to their migratory strategies (Table 2a, Table S4), although the relationships were mostly not significant when considering each species separately (Supplementary Tables S3 and S5).

Carry-over effect

The carry-over effect of climatic conditions at sub-Saharan non-breeding grounds on long-distance migrants' breeding productivity proved insignificant, although some indication of a positive relationship was found between breeding productivity and AET/PET in the southern part of non-breeding range (Table 2b), which became significant when random slope was not included in the model (Table S2b). Insignificant relationships were also observed in separate analyses for every species (Supplementary Table S5).

Table 2: Relationships between breeding productivity of long-distance migrants and climatic variables reflecting (a) spring phenology at breeding grounds and (b) water availability at non-breeding grounds (indicating so called carry-over effect) estimated by Bayesian meta-analytic models. Each variable was tested in a single model taking also the potential effect of population density into account. Model performance was assessed by Deviance Information Criterion (DIC) and Penalized Expected Deviance (PED). Significant relationships (95% confidence limits not overlapping zero) are in bold. See Methods section for more details on model formulation and variable characteristics.

Climatic variable	Effect of climatic variables				Effect of population density			Model characteristics			
	slope	2.5%	97.5%	R^2_var[1]	slope	2.5%	97.5%	DIC	PED	ΔDIC	ΔPED
a) Climatic variables at breeding grounds:											
GDD5[2]	**-0.119**	**-0.209**	**-0.022**	0.62	**-0.629**	**-1.005**	**-0.255**	102.0	139.3	0.0	0.0
early spring temperature[3]	-0.103	-0.207	0.009	0.44	**-0.614**	**-0.997**	**-0.224**	107.9	150.9	5.9	11.6
late spring temperature[4]	-0.030	-0.118	0.057	-0.03	**-0.439**	**-0.820**	**-0.046**	114.6	169.7	12.5	30.3
Salix caprea[5]	0.112	-0.007	0.220	0.57	**-0.591**	**-0.966**	**-0.212**	104.9	143.3	2.8	4.0
Tilia cordata[5]	0.094	-0.024	0.198	0.50	**-0.583**	**-0.941**	**-0.196**	106.8	150.8	4.7	11.4
Sambucus nigra[5]	-0.015	-0.118	0.084	-0.06	**-0.417**	**-0.809**	**-0.016**	115.1	176.8	13.1	37.4
b) Climatic variables at non-breeding grounds:											
AET/PET[6] whole range[7]	0.050	-0.063	0.165	-0.03	**-0.433**	**-0.812**	**-0.039**	113.9	168.2	11.9	28.8
AET/PET[6] Sahelian part[8]	0.014	-0.072	0.106	-0.09	**-0.421**	**-0.813**	**-0.017**	115.3	173.0	13.3	33.7
AET/PET[6] south of Sahel[9]	0.175	-0.031	0.390	0.10	**-0.490**	**-0.866**	**-0.107**	112.6	163.1	10.6	23.8

[1] proportion of variance explained by the climate variable, after removing the variance explained by density dependence (see Methods for details)

