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Linking events through the annual cycle in migratory songbirds:

causes and consequences of different spatiotemporal strategies

Ph.D. Thesis

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I declare that this thesis is my original work and has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My contribution to each of the chapters comprising this work is expressed through the authorship order of the included chapters and author's contribution statements complementing the chapters.

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Abstract

Each year animals move across and between continents to track seasonal changes in resource availability and abundance to improve their survival and reproductive opportunities. Birds represent one of the largest animal group that engage in these global-scale migration events. Afro-Palearctic bird migration system is estimated to facilitate more than 2 billion individual birds that link ecological communities of the two continents.

Recent advances in tracking technology, like light-level geolocators, have enabled us to follow even the smallest of individual migrants as they complete their annual cross-continental journeys. This has opened a new era in bird migration research allowing us to gain unique insights into spatiotemporal organization of full annual cycles of individual songbirds. Furthermore, these technological advances allow for estimation of migratory connectivity between breeding and non-breeding populations as well as linking spatially and temporarily distinct phases of the annual cycles of migratory birds.

In my dissertation I couple geolocator tracking with stable isotope signatures, breeding data, and environmental variables to unravel spatiotemporal migration strategies and identify the importance of carry-over effects operating in wild populations of long-distance migrants. I reveal how annual events are interlinked with one another and the environment on the level of individual birds, populations, and species. I use three Afro-Palearctic migratory birds – Tawny Pipit *Anthus campestris*, Collared Flycatcher *Ficedula albicollis*, and Semi-collared Flycatcher *F. semitorquata* – as model species.

Besides answering trivial questions of where and when each of the model species migrate, I found that there is a great deal of variation in the migration strategies among individuals and populations. Breeding site phenology is the main driver of migratory schedules on a population level, while individual variation in timing of migratory episodes are mediated via carry-over effects of previous breeding effort and conditions experienced at the non-breeding sites. Crossing of the Sahara Desert, which majority of the successful migrants accomplish in a single endurance flight, serves as a gateway between Europe and Africa for long-distance migratory birds. Only after the cross-desert flight, environmental and phenological cues can be picked up and used for accurate timing of spring migration and timely arrival for breeding.

Studies from the perspective of full annual cycles are still underrepresented in animal ecology research. The chapters comprising this dissertation adds only a drop in the vast pool of knowledge in animal migration ecology. However, such information is of topmost priority for understanding the drivers of population dynamics as many migratory species are currently declining.

Keywords: long-distance migrant, migration strategy, annual cycle, carry-over effects, migratory connectivity

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Abstrakt

Každoročně živočichové podnikají dlouhé přesuny mezi kontinenty. Přizpůsobují se tak sezónním změnám v dostupnosti zdrojů a jejich početnosti, a to vše v zájmu přežití a snahy o reprodukci. Ptáci představují jednu z nejpočetnějších skupin, které podstupují takové globální migrační přesuny. Mezi Evropou a Afrikou se každoročně přesouvají více jak dvě miliardy ptáků.

Recentní pokroky ve vývoji sledovací techniky, jako například geolokátorů, nám umožnily sledovat pohyby mezi kontinenty i u těch nejmenších ptáků. Tento technický pokrok nám tak otevírá nové možnosti pro výzkum ptačí migrace a to na úrovni jedinců a organizace jejich celoročních cyklů. Dále tak můžeme lépe porozumět konektivitě mezi populacemi, tj. jak jsou různé populace propojeny na zimovištích a hnízdištích.

Za účelem odhalení časoprostorových migračních strategií u ptáků kombinuji, ve své disertační práci, hnízdní data a environmentální proměnné s daty získanými pomocí geolokátorů a analýzy stabilních izotopů z peří. Zároveň zhodnocuji význam tzv. carry-over efektů v průběhu ročního cyklu u dálkových migrantů. Na úrovni jedinců, populací a druhů odhaluji, jak jsou jednotlivé fáze ročního cyklu vzájemně propojené a také ovlivněné prostředím. Jako modelové druhy jsem použil tři dálkové migranty: lindušku úhorní *Anthus campestris*, lejska bělokrkého *Ficedula albicollis* a lejska černokrkého *Ficedula semitorquata*.

Vedle odpovědí na základní otázky typu kam a kdy každý z modelových druhů táhne, jsem zjistil, že je značná variabilita v migračních strategiích mezi jedinci i mezi populacemi. Například fenologie na hnízdišti byla hlavním faktorem určujícím načasování migrace na populační úrovni, kdežto individuální rozdíly v časování jednotlivých migračních událostí byly poháněny carry-over efekty na základě předchozího hnízdního úsilí a také podmínkami, kterým byli jedinci vystaveni v průběhu tahu nebo na zimovišti. Dalším poznatkem je, že většina drobných pěvců překonává Saharu v jednom non-stop letu. Zdá se, že teprve po překonání této bariéry ptáci využívají environmentální a fenologické indikátory k doladění příletu na hnízdiště.

Studií, které sledují celoroční cyklus života živočichů, je stále poměrně poskrovnu. Poznatky, které představuji v jednotlivých kapitolách své dizertace, jsou pouze kapkou v moři vědomostí o migraci živočichů. Přesto jsou ale tyto informace klíčem k porozumění populační dynamiky celé řady tažných druhů a to zejména v souvislosti s recentním poklesem početností u mnohých dálkových migrantů.

Klíčová slova: dálkový migrant, migrační strategie, roční cyklus, carry-over efekty, ptačí migrace

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Contents

Chapter 1

General introduction:
There and back again

Martins Briedis

Introduction

Every year billions of animals engage into a phenomenon we call migration. Among those, birds are especially praised for their remarkable migratory ability and diversity. Birds of all shapes and sizes travel across the globe twice a year connecting and shaping ecological communities wherever they pass through.

In my thesis, I look into the astonishing migratory patterns of Afro-Palearctic migratory birds revealing a fraction of details of their annual cycles. I will follow and take you with me on journeys of individual birds as they complete their annual cross-continental migrations, passing countless country borders and ultimately linking Europe to Africa. I will focus on a number of species giving not only the general information of where they go and when they migrate, but also how they get there. I take a closer look at the barrier crossing strategies, links between different phases of the annual cycles of individual birds and populations, as well as connections between the migrants and the environment.

It has been proven time and time again – we care for what we know, understand and are connected to. Building a knowledge means raising awareness.

There and back again: a bird's tale

Annual cycles of migratory birds are optimized to the seasonal patterns of changing environmental conditions. Long-distance migratory birds travel thousands of kilometres between their temperate breeding grounds and tropical – sub-tropical non-breeding regions. By doing so they are able to track seasonal changes in resource availability and increase their survivorship (Thorup et al. 2017). They exploit the relatively short but productive summers of high latitudes to rise their young and (in some species) moult their feathers, and escape the unfavourable winter conditions by traveling to more hospitable regions which are typically found in lower latitudes.