[2] growing degree days - accumulated temperature above 5°C

[3] mean temperature in March and April

[4] mean temperature in May and June

[5] julian date of 10% leaf unfolding

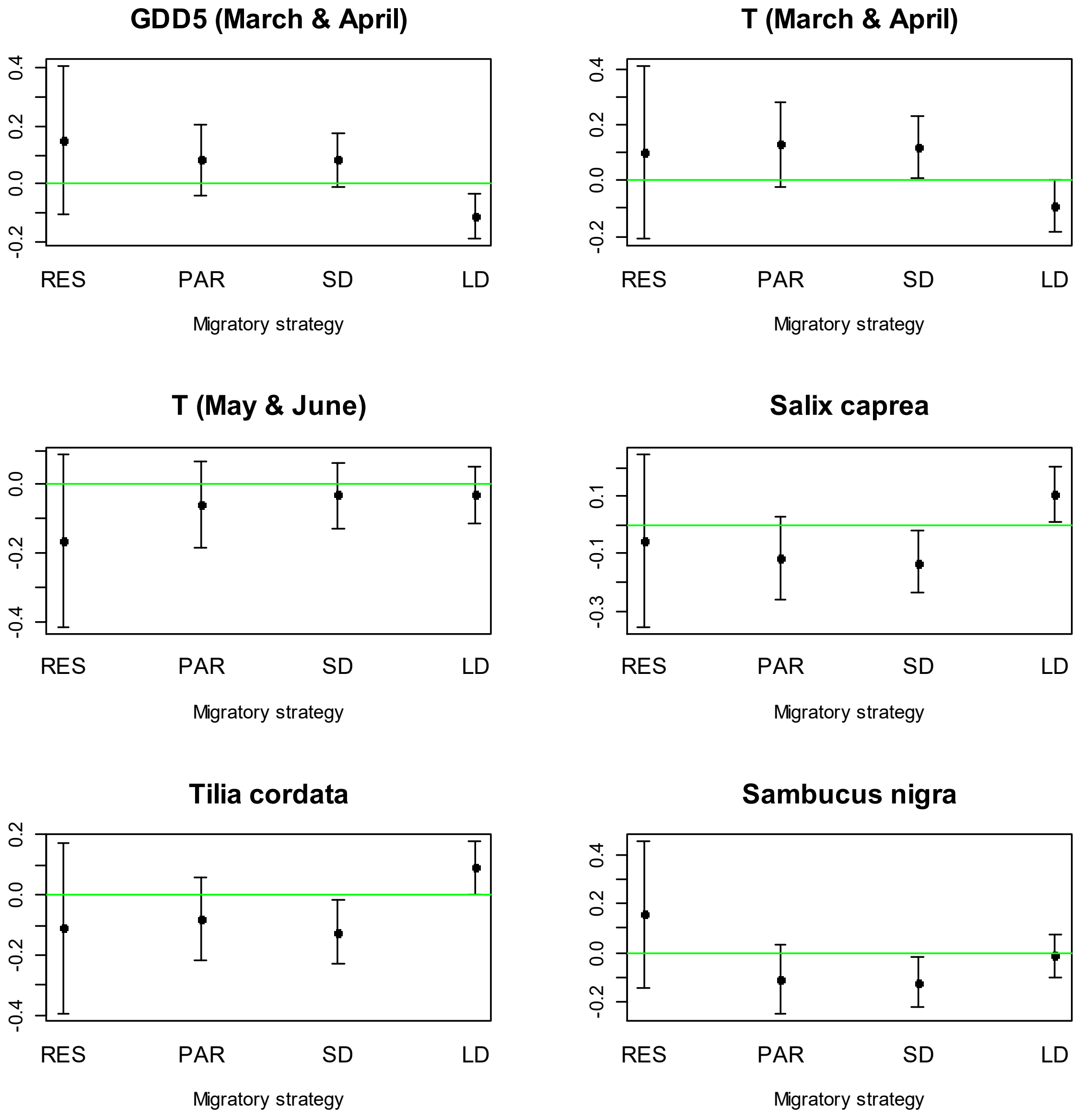
[6] ratio of actual to potential evapotranspiration in species' sub-Saharan non-breeding ranges

[7] whole species' sub-Saharan non-breeding ranges (see Supplementary Fig. 1)

[8] Sahelian part of species' sub-Saharan non-breeding ranges (see Supplementary Fig. 1)

[9] south-of-Sahelian part of species' sub-Saharan non-breeding ranges (see Supplementary Fig. 1)

Fig. 2: Relationships between breeding productivity of bird groups defined by different migratory strategies and climatic variables reflecting spring phenology at breeding grounds estimated by Bayesian meta-analytic models. Each variable was tested in a single model taking also the potential effect of population density into account (see Table S4 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.



Adult survival

Long-distance migrants' adult survival was higher in years with higher AET/PET (i.e. higher water availability) in Sahel part of sub-Saharan non-breeding grounds (Table 3). When considering the southern part of the sub-Saharan non-breeding ground or the sub-Saharan region as a whole, the relationships to adult survival were also positive but not significant (Table 3).

Relationships were more diverse when focusing separately on each species (Table S6), but only the positive ones were strong enough to be significant according to the 95% confidence limits: *Phylloscopus trochillus* and *Sylvia communis* had significantly higher adult survival in years with higher AET/PET and *Acrocephalus schoenobaenus* almost significantly so.

Linking demographic parameters with population dynamics

The analysis of the population growth rates of long-distance migrants showed that, when assessed across all species together, both breeding productivity (estimate = 0.347, SE = 0.202) and adult survival (estimate = 0.530, SE = 0.320) had positive effect on their population growth. However, only the adult survival was significant and explained higher proportion of variability in population growth rates (R^2_var = 35.3 %) than the breeding productivity (R^2_var = 22.4 %).

Both breeding productivity and adult survival had significant effects on population growth rates in separate models for particular species and their relative importance was species-specific (Table S7). For example, population growth of *Acrocephalus schoenobaenus* was limited by survival, while population growth of *Sylvia curruca* by productivity and population growth of *Acrocephalus scirpaceus* by both these factors (Table S7).

Table 3: Relationships between adult survival of long-distance migrants and water availability in non-breeding grounds estimated by Bayesian meta-analytic models. Each variable was tested in a single model. Significant relationships (95% confidence limits not overlapping zero) are in bold. See Methods section for more details on model formulation and variable characteristics.

Climatic variable	slope	2.5%	97.5%	R^2_dev[1]
AET/PET[2] whole range[3]	0.149	-0.016	0.326	0.151
AET/PET[2] Sahelian part[4]	**0.203**	**0.026**	**0.418**	**0.206**
AET/PET[2] south of Sahel[5]	0.079	-0.104	0.251	0.123

[1] proportion of deviance explained (see Methods for details)

[2] ratio of actual to potential evapotranspiration expressed in species' sub-Saharan non-breeding ranges

[3] whole species' sub-Saharan non-breeding ranges (see Supplementary Fig. 1)

[4] Sahelian part of species' sub-Saharan non-breeding ranges (see Supplementary Fig. 1)

[5] south-of-Sahelian part of species' sub-Saharan non-breeding ranges (see Supplementary Fig. 1)

Discussion

Our study aimed to find the links between demographic parameters and climate variation to explain population changes of long-distance migrants. We found strong relationships between climate and migrants' breeding productivity which was lower in years with more advanced spring phenology. At the same time, the effect of climate in non-breeding grounds on adult survival was weaker and the conditions in Sahel played the crucial role manifested by the higher survival under the conditions of the higher water availability. In contrast, we did not find a significant carry-over effect of non-breeding climatic conditions on breeding productivity of migrants. Population model considering the key demographic parameters showed that both breeding productivity and adult survival were important predictors of population changes of migrants but the adult survival was significant. The climatically driven dynamics investigated here is thus most likely not the only driver of the continuing declines of long-distance migrants.

Our results provide a clear support for the hypothesis that the breeding productivity of long-distance migrants is negatively affected by the advancement of spring phenology due to the phenologic mismatch (Both et al., 2006). This hypothesis predicts different impacts on species with different migratory strategies. Residents and short-distance migrants, i.e. species with more flexible timing of their annual cycle, should benefit from higher spring temperatures and earlier onset of the vegetation phenophases by earlier breeding (Wright et al., 2009). In contrast, long-distance migrants cannot adjust their breeding to the spring advancement adequately due to their innate migration schedule (Møller et al., 2008) and they thus face suboptimal conditions for breeding resulting in a lower offspring survival and, consequently, in a lower breeding productivity (Both et al., 2006). Although the phenologic mismatch hypothesis attracted high interested of researchers and was tested by numerous studies (e.g. Clausen & Clausen, 2013; Reed et al., 2013; Eglington et al., 2015; Visser et al., 2015), we are not aware of any tests of the key mechanism, i.e. the links between climate and breeding productivity using a set of multiple species with different migratory strategies. Our results confirm the predictions of this hypothesis observing strongly negative response in long-distance migrants and neutral or positive responses in resident species, partial and short-distance migrants. This provides an important mechanistic background for recent extensions of the hypothesis to the investigations of population dynamics (e.g. Both et al., 2010; Jones & Cresswell, 2010; Pearce-Higgins et al., 2015).

Spring phenology can be described in numerous ways: some studies use temperature variables directly reflecting weather conditions (e.g. Pearce-Higgins et al., 2015), while others focus on various measures based on the progress of the vegetation development (e.g. Kolarova et al., 2014). It might be argued that the latter variables are biologically more relevant because they show how the spring phenology is actually perceived by organisms the birds are dwelling on, whereas temperatures *per se* are less important for birds (Reif et al., 2010). We found that birds' breeding productivity was most tightly related to GDD5 and unfolding of *Salix caprea* and *Tilia cordata* indicating the support for this expectation. On the other hand, results for *Sambucus nigra* were less convincing. This discrepancy among the focal woody plant species might be caused by very high sensitivity of this shrub species to temperatures (Mazer et al., 2015) leading to its extremely early onset of leaf unfolding in some years which is probably not reflected by the start of bird breeding. Birds most likely respond to the development of the ecosystem as a whole, which is better captured by the phenology of tree species with later onset of unfolding, here represented by *Salix caprea* and *Tilia cordata*. In any case, we have shown that selection of the variable reflecting spring phenology can have important impact on results and we recommend focusing on those with higher biological relevancy. Concerning the specific effect of spring temperature on migrants' breeding productivity, we found a clear difference between early and late spring temperatures showing the importance of the former ones. This is in accord with the expectation that thermal conditions at the beginning of bird breeding are decisive for the eventual occurrence of phenologic mismatch, whereas late season temperatures are less important (Bowers et al., 2016). As temperatures generally grow over the course of the season, it is logical that their limiting effect declines in later phases.