The vast majority of long-distance migrants are nocturnal and fly solitary, rather than congregating in groups (Newton 2008). This leads to a situation when young first-time migrants need to orientate themselves and find the desired non-breeding regions on their own. The migration routes and non-breeding regions are innate and even translocated birds most often can adjust and re-orientate themselves (Holland 2014; Willemoes et al. 2015). For large-scale orientation purposes birds use three compass systems – the solar, the stellar, and the magnetic compass (Chernetsov 2015).

Along their way migrants have to optimize their migration routes and schedules according to the environmental factors, like prevailing winds, temperatures, and food availability. Additionally, they have to cross inhospitable areas like deserts and seas where food, shelter and other vital resources are scarce or lack completely (Moreau 1961). Migratory journeys of birds typically comprise of relatively short flight bouts and prolonged stopovers (Hedenström and Alerstam 1997). Local knowledge of suitable stopover sites capable of providing enough resources to fuel to the next flight bout is crucial. Mortality during migration is typically higher compared to the stationary breeding and non-breeding periods (Sillett and Holmes 2002; Lok et al. 2015). Furthermore, young, inexperienced first-time migrants typically show higher mortality rates than experienced adult individuals (Newton 2008).

BOX 1 ANNUAL CYCLES OF MIGATORY BIRDS

An annual cycle refers to a set of events that regularly take place at the same time of the year. In the annual cycles of migratory birds, events that are typically looked at are breeding, migration, wintering and moult. The onset of breeding is typically linked to local phenological events at the breeding site and timed so that the chicks hatch and fledge at the time when food is most abundant. Migratory species differ in their life history strategies with some moulting their feathers while still at the breeding sites after the completion of the breeding cycle (e.g., *Ficedula* flycatchers), while the others moult at their wintering sites after completion of the post-nuptial (autumn) migration (e.g., *Acrocephalus* warblers). Some species may moult several times a year undergoing complete moult first, followed by a partial moult later or *vice versa*. Non-breeding residency or wintering period is followed by a pre-nuptial (spring) migration with birds returning to their breeding areas. Setting the start and end points of annual routines is largely arbitrary and annual cycles should rather be viewed as a continuous set of events which are interlinked with one another.

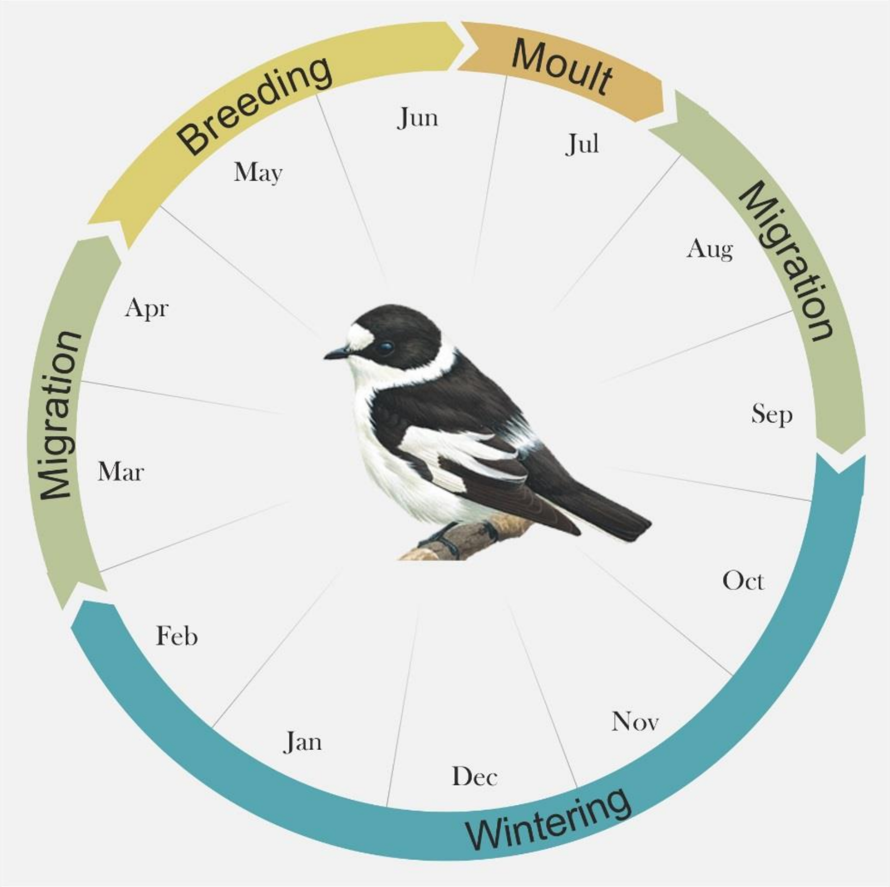


Figure B1. Annual cycle of Collared Flycatcher *Ficedula albicollis.* Flycatcher illustration © Birds of Armenia Project.

After the non-breeding residency period in the tropics, successful, surviving individuals return to their natal or previous breeding sites – a phenomenon called philopatry (Greenwood 1980). How exactly they are able to find their natal origins is still unknown. Nevertheless, this allows to follow individual birds throughout their reproductive lifetime as the likelihood of encountering the same individuals each year is relatively high.

Birds have to time their arrival at the breeding grounds not only in respect to the environmental conditions (Both and Visser 2001), but also to what their conspecifics are doing. Arriving at the breeding sites first, allows to secure the prime quality territories and gain higher overall fitness (Kokko 1999). Yet, long-distance migrants breeding in Europe are only short visitors at the temperate latitudes and spend most of the year away from their breeding sites. Some spend as little as a few days or weeks at a given breeding location before moving on (Kempenaers and Valcu 2017).

Both spatial and temporal aspects are essential for successful organization of birds' annual cycles (Box 1). Migratory birds need to time their visits at particular locations to match the resource availability (Thorup et al. 2017). The optimal migration theory suggests that birds should minimize the energy expenditure and maximize the total migration speed i.e., minimize the total migration duration, when moving between different sites of residency (Alerstam 2011). Thus, in both seasons birds should follow the time minimization migration strategy and complete their migration swiftly (Hedenström 2008). Under a theoretically ideal scenario, an individual would complete its entire migratory journey in a single long-distance flight. This would allow to reduce the likelihood of morality and to outcompete conspecifics for early arrival. Typically, long-distance migrants cannot complete the entire length of the journey in a single flight and need to stop over, sometimes multiple times, for refuelling (Hedenström and Alerstam 1997) and/or due to unfavourable weather conditions (Tøttrup et al. 2012). Nevertheless, there are several examples of birds completing their annual migratory journeys in a single long-distance endurance flight (Gill et al. 2009; Alves et al. 2016; Xenophontos et al. 2017). Resources and suitable stopover sites for refuelling are distributed unevenly across the migratory flyways, leading to the great diversity of migratory strategies we see today.