Influence of climatic conditions in non-breeding grounds on migrants' survival was suggested for decades (e.g. Winstanley, Spencer & Williamson, 1974; Peach, Baillie & Underhill, 1991). Numerous studies tested their effects using single species (e.g. Eraud et al., 2009, Salewski et al., 2013; Morrison et al., 2016) or inferred their influence on migrants' population dynamics without a specific test for the relationships to adult survival (Ockedon et al., 2012). However, broader formal assessments of a general validity these relationships were lacking (but see Johnston et al., 2016). Here we show that the influence of climatic conditions in sub-Saharan non-breeding grounds, expressed as water availability, were significant for the northern (Sahelian) part, but not for the southern part of the non-breeding ranges. The key importance of the moisture in Sahel is expectable given relatively lower water availability and thus its stronger limiting effect on organisms in the northern part of sub-Saharan Africa compared to southern regions (Zwarts et al., 2009). In addition, virtually all trans-Saharan migrants have to stop in Sahel to restore the reserves before crossing the Sahara desert (Tøttrup et al., 2012). Drought events in Sahel has thus serious consequences even for the species spending the winter further south in the Southern hemisphere (Tøttrup et al., 2012; Risely et al., 2015).

In contrast to the importance of the non-breeding grounds' climate for adult survival, we did not detect much significant carry-over effects of water availability in non-breeding grounds on breeding productivity. The lower predictive power of these relationships was also reported in the other studies (e.g. Woodworth et al., 2017) and can be explained by rather indirect causal pathways that act in these relationships when other factors affecting breeding productivity can balance the adverse effects of the water stress in non-breeding grounds. For example, when the water availability is limited resulting in increased migrants' mortality during winter and poor body condition of those who survived, then if the birds are able to arrive successfully to the breeding grounds, they can enjoy the conditions of less intensive intraspecific competition and have thus more resources available to exploit (Calvert, Walde & Taylor, 2009). In turn, their body condition improves and no adverse consequences on breeding performance may be observed. Indeed, the importance of intraspecific competition for breeding performance was frequently reported (e.g. Reed et al., 2013; Woodworth et al., 2017) and our results showing a strong negative density dependent population regulation support this explanation.

Our study, for the first time, quantifies the influence of breeding productivity and adult survival on migrants' population changes using multiple species. Considering each species separately, either of the demographic parameters was more important: breeding productivity had stronger relations to population growth in *Sylvia* warblers, whereas the reverse was true for *Acrocephalus schoenobaenus* and *A. palustris*. However, when tested across all species, only the adult survival was significantly related to migrants' population change accounting for ca 10% more variability than breeding productivity. Therefore, our results indicate that the adults' survival is a more limiting component of long-distance migrants' population dynamics than the breeding productivity. Viewing this result in the light of ongoing climatic changes, it seems that the effects of climate warming at breeding grounds are less important than the conditions of at non-breeding grounds.

Interestingly, this finding contrasts with our results showing tighter relationships between breeding productivity and climate on breeding grounds than between adult survival and climate on non-breeding grounds. This discrepancy may be caused by the lack of precise spatial data for non-breeding grounds where the exact location of wintering areas for sub-Saharan migrants is known with a large amount of uncertainty (Cepák et al., 2008). This imprecision could weaken the link between spatially specific climatic data and the adult survival. As an alternative (but not mutually exclusive), it is possible that other factors than climate are involved in setting the limits for migrants' survival in sub-Saharan Africa. Indeed, due to explosive human population growth and rapid economic development, land use changes in this region result in marked habitats changes in birds' non-breeding grounds with marked imprints on their populations (Stevens et al., 2010; Koleček et al., 2017) that are at least partly independent of annual variation in water availability. Moreover, climatic and other factors impacting bird mortality may interact making the relationships between water availability and adult survival even more complex (Sirami et al., 2017).

In conclusion, we found that both breeding productivity and adult survival were important for population dynamics of long-distance migrants, but only the latter relationship was significant suggesting the key influence of non-breeding conditions on migrants' populations, as frequently assumed but seldom tested in many recent studies (e.g. Vickery et al., 2014). We were also able to demonstrate strong relationships between spring phenology and breeding productivity of long-distance migrants. By contrasting these migrants to species with other migratory strategies, we provide convincing support for the mechanism of the phenologic mismatch hypothesis, which has never been validated using a larger set of species. Finally, we confirmed the hypothesis that the lower water availability at Sahelian non-breeding grounds adversely affected adults' survival, but this limitation did not carry-over to the lower breeding productivity. Although our data originate from a single central European country, the conceptual and analytical framework developed by this study opens a new field for research at the continental and global scales.

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References

Adamik, P., Emmenegger, T., Briedis, M., Gustafsson, L., Henshaw, I., Krist, M., Laaksonen, T., Liechti, F., Prochazka, P., Salewski, V. & Hahn, S. (2016) Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Scientific Reports, 6,* 21560.