BOX 2 MIGRATORY CONNECTIVITY

Migratory connectivity defines the extent to which individuals of different breeding populations mix and form non-breeding populations. It is described along a continuum where one end represents complete segregation of different populations (i.e., strong migratory connectivity) while the other end defines complete mixing of different populations (i.e., weak migratory connectivity) (Webster et al. 2002). The strength of migratory connectivity has direct implications for conservation biology where stronger connectivity is associated with higher degree of vulnerability (Taylor and Norris 2010; Iwamura et al. 2013; Cresswell 2014). Meta-analyses of individually tracked long-distance migrants have revealed generally weak migratory connectivity between breeding and non-breeding populations (Finch et al. 2017).

In a classical sense migratory connectivity is understood as geographic mixing of different breeding populations at the non-breeding grounds (Marra et al. 2006). Where migratory animals spend the non-breeding period is only one of the aspects which furthermost might highly depend on variability in migration strategies (i.e., migration routes, stopover usage and phenology) among individuals. The largest mortality often occurs during migration (Sillett and Holmes 2002; Newton 2008; Lok et al. 2015), therefore understanding which migration routes and stopover areas are used by which populations is of high priority.

Geographic aspect of migratory connectivity is, however, only one part of how we perceive animal movements. Bauer et al. (2015) argue that we should integrate timing of annual events as a third dimension when looking at migratory connectivity. While populations can overlap spatially in their site usage, it might not be the case temporarily. In other words, the same sites might be used by different populations at different times. Such patterns of migratory connectivity can have various consequences on individual fitness, population dynamics, gene flow, and parasite transmission.

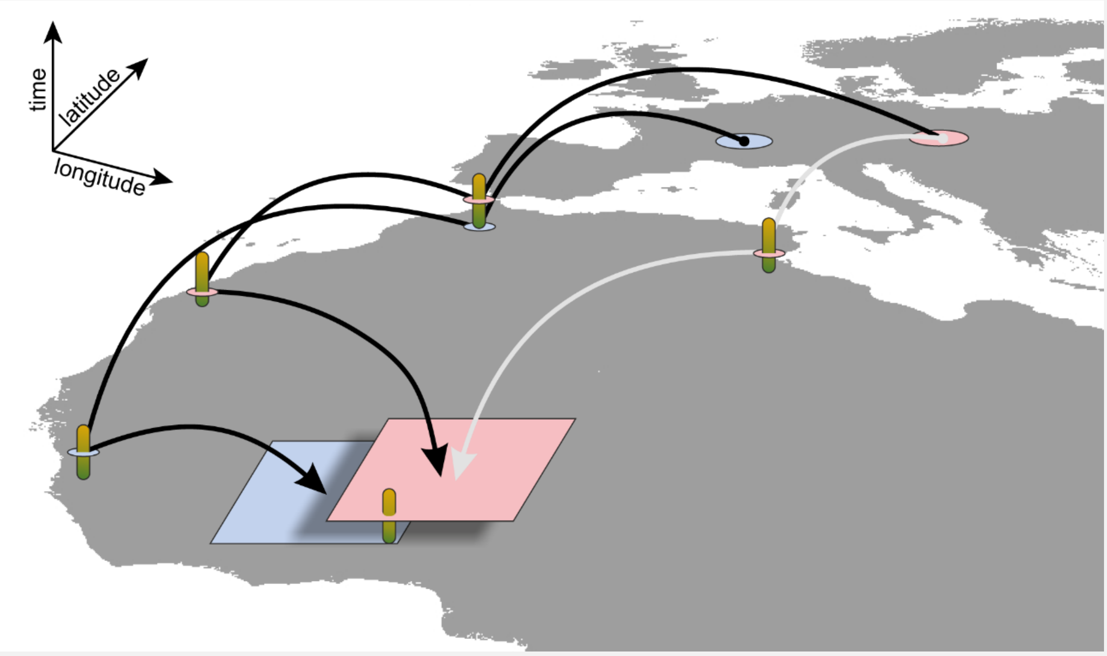


Figure B2. Migratory connectivity in a hypothetical bird species shown as connectivity at breeding and non-breeding grounds, migration routes, stopover sites, and phenology of site usage. Different breeding populations (blue and red ellipses) might use the same migratory flyway (black arrows) but can spatially and temporarily vary/overlap in respect to the stopover and non-breeding site usage. Similarly, individuals of the same breeding population (red ellipse) can differ in migratory routes (black and white arrows) and stopover usage, resulting in migratory divide and ‘weak’ connectivity *en route*.

For many species the structure of breeding-populations is known to be very tight with the same individuals returning to the same locations each season (Greenwood 1980). On the contrary, our knowledge about the non-breeding populations is still relatively scarce. The concept of migratory connectivity (Box 2) has really come about during the last few decades. Recent advances in individual-based tracking systems, have enabled us to follow migratory animals as they complete their annual journeys. This has boosted research in animal migration ecology, particularly in small bodied songbirds, allowing us to link breeding populations to non-breeding populations.

Individual-based tracking technologies, like geolocators (Box 3), and remote sensing techniques enable us to look into not only broad scale migration patterns, but also individual level experiences across the annual cycle. While animal tracking provides us with the information on where and when animals go, methods like stable isotope analyses can provide us with the information about the conditions animals experience on site, for example, their diet composition (Hobson and Clark 1992). Stable isotopes of winter-grown tissue can also be used to infer environmental conditions at the wintering sites to further study seasonal interactions and link different events across the animal's annual cycle (Marra et al. 1998). It is well documented that individual experiences in one season can carry consequences on individual's performance in the following seasons via carry-over effects (Harrison et al. 2011; Box 4). Thus, the annual cycles of animals should be considered as unified sequences of mutually interlinked events, rather than separate happenings, even if the events are spatially and temporarily segregated.

These seasonal large-scale movements of birds have long fascinated humans. Now with the help of technology we are able to follow bird migration and look into the details more closely than ever before. We can gain an in-depth understanding of when birds migrate, where they go, how they get there. Thus, we can also monitor how human-induced activities like habitat modification and climate change influence migratory animals and if they are able to adapt to the changing environment. We can get a glimpse in their lives on the move and away from the breeding sites before they once again return the following spring.

BOX 3 LIGHT-LEVEL GEOLOCATORS

Geolocation by light is based on a simple principle of differences in daylight patterns across geographically distinct regions of the world. This method relies on information of local sunrise and sunset times which are used to calculate geographic coordinates via standard astronomical equations (Montenbruck and Pfleger 2010). In short, local noon/midnight time is used to determine longitude, while day length/night length is used to determine latitude.

A geolocator is an archival data logging device that records ambient light intensity. Geolocator is mounted on a bird's back using a back-pack like harness or fitted on a bird's leg similar as a bird ring. This tiny gadget, weighing mere 0.6 g, stores the light data on board adding a time-stamp to each measurement. After the bird has completed its migration and returned to the breeding site the following spring, the geolocator can be retrieved and data downloaded. Sunrise and sunset times are most often determined using the 'threshold method' (Lisovski and Hahn 2012). The accuracy of the calculated geographic coordinates highly depends on the shading of the light sensor by vegetation, weather, topography, and behaviour of the bird (Lisovski et al. 2012). Consistent shading patterns can be corrected for by fitting an appropriate sun elevation angle to the determined sunrise/sunset times.