Ambrosini, R., Saino, N., Rubolini, D. & Moller, A.P. (2011) Higher degree-days at the time of breeding predict size of second clutches in the barn swallow. *Climate Research, 50,* 43–50.

Baillie, S.R. (1990) Integrated population monitoring of breeding birds in Britain and Ireland. *Ibis, 132,* 151–166.

Baillie, S.R., Green, R.E., Boddy, M. & Buckland, S.T. (1986) *An evaluation of the Constant Effort Sites Scheme*. BTO Research Report No. 21. BTO Thetford, Norfolk, UK.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters, 15,* 365–377.

Bello, F. de, Berg, M.P., Dias, A.T.C., Diniz-Filho, J.A.F., Götzenberger, L., Hortal, J., Ladle, R.J. & Lepš, J. (2015) On the need for phylogenetic 'corrections' in functional trait-based approaches. *Folia Geobotanica, 50,* 349–357.

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

Bowers, E.K., Grindstaff, J.L., Soukup, S.S., Drilling, N.E., Eckerle, K.P., Sakaluk, S.K. & Thompson, C.F. (2016) Spring temperatures influence selection on breeding date and the potential for phenological mismatch in a migratory bird. *Ecology, 97,* 2880–2891.

Calvert, A.M., Walde, S.J. & Taylor, P.D. (2009) Nonbreeding-Season Drivers of Population Dynamics in Seasonal Migrants: Conservation Parallels Across Taxa. *Avian Conservation and Ecology, 4,* 71–97.

Cayton, H.L., Haddad, N.M., Gross, K., Diamond, S.E. & Ries, L. (2015) Do growing degree days predict phenology across butterfly species? *Ecology, 96,* 1473–1479.

Cepák, J., Klvaňa, P., Škopek, L., Schröpfer, L., Jelínek, M., Hořák, D., Formánek, J. & Zárybnický, J. (2008) *Czech and Slovak Bird Migration Atlas.* Aventinum, Praha.

Cepák J. & Škopek J. (2005) CES project in the Czech Republic in 2004. *Zprávy ČSO, 60,* 62–65.

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

Cramp, S. (1977) *Handbook of the Birds of Europe, the Middle East and North Africa : The Birds of the Western Palearctic*. Oxford University Press.

Czech Hydrometeorological Institute. (2009) Návod pro činnost fenologických stanic - lesní rostliny [Methodical instructions for phenological stations – forest plants]. METODICKÝ PŘEDPIS č. 10.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I. & Jiguet, F. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change, 2,* 121–124.

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

Eglington, S.M., Julliard, R., Gargallo, G., van der Jeugd, H.P., Pearce-Higgins, J.W., Baillie, S.R. & Robinson, R.A. (2015) Latitudinal gradients in the productivity of European migrant warblers have not shifted northwards during a period of climate change. *Global Ecology and Biogeography, 24,* 427–436.

Eraud, C., Boutin, J.M., Riviere, M., Brun, J., Barbraud, C. & Lormee, H. (2009) Survival of Turtle Doves Streptopelia turtur in relation to western Africa environmental conditions. *Ibis, 151,* 186–190.

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.

Gelman, A. & Rubin, D.B. (1992) Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science, 7,* 457–472.

Gilroy, J.J., Gill, J.A., Butchart, S.H.M., Jones, V.R. & Franco, A.M.A. (2016) Migratory diversity predicts population declines in birds. *Ecology Letters, 19,* 308–317.

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.

Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. & Weimerskirch, H. (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews, 83,* 357–399.

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.

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.

Jørgensen, P.S., Böhning-Gaese, K., Thorup, K., Tøttrup, A.P., Chylarecki, P., Jiguet, F., Lehikoinen, A., Noble, D.G., Reif, J., Schmid, H., van Turnhout, C., Burfield, I.J., Foppen, R., Voříšek, P., van Strien, A., Gregory, R.D. & Rahbek, C. (2016) Continent-scale global change attribution in European birds - combining annual and decadal time scales. *Global Change Biology, 22,* 530–543.

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.

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.

Kolarova, E., Nekovar, J. & Adamik, P. (2014) Long-term temporal changes in central European tree phenology (1946-2010) confirm the recent extension of growing seasons. *Internation Journal of Biometeorology, 58,* 1739–1748.

Koleček J., Procházka P., El-Arabany N., Tarka M., Ilieva M., Hahn S., Honza M., de la Puente J., Bermejo A., Gürsoy A., Bensch S., Zehtindjiev P., Hasselquist D. & Hansson B. (2016) Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology, 47,* 756-767.

Koleček, J. Procházka, P., Ieronymidou, C., Burfield, I.J. & Reif, J. (2017) Non-breeding range size predicts the magnitude of population trends in trans-Saharan migratory passerine birds. *Oikos,* in press.