Geolocators were first used on small-bodied songbirds only in 2007 (Stutchbury et al. 2009). Since then these devices have been used increasingly to study migration and wintering ecology of various passerine and near-passerine birds.

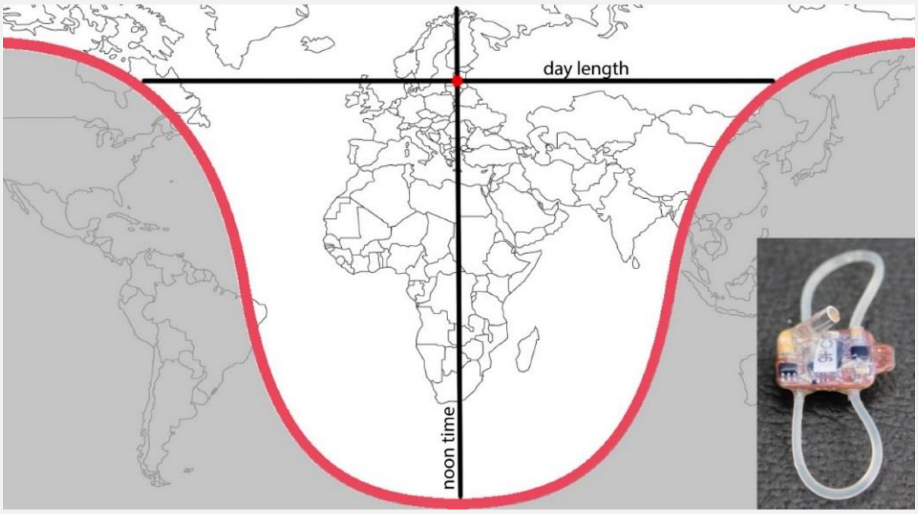


Figure B3. The principle of geolocation by light. Longitudinal position is obtained from local noon time, latitude – from day length. Red line on the map indicates transition between day (transparent) and night (shaded area). Bottom right: geolocator model GDL2.0 (Swiss Ornithological Institute) with a 7mm light stalk and an elastic silicon leg-loop harness.

BOX 4 CARRY-OVER EFFECTS

Annual cycles of migratory animals consist of various spatially- and temporally-distinct episodes, like reproduction, moult, migration, and non-breeding residency. Nevertheless, these events are linked to each other physiologically and ecologically, and preceding events may have profound consequences on the following life history phases (Harrison et al. 2011). Carry-over effects are defined as events and processes taking place in one season which result in individuals making a transition between the seasons in a different state of condition, ultimately affecting their performance (Norris and Marra 2007; Harrison et al. 2011).

For long-distance migratory birds this means that experiences at their tropical non-breeding grounds may carry over across seasons and continents to influence events taking place at their temperate breeding grounds and *vice versa*. For instance, residing in sub-optimal habitat at non-breeding areas can result in delayed spring migration, consequently negatively affecting breeding performance the following season (Marra et al. 1998; Norris et al. 2004). Habitat quality, social status, population density, and breeding effort have been identified among the main drivers of carry-over effects (Harrison et al. 2011). To disentangle true carry-over effects from individuals' intrinsic quality, researchers need to implement experimental approaches in their study design.

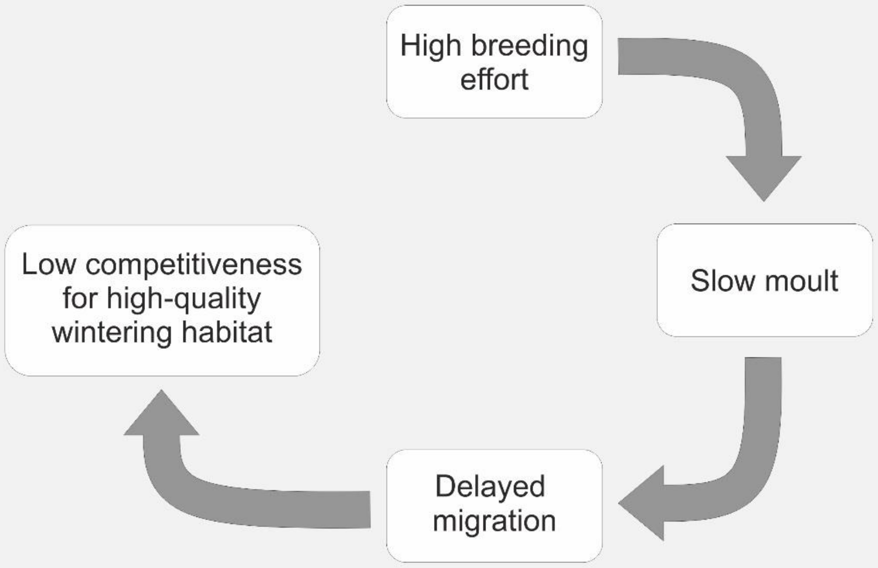


Figure B4. A theoretical example of how carry-over effects form the breeding season may affect the subsequent annual cycle events in a migratory species.

Thesis focus

Thus far, over 70% of the published studies on birds have been focused solely on the breeding period and only 6–7% of the studies take a multi-season year-round approach. Furthermore, only slightly more than 5% of the studies examine seasonal interactions (Marra et al. 2015). In respect to migratory birds, this means that we still know relatively little about the migration and non-breeding periods, which comprise up to 9–10 months of the year for some long-distance migrants.

The technological development in the last decade has opened new horizons in bird migration research. For some species just one year of tracking has provided more data on their migration and non-breeding periods than 100 years of scientific bird ringing. Tracking data also allow us to get a clearer picture of the annual cycles of individual migrants. Furthermore, if we want to know not only where and when birds go but also how they get there, we need to look into their movement patterns in connection with the environment, migrants' own physical state, and past experiences leading up to the migration.

The key aims of my thesis are (1) to provide a comprehensive knowledge of migration patterns and organization of the annual cycles of the three study species – Tawny Pipit, Semi-collared Flycatcher, and Collared Flycatcher, (2) to gain deeper understanding of the interactions between the long-distance migrants and the environment, and (3) to examine year-round seasonal interactions of individual migrants.

Study systems

An estimated 2.1 billion passerine and near-passerine birds migrate from Europe to sub-Saharan Africa each autumn (Hahn et al. 2009). This makes Afro-Palearctic migratory system the world's largest bird migration network (Moreau 1972; Newton 2008). Migratory birds link ecological communities of the two continents altering diversity and stability of the local communities (Bauer and Hoye 2014). They transform various trophic levels by foraging as well as becoming prey for the resident animals.