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.

Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics, 41,* 321–350.

Mazer, S.J., Gerst, K.L., Matthews, E.R. & Evenden, A. (2015) Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem. *Ecosphere, 6,* 98.

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., Robinson, R.A., Butler, S.J., Clark, J.A. & Gill, J.A. (2016) Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. *Proceedings of The Royal Society of London B, 283,* 20161387.

Mu, Q., Zhao, M. & Running, S.W. (2011) Improvements to a MODIS global terrestrial evapotranspiration algorithm. *Remote Sensing of Environment, 115,* 1781–1800.

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.

Ockendon, N., Hewson, C.M., Johnston, A. & Atkinson, P.W. (2012) Declines in British-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird Study, 59,* 111–125.

Pannekoek, J. & Van Strien, A. (2005) *TRIM 3 Manual (TRends and Indices for Monitoring Data).*

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.

Pecl, G.T., Araujo, M.B., Bell, J.D., Blanchard, J. *et al.* (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science, 355,* eaai9214.

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

Plummer, M. (2008) Penalized loss functions for Bayesian model comparison. *Biostatistics, 9,* 523–539.

Pradel, R., Hines, J.E., Lebreton, J.D. & Nichols, J.D. (1997) Capture-recapture survival models taking account of transients. *Biometrics, 53,* 60–72.

R Core Development Team. (2016) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL http: //www.R-project.org/.

Reed, T.E., Grotan, V., Jenouvrier, S., Saether, B.-E. & Visser, M.E. (2013) Population Growth in a Wild Bird Is Buffered Against Phenological Mismatch. *Science, 340,* 488–491.

Reif, J. (2013) Long-Term Trends in Bird Populations: A Review of Patterns and Potential Drivers in North America and Europe. *Acta Ornithologica, 48,* 1–16.

Reif J., Telenský T., Šťastný K., Bejček V. & 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.

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., Julliard, R & Saracco, J.F. (2009) Constant effort: studying avian population processes using standardized ringing. *Ringing & Migration, 24,* 199–204.

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.

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.

Salewski, V., Hochachka, W.M. & Fiedler, W. (2013) Multiple Weather Factors Affect Apparent Survival of European Passerine Birds. *PLoS ONE, 8,* e59110.

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.

Šímová, I. & Storch, D. (2017) The enigma of terrestrial primary productivity: measurements, models, scales and the diversity–productivity relationship. *Ecography, 40,* 239–252.

Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L. & Martin, J.L. (2017) Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. *Global Ecology and Biogeography, 26,* 385–394.

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

Stephens P.A., Mason L.R., Green R.E., Gregory R.D., Sauer J.R., Alison J., Aunins A., Brotons L., Butchart S.H.M., Campedelli T., Chodkiewicz T., Chylarecki P., Crowe O., Elts J., Escandell V., Foppen R.P.B., Heldbjerd H., Herrando S., Husby M., Jiguet F., Lehikoinen A., Lindström A., Noble D.G., Paquet J.-Y., Reif J., Sattler T., Szep T., Teufelbauer N., Trautmann S., Van Strien A.J., Van Turnhout C.A.M., Vorisek P. & Willis S.G. (2016) Consistent response of bird populations to climate change on two continents. *Science, 352,* 84–87.

Stevens, M., Sheehan, D., Wilson, J., Buchanan, G. & Cresswell, W. (2010) Changes in Sahelian bird biodiversity and tree density over a five-year period in northern Nigeria. *Bird Study, 57,* 156–174.

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.

Thaxter, C.B., Joys, A.C., Gregory, R.D., Baillie, S.R. & Noble, D.G. (2010) Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation, 143,* 2006–2019.

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.

Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science, 348,* 571–573.

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., Gienapp, P., Husby, A., Morrisey, M., de la Hera, I., Pulido, F & Both, C. (2015) Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *PLoS Biology, 13,* e1002120.

Westoby, M., Leishman, M. & Lord, J. (1995) Further Remarks on Phylogenetic Correction. *Journal of Ecology, 83,* 727–729.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study, 46,* 120–139.

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

Woodworth, B.K., Wheelwright, N.T., Newman, A.E., Schaub, M. & Norris, D.R. (2017) Winter temperatures limit population growth rate of a migratory songbird. *Nature Communications, 8,* 14812.

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.

Table S1: Characteristics of the species involved in this study: migratory strategy (LD - long-distance migrants, SD - short-distance migrants, PAR - partial migrants, RES - residents), total number of adult individuals captured (total capture), total number of individuals captured in two different years (recapture) and location of wintering grounds (W - Western Africa, E - Eastern Africa, S - Southern Africa, C - Central Africa). Last two characteristics are shown for LDMs only due to their relevance for further analysis.