A crucial part comprising the Afro-Palearctic bird migration system is the Sahara Desert and the Mediterranean Basin – large inhospitable barriers separating the tropics from the temperate regions. For decades there has been a debate over how small-bodied birds are able to cross them successfully and what might be the appropriate strategy for barrier crossing – a non-stop flight spanning tens of hours (Moreau 1961) or an intermittent strategy by flying at night and resting during the day (Biebach et al. 1986; Bairlein 1988; Schmaljohann et al. 2007). The chosen strategy may also be opportunistic depending on availability of suitable stopover sites along the way and differ among species, individuals and flyways.

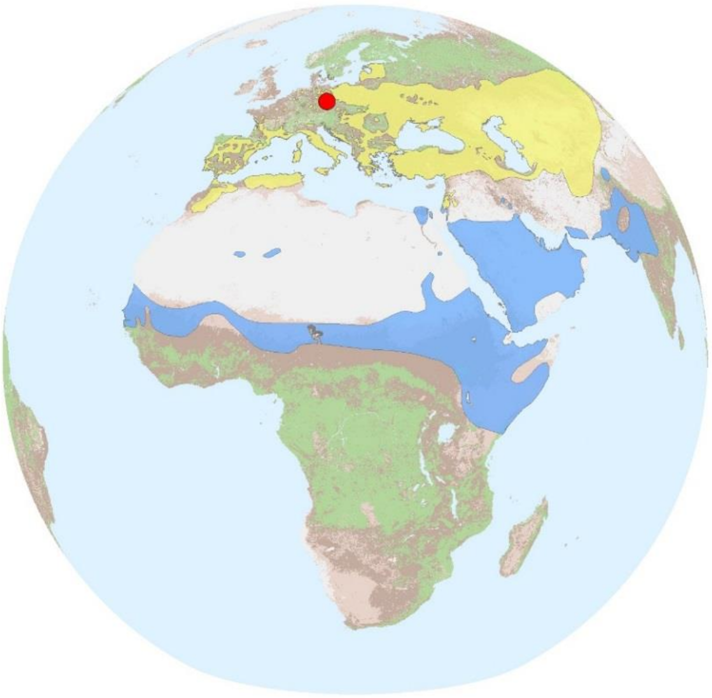
The three central study species of this dissertation differ in their non-breeding residency destinations and migration ecology representing each of the three major flyways connecting Europe and sub-Saharan Africa – the western, the central and the eastern flyways.

Tawny Pipit

The Tawny Pipit *Anthus campestris* is an insectivorous passerine long-distance migrant of the family *Motacillidae*. Its breeding range spans from southern and eastern Europe to Central Asia (Fig. 1). Tawny Pipit is currently listed as Least Concern by the IUCN Red list (IUCN 2016). However, the central European breeding populations are patchily distributed, and in recent decades have faced severe declines across Germany (Sudfeldt et al. 2013), Poland (Sikora et al. 2007) and the Czech Republic (Šťastný et al. 2006). Tawny Pipits are habitat specialists, and during the breeding season prefer dry, sandy, steppe-like habitats (Cramp 1988).

Whilst Tawny Pipits are known to spend the non-breeding period in arid regions from Western Sahel to the Middle East (Cramp 1988; BirdLife International and NatureServe 2011), our knowledge of habitat preference during the non-breeding period is limited. Consequently, data on population-specific non-breeding areas, and thus migratory connectivity, and temporal organization of the annual cycle are lacking.

As part of my thesis (Chapter 2), I studied Tawny Pipits from a breeding population in central Europe, Czech Republic (50°30′N, 13°50′E; Fig. 1). This population breeds in active open-type lignite mines – a highly disturbed and dynamic manmade habitat. The population is relatively small and isolated with no more than 200 breeding pairs annually.



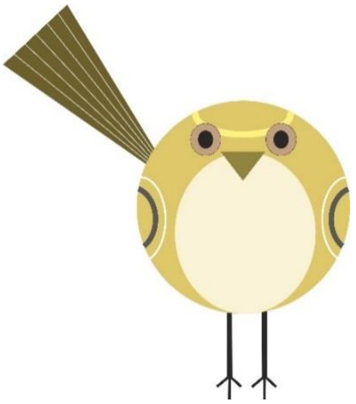
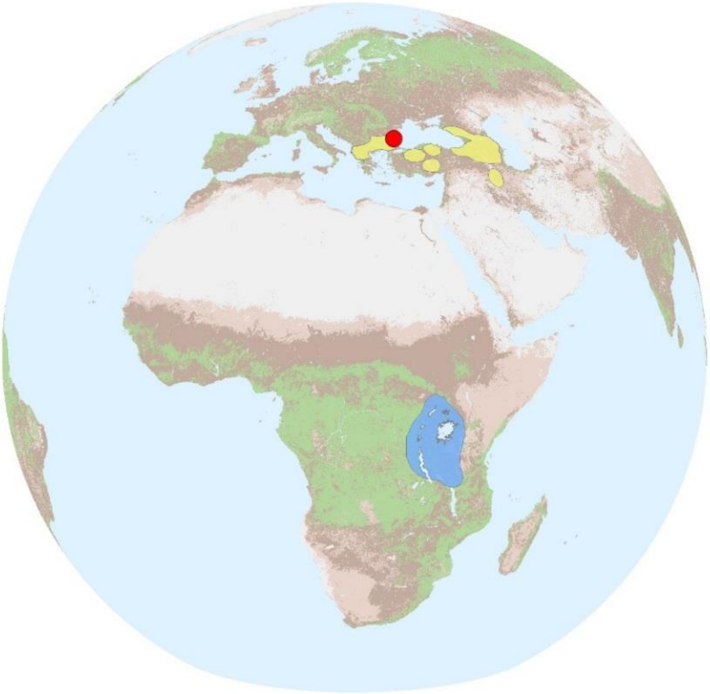


Figure 1. Distribution map of Tawny Pipit *Anthus campestris*. Breeding range is marked in yellow, non-breeding range in blue (BirdLife International and NatureServe 2011). Red dot denotes breeding site of the studied population.

Semi-collared Flycatcher

The Semi-collared Flycatcher *Ficedula semitorquata* is an insectivorous long-distance migrant of the family *Muscicapidae*. It's breeding range spans between 35° and 45° latitude in the Southeast Europe from Albania in the west to the Caspian Sea in the east (Fig. 2; Cramp and Perrins 1993; BirdLife International and NatureServe 2011). During a recent reassessment of the IUCN Red List, its threat status was reclassified from Near Threatened to Least Concern, however, the global population is still declining (IUCN 2015). Until recently the species was considered a subspecies of the relatively well-studied Collared Flycatcher (Sætre et al. 2001). Therefore, little is known about the species' ecology. Spatiotemporal aspects of migration and non-breeding period are particularly obscure.

For my thesis (Chapters 3 and 6), I studied a Semi-collared Flycatcher population breeding in Eastern Bulgaria (42°55′N, 27°48′E; Fig. 2). The population is breeding in artificial nest boxes situated in an open woodland dominated by Hungarian Oak *Quercus farnetto*. During the breeding season birds suffer high predation pressure from Forest Dormouse *Dryomys nitedula*. Size of the studied population varies around 100 breeding pairs annually.



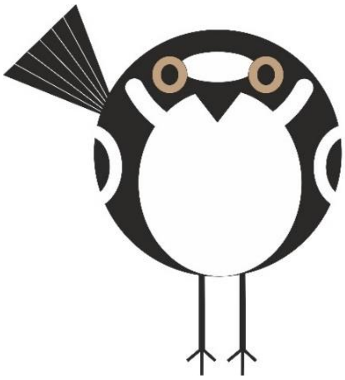


Figure 2. Distribution map of Semi-collared Flycatcher *Ficedula semitorquata*. Breeding range is marked in yellow, non-breeding range in blue (BirdLife International and NatureServe 2011). Red dot denotes breeding site of the studied population.

Collared Flycatcher

The Collared Flycatcher *Ficedula albicollis* is an insectivorous long-distance trans-Equatorial passerine migrant of the family *Muscicapidae*. Collared Flycatcher breeds across large areas of the Central and Eastern Europe and migrate to Southern and Central Africa during the Northern Hemisphere winter (Fig. 3; Cramp and Perrins 1993; BirdLife International and NatureServe 2011). It is listed as Least Concern by the IUCN Red list and the global population size is increasing (IUCN 2016). The species breeding ecology has been studied extensively with Collared Flycatcher often serving as a model species for a wide range of ecological studies (e.g., Gustafsson and Sutherland 1988; Gustafsson et al. 1995). Despite the large numbers of Collared Flycatchers ringed each year in Europe, thus far there have only been five ring recoveries from sub-Saharan Africa (Hölzinger 1993), leaving a gap in our knowledge about the species non-breeding ecology.

For my thesis (Chapters 4, 5 and 7), I look into migration patterns and organizations of the annual cycle of two Collared Flycatcher populations. The Central European study population in the Czech Republic (49°50′N, 17°13′E; Fig. 3) breeds in artificial nest boxes situated in deciduous woodland dominated by European Beech *Fagus sylvatica* and English Oak *Quercus robur*. The Northern European study population on the Baltic island of Gotland, Sweden (57°01′N, 18°16′E) breeds in deciduous (mainly ash-oak-hazel) forests. Both populations are a subject of long-term studies spanning several decades.

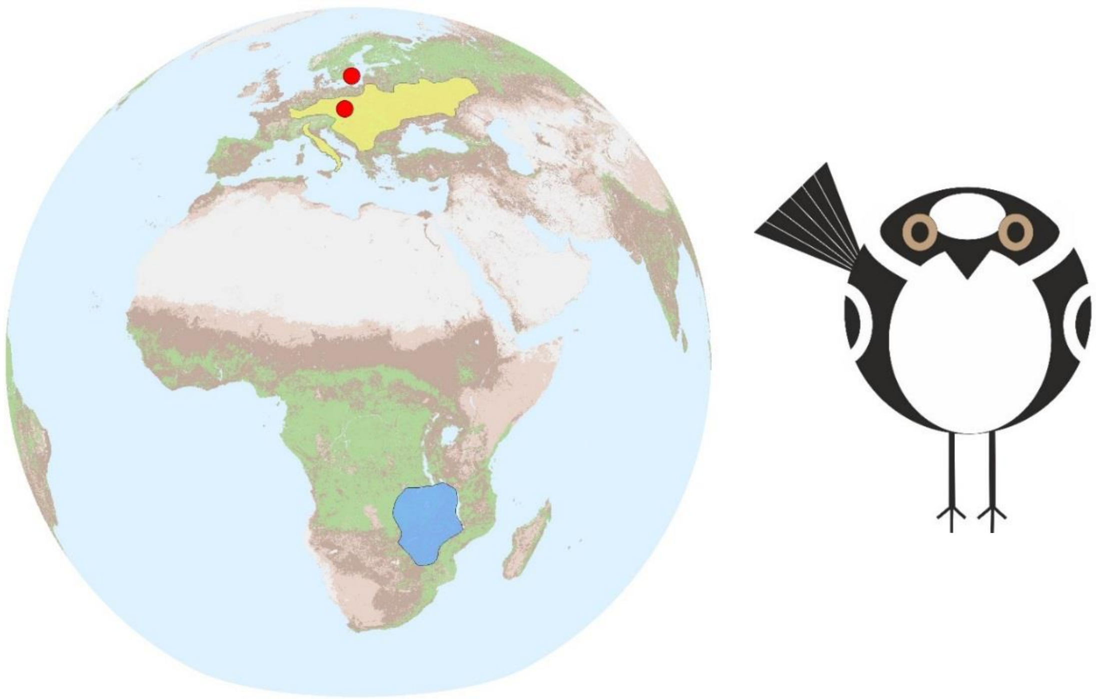


Figure 3. Distribution map of Collared Flycatcher *Ficedula albicollis*. Breeding range is marked in yellow, non-breeding range in blue (BirdLife International and NatureServe 2011). Red dots denote breeding sites of the studied populations.

Thesis outline

As stated earlier, the Afro-Palearctic bird migration system consists of three major flyways – the western, the central and the eastern flyway. In **Chapter 2**, I start out on the western flyway by looking at the annual cycle and migration strategies of the Tawny Pipit. In 2013 we equipped 35 adult breeders with geolocators at our Central European study site. A year later in 2014, we obtained tracking data of six individuals revealing that the birds migrated and spent the northern hemisphere winter in the Sahel zone in Western Africa. During the both migration seasons the majority of the birds followed a migration route through the Iberian Peninsula utilizing stopover sites in Northern Africa. In autumn, three of the six tracked birds crossed the Sahara Desert inland, and the other three followed the Atlantic coastline, while all individuals flew along the coastline in spring. During the wintering period we observed high site itinerancy with five individuals moving westward in mid-winter and thus, utilizing two main wintering sites. On average the tracked individuals spent only ¼ of the year at the European breeding sites. Another ¼ was spent on annual migrations, while ½ of the year was spent at the wintering sites in the Western Sahel. We discuss the choice of migration routes and wintering areas in respect to the breeding longitude. We also provide rainfall data from the Western Sahel to gain deeper understanding of the observed non-breeding site itinerancy.

In **Chapter 3**, I move from the western to the eastern flyway, and look into the annual cycle of the Semi-collared Flycatcher. We again used light-level geolocators to track the flycatcher migration between a breeding site in Eastern Bulgaria and wintering locations in Central Africa. By tracking the birds over two consecutive seasons, we confirm the location of wintering sites in Eastern-Central Africa and reveal a clock-wise loop migration system where autumn migration routes lay east from the spring migration routes. The tracked individuals on average spent about seven months in the sub-Saharan Africa, while only five months were spent north of the Sahara Desert (including three months at the breeding sites). During the migration periods all birds congregated at certain stopover regions indicating high migratory connectivity *en route*. Such migratory strategy may increase the vulnerability of this already declining species as habitat degradation at these stopover hotspots may affect birds of different origins from across the breeding range.