Species	Migratory strategy	Total capture	Recaptured	Wintering grounds
Acrocephalus arundinaceus	LD	737	33	W
Acrocephalus palustris	LD	2682	117	E,S
Acrocephalus scirpaceus	LD	8977	753	W
Acrocephalus schoenobaenus	LD	3553	271	E
Lanius collurio	LD	454	13	E,S
Locustella luscinioides	LD	372	18	E
Locustella naevia	LD	399	14	W
Phylloscopus trochilus	LD	611	39	W
Sylvia borin	LD	1019	88	W,E,C
Sylvia communis	LD	821	75	W,E
Sylvia curruca	LD	492	60	E
Carduelis chloris	PAR	558		
Parus caeruleus	PAR	1148		
Parus major	PAR	928		
Turdus merula	PAR	967		
Emberiza citrinella	RES	776		
Emberiza schoeniclus	SD	1629		
Erithacus rubecula	SD	364		
Fringilla coelebs	SD	310		
Luscinia svecica	SD	520		
Phylloscopus collybita	SD	1815		
Prunella modularis	SD	470		
Sylvia atricapilla	SD	3536		
Turdus philomelos	SD	448		

Table S2: Relationships between breeding productivity of long-distance migrants and climatic variables reflecting (a) spring phenology at breeding grounds and (b) water availability at non-breeding grounds (indicating so called carry-over effect) estimated by Bayesian meta-analytic models, the variant with random intercept only (i.e. without random slope effect). Each variable was tested in a single model taking also the potential effect of population density into account. Model performance was assessed by Deviance Information Criterion (DIC) and Penalized Expected Deviance (PED). Significant relationships (95% confidence limits not overlapping zero) are in bold. See Methods section for more details on model formulation and variable characteristics.

Climatic variable	Effect of climatic variables				Effect of population density			Model characteristics			
	slope	2.5%	97.5%	R^2_var[1]	slope	2.5%	97.5%	DIC	PED	ΔDIC	ΔPED
a) Climatic variables at breeding grounds:											
GDD5[2]	**-0,125**	**-0,192**	**-0,057**	0,56	**-0,597**	**-0,951**	**-0,230**	102,0	133,1	0,0	0,0
early spring temperature[3]	**-0,110**	**-0,192**	**-0,026**	0,38	**-0,601**	**-0,979**	**-0,212**	107,3	144,5	5,3	11,4
late spring temperature[4]	-0,028	-0,102	0,045	-0,03	**-0,433**	**-0,814**	**-0,043**	113,2	163,9	11,2	30,8
Salix caprea[5]	**0,124**	**0,046**	**0,201**	0,50	**-0,567**	**-0,936**	**-0,195**	105,1	138,9	3,1	5,8
Tilia cordata[5]	**0,105**	**0,028**	**0,183**	0,42	**-0,544**	**-0,914**	**-0,168**	107,2	144,9	5,2	11,8
Sambucus nigra[5]	-0,010	-0,094	0,073	-0,04	**-0,423**	**-0,816**	**-0,027**	113,4	168,3	11,4	35,2
b) Climatic variables at non-breeding grounds:											
AET/PET[6] whole range[7]	0,047	-0,047	0,143	0,01	**-0,430**	**-0,811**	**-0,043**	112,1	165,9	10,1	32,8
AET/PET[6] Sahelian part[8]	0,010	-0,065	0,087	-0,05	**-0,425**	**-0,810**	**-0,030**	113,3	166,6	11,3	33,5
AET/PET[6] south of Sahel[9]	**0,164**	**0,002**	**0,322**	0,07	**-0,467**	**-0,833**	**-0,087**	111,2	159,6	9,1	26,5

[1] proportion of variance explained by the climate variable, after removing the variance explained by density dependence (see Methods for details)

[2] growing degree days - accumulated temperature above 5°C

[3] mean temperature in March and April

[4] mean temperature in May and June

[5] julian date of 10% leaf unfolding

Table S3: Relationships between breeding productivity of long-distance migrants and climatic variables reflecting spring phenology at breeding grounds estimated by Bayesian meta-analytic models. Each variable was tested in a single model taking also the potential effect of population density into account. Significant relationships (95% confidence limits not overlapping zero) are in bold. See Methods section for more details on model formulation and variable characteristics.

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Table S4: Relationships between breeding productivity of bird groups defined by different migratory strategies and climatic variables reflecting spring phenology at breeding grounds estimated by Bayesian meta-analytic models. Each climatic variable was tested in a single model taking also the potential effect of population density (estimated across all bird groups together) into account. Significant relationships (95% confidence limits not overlapping zero) are in bold. Model performance was assessed by Deviance Information Criterion (DIC) and Penalized Expected Deviance (PED). See Methods section for more details on model formulation and variable characteristics.