In **Chapter 4**, I shift back to the west and to my third study species, the Collared Flycatcher, representing the central Afro-Palearctic flyway. We investigate the importance of breeding site latitude on the organization of the annual cycle by comparing the migration tracks of Swedish and Czech breeding populations. We expose how phenology at the breeding sites dictates the timing of events across the entire annual cycle. The southern study population always completed the annual events i.e., breeding, start and finish of the migrations earlier compared to their counterparts breeding at higher latitude. Even though, the temporal schedules of the two populations were different, spatial organization of the annual cycle was fairly similar with both populations using similar migration routes and wintering regions. Such spatiotemporal pattern of the annual cycle suggests that annual schedules of long-distance migrants are predominantly under endogenous control and are mainly driven by spring phenology at breeding sites. Furthermore, we found that wintering sites of both populations laid west from the previously known wintering distribution which calls for re-evaluation of the species' non-breeding range.

After answering the trivial questions of where and when each of my study species migrate, I take a broader look at how they get there. More specifically, in **Chapter 5** we look into barrier crossing strategies of four small-bodied passerine species as they are crossing the Sahara Desert and the Mediterranean Sea. The chosen range of study species (Collared Flycatcher, Pied Flycatcher, Reed Warbler, and Aquatic Warbler) represents all three Afro-Palearctic flyways. We found that these otherwise typical nocturnal migrants often prolong their migration into the day or even fly non-stop for up to 70–80 hours while crossing an ecological barrier. The prolonged daytime flights were more frequent in spring suggesting tighter migration schedules, possibly associated with higher pressure for early arrival at the breeding sites. As we observed the prolonged diurnal flight in the vast majority of the tracked individuals, we discuss the possibility that this might be the prevailing barrier crossing strategy yielding the lowest mortality. Nevertheless, the light pattern data recorded by the geolocators also revealed a high degree of variability among the individuals, thus birds may act opportunistically and make a daytime stopover in Sahara if encountering a suitable resting site.

Further in **Chapter 6**, I look at how migratory birds cope with weather extremes faced during their migrations. We used Semi-collared Flycatcher as our model species and compared tracking data of two consecutive spring seasons. The spring of 2014, when the first group of tagged birds returned back to Europe, was exceptionally warm in the Mediterranean Basin and at the breeding site of the flycatchers. In contrast, the spring of 2015 when the second group of tagged birds returned, was exceptionally cold, delaying plant phenology for several weeks. Such extreme and contrasting conditions present an ideal opportunity to study phenotypic plasticity in a natural setting. We found that in both years flycatchers started their spring migration from the wintering sites in Eastern-Central Africa and crossed the Sahara Desert at approximately the same time. However, when reaching the Mediterranean Basin where the first cues for weather and environmental conditions of the temperate regions can be assessed, the flycatchers adopted different strategies. In the warm spring of 2014, birds quickly continued their migration and returned to their breeding sites, while in the cold spring of 2015 birds spent a prolonged period in the Mediterranean Basin waiting for improved weather conditions before returning to their breeding sites. Additionally, we observed a lower apparent individual survival in the cold spring, suggesting that some individuals lacked an appropriate response strategy or may have chosen an inappropriate response to the cold weather. Males and older individuals that typically migrate earlier paid a higher cost and suffered a higher degree of mortality compared to females and younger birds.

As climate change is predicted to bring an increasing number of extreme weather events, animals’ ability to flexibly adjust their behaviour seems to be an essential necessity for survival. Long-distance migratory birds are especially challenged in their responses to weather extremes as they have limited or no ability to predict the weather at their distant breeding areas while residing in the tropics. The onset of spring migration in long-distance migrants is determined by photoperiod and endogenously controlled circannual rhythms. While on migration, combining the internal clock with external cues from the environment seems to be vital to withstand the changing climate.

In **Chapter 7**, I take a closer look at the annual cycles of the tracked Collared Flycatchers from the Central European breeding population and examine how carry-over effects from the breeding and non-breeding seasons modify individual timing of migration. We used the number of fledglings as a gauge for the parental investment with higher number of fledglings corresponding to a higher parental investment. To infer the non-breeding habitat quality and to assess the carry-over effects from the non-breeding season, we used stabile isotope (δ2H) signatures of the winter-grown feathers. We found that individuals with higher absolute parental investment delayed their autumn migration, had shorter non-breeding residency period and advanced spring migration compared to the individuals with lower breeding effort. Timing of spring events, particularly the onset of breeding, were more dependent on the conditions at the non-breeding areas, rather than the previous parental investment. We also observed a strong "domino effect" (i.e., high dependency of the timing of consecutive events) for intra-seasonal events, but it was weaker for inter-seasonal events. Thus, it seems that the costs of previous breeding could be overcome during the wintering period.

We also conducted a brood manipulation experiment to disentangle the true carry-over effects from individuals' intrinsic quality. Brood size of the geolocator-tagged males were experimentally increased or reduced by one chick prior to the tracking of migration. We did not find unambiguous differences in the annual schedules between the individuals of reduced and increased broods; however, the latter were earlier with Sahara crossing in spring and arrival at the breeding grounds.

These results demonstrate that annual schedules of individual migratory birds depend on both, their previous parental investment and the environmental conditions at the non-breeding residency areas. Our findings highlight the tight links between spatially- and temporally-distinct phases of the annual cycles of migrants.

Conclusions

The studies comprising this thesis look into spatiotemporal migration strategies of selected long-distance migrants spanning across all major flyways linking Europe to Africa. We revealed different approaches of how these migrants cope with their annual movements and the encountered environmental challenges. Among those, Tawny Pipits adopted non-breeding site itinerancy while in sub-Saharan Africa, Semi-Collared Flycatchers migrate in a clock-wise loop fashion using different migration pathways and stopover sites in autumn and spring, and different populations of Collared Flycatchers have different migration scheduled that are linked to their breeding site phenology. Carry-over effects from the breeding and non-breeding seasons can have severe consequences on the annual schedules of individual migrants, thus seasonal interactions play an important role in individuals’ annual cycles. An effective barrier crossing strategy and phenotypic plasticity en route can be the key issues that decide between successful breeding and mortality.

As more and more data are accumulated on different species and populations, we also need to start looking into migratory patterns and migratory connectivity discriminating between specific age and sex classes. Juvenile migrants can adopt different spatiotemporal strategies in contrast to their adult conspecifics e.g., by migrating at different time and using different migration routes (Hake et al. 2003; Crysler et al. 2016). Similarly, males and females may adopt contrasting migratory patterns (Tøttrup and Thorup 2008) and reside at different non-breeding areas (Cristol et al. 1999), resulting in different environmental factors encountered by both sexes. Such differences among age and sex classes can have a large influence on how we perceive migratory connectivity from a conservation perspective.