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Table S5: Relationships between breeding productivity of long-distance migrants and climatic variables reflecting water availability at non-breeding grounds (indicating so called carry-over effect) estimated by Bayesian meta-analytic models. Water availability was expressed using ratio of actual to potential evopotranspiration (AET/PET) calculated separately for species' whole sub-Saharan non-breeding ranges, Sahelian parts of species' sub-Saharan non-breeding ranges (north of the 13° northern latitude) and south of the Sahelian parts of species' sub-Saharan non-breeding ranges (south of the 13° northern latitude). Each variable was tested in a single model taking also the potential effect of population density into account. Significant relationships (95% confidence limits not overlapping zero) are in bold. See Methods section for more details on model formulation and variable characteristics.

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Table S6: Relationships between adult survival of long-distance migrants and water availability in non-breeding grounds estimated by Bayesian meta-analytic models. Water availability was expressed using ratio of actual to potential evapotranspiration (AET/PET) calculated separately for species' whole sub-Saharan non-breeding ranges, Sahelian parts of species' sub-Saharan non-breeding ranges (north of the 13° northern latitude) and south of the Sahelian parts of species' sub-Saharan non-breeding ranges (south of the 13° northern latitude). Each variable was tested in a single model. Significant relationships (95% confidence limits not overlapping zero) are in bold. See Methods section for more details on model formulation and variable characteristics.

Species	AET/PET (whole range)			AET/PET (Sahelian part)			AET/PET (south of the Sahelian part)		
	slope	2.5%	97.5%	slope	2.5%	97.5%	slope	2.5%	97.5%
Acrocephalus arundinaceus	-0.183	-0.824	0.459	-0.129	-0.755	0.498	-0.266	-0.937	0.404
Acrocephalus palustris	0.144	-0.077	0.365	0.197	-0.097	0.492	0.127	-0.132	0.386
Acrocephalus scirpaceus	0.090	-0.036	0.217	0.067	-0.055	0.189	0.126	-0.005	0.258
Acrocephalus schoenobaenus	0.168	-0.008	0.345	0.178	-0.005	0.362	0.112	-0.050	0.275
Phylloscopus trochilus	**0.769**	**0.108**	**1.429**	**0.757**	**0.102**	**1.412**	**0.724**	**0.076**	**1.372**
Sylvia borin	-0.048	-0.513	0.418	0.214	-0.195	0.622	-0.288	-0.701	0.124
Sylvia communis	0.332	-0.238	0.902	**0.722**	**0.107**	**1.338**	-0.067	-0.473	0.338
Sylvia curruca	0.212	-0.266	0.689	0.197	-0.321	0.716	0.131	-0.259	0.521

Table S7: The effects breeding productivity (left column) and adult survival (right column) on annual population growth rate of long-distance migrants estimated by generalized mixed-effects models. Significant relationships (95% confidence limits not overlapping zero) are in bold. Note that the adult survival was not estimated in three species due to small sample size. See Methods section for more details on model formulation and variable characteristics.

Species	Breeding productivity				Adult survival			
	Slope	2.50%	97.50%	R^2_var	Slope	2.50%	97.50%	R^2_var
Acrocephalus arundinaceus	0.529	-0.122	1.198	0.66	0.560	-0.537	1.572	0.47
Acrocephalus palustris	-0.493	-1.419	0.429	0.16	0.590	-0.212	1.339	0.49
Acrocephalus scirpaceus	**0.886**	**0.426**	**1.376**	0.85	**0.869**	**0.375**	**1.378**	0.81
Acrocephalus schoenobaenus	0.209	-0.824	1.256	-0.06	**0.683**	**0.262**	**1.184**	0.83
Lanius collurio	0.067	-0.945	1.005	0.16				
Locustella luscinioides	-0.067	-1.110	0.936	0.05				
Locustella naevia	-0.007	-0.862	0.861	0.19				
Phylloscopus trochilus	0.074	-1.028	1.087	0.12	-0.407	-1.707	0.759	0.06
Sylvia borin	0.555	-0.020	1.104	0.69	0.314	-1.054	1.398	0.20
Sylvia communis	-0.233	-1.210	0.994	0.23	0.443	-1.506	2.236	0.00
Sylvia curruca	**0.638**	**0.001**	**1.330**	0.71	0.515	-0.703	1.575	0.30

Fig. S1: Regional classification of sub-Saharan Africa according to Cepak *et al.* (2008): W – West Africa, E – East Africa, S – South Africa, C – Central Africa. The thin line shows the borderline of 13°N delimitating the Sahel from the southern part of the non-breeding grounds.