However, we also need to understand the limitations of different study methods. For instance, in studies where migration and non-breeding information is obtained via non-transmitting data loggers, like geolocators, we get access only to information of the successful-surviving individuals, possibly biasing the sub-sample of the overall population. Similarly, when ring recovery data are used the sample is biased to locations and times with the highest catching/ringing effort. Despite being a powerful tool for migration studies, such methods do not provide the crucial information on areas and time that are associated with increased mortality.

Knowing where and when certain populations reside is crucial for developing appropriate conservation measures. Such knowledge, even on species that are currently 'doing well', is important for future references and detecting changes in long-term. Common species can also serve as so called 'model species' for investigating more complex issues of bird migration, like seasonal interactions and carry-over effects. Thus, building a comprehensive knowledge can go a long way in protecting migratory species as well as predicting consequences of future climate change.

Concluding remarks

Life on the move provides more opportunities and allows to explore a far greater variety of resources. The challenge is to keep up with the ever moving animals. Our ability to follow migratory birds as they complete their thousand-mile journeys across countries and continents is essential if we aim to understand the experiences migrants go through each year. Annual migrations and non-breeding season of migratory birds are still relatively uncharted areas and there are still a great deal of natural history questions waiting to be answered.

Studying animal movement is all but dull.

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Chapter 2

Annual cycle and migration strategies of a habitat specialist, the Tawny Pipit *Anthus campestris*, revealed by geolocators

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Abstract

Habitat specialist species occupy narrow ecological niches, typically utilizing similar habitat types throughout the annual cycle. Their strict requirements for specific habitats may make them vulnerable to environmental changes, especially in small, local populations. Therefore, detailed knowledge of the species' ecology is crucial for conservation purposes. In this study, we used light-level geolocators to identify migration routes and non-breeding areas of a distinct specialist for dry habitats, the Tawny Pipit *Anthus campestris*, from a currently declining central European breeding population. During autumn and spring migration, the majority of the birds followed a route along the northwest of the Alps and via the Iberian Peninsula, with stopover sites mainly in northern Africa. In each migration season, however, one of two different individuals took a detour around the eastern side of the Alps. When crossing the main ecological barrier, the Sahara Desert, three of six birds followed the Atlantic coastline in autumn, whereas all five birds migrated near the coast in spring. Non-breeding areas of all tracked pipits were uniformly located in the Western Sahel, with five of six birds utilizing two main non-breeding sites, the second of which was always located west of the first. On average, the tracked birds spent 48% of the year at the nonbreeding areas, 27% on migration, and 25% at the breeding site. Our findings demonstrate strong migratory connectivity in Tawny Pipits which may have future implications for conservation of this long-distance migrant.

Keywords: Annual cycle, Geolocation, Habitat specialist, Long-distance migrant, Migratory strategy

Introduction

Habitat preference and condition throughout the annual cycle play a key role in successful breeding performance, survival and population longevity for all species (Wiens 1992). Species are usually categorized in two groups according to their habitat preference: habitat generalists, that use a wide range of diverse habitats, and habitat specialists, that rely on one or a few similar habitat types (McPeek 1996). In the case of migratory animals, it is important to understand their habitat preference and use throughout the entire annual cycle. Another important aspect for migrants is migratory connectivity—the extent to which animals from the same breeding area migrate to the same non-breeding area (Webster et al. 2002). Strong migratory connectivity in combination with habitat specialization are associated with high vulnerability, as habitat deterioration in either breeding or non-breeding areas can result in severe population decline (Bauer et al. 2015; Cresswell 2014).

Migratory strategy and availability of suitable habitats *en route* can also play a key role in population dynamics of habitat specialists. During migration between Europe and sub-Saharan Africa, birds can face several ecological barriers, including the Alps, the Pyrenees, the Mediterranean Sea and the Sahara Desert. Therefore, choosing the optimal migratory strategy in terms of routes, detours, stopovers and migration schedule, along with flexibility to adjust for local conditions, is critical for minimizing mortality risk and maintaining body condition during the non-breeding season (Alerstam 2011). The choice of migratory strategy may be greatly dependent on food availability *en route* and on the animal's body condition. Recent studies have shown that individuals from the same breeding population can exhibit a high degree of versatility in their migration strategies and non-breeding areas (Delmore et al. 2012; Lemke et al. 2013; Trierweiler et al. 2014). Moreover, the same individual can adopt different strategies in different migration seasons (Tøttrup et al. 2012).

In this study, we tracked a sub-Saharan migrant, the Tawny Pipit *Anthus campestris*, from a breeding population in central Europe by means of light-level geolocation. The central European population of Tawny Pipits is patchily distributed, and in recent decades has faced a severe decline across Germany (Sudfeldt et al. 2013), Poland (Sikora et al. 2007) and the Czech Republic (Šťastný et al. 2006). Tawny Pipits are habitat specialists, and during the breeding season inhabit dry, sandy, steppe-like habitats; however, our knowledge of the non-breeding period is limited. Whilst the Tawny Pipits are known to spend the non-breeding period in arid regions from Western Sahel to the Middle East (Cramp 1988), data on population-specific non-breeding areas, and thus migratory connectivity and temporal organization of the annual cycle, are lacking. The aims of this study were to identify migration routes and non-breeding residency areas and to evaluate seasonal and individual differences in migration strategies of a central European population of Tawny Pipits. We expect that Tawny Pipits, as dry and open habitat specialists, spend the non-breeding period in the northernmost part of Sahel, while utilizing inhospitable habitats during migration (BirdLife International and NatureServe 2011; Cramp 1988).

Methods

We studied the annual cycle of a Tawny Pipit population breeding in northern Bohemia, the Czech Republic (50°30′N, 13°50′E). The studied population breeds in active open-type lignite mines—a highly dynamic, manmade habitat. The population is isolated and relatively small, with no more than 200 breeding pairs.

In 2013, we captured 35 breeding adults (25 males, 10 females) using mist-nets and perch and walk-in traps, and equipped the birds with geolocators (model GDL2.0, manufacturer: Swiss Ornithological Institute). The geolocators were fitted on each bird’s back using a leg-loop silicone harness. The mass of the device including the harness was 0.66 ± 0.03 (SD) g, which is less than 5% of the lean body mass of the birds (mean ± SD, males 25.52 ± 1.74 g, females 23.65 ± 2.02 g). All tagged birds were additionally fitted with aluminium and colour leg-rings. Ringed-only birds were used as a control group to account for return rates. During the 2014 breeding season we successfully recaptured eight (six males, two females) previously tagged birds and retrieved the geolocators. An additional eight (seven males, one female) previously tagged birds were observed in the area, but we failed to recapture them. We carefully inspected the recaptured birds for any signs of feather or skin abrasion caused by the geolocators, but generally found no damage except for some abraded feathers directly underneath the area where the geolocator was positioned. Only one male had a small amount of dry pus under the geolocator.

In 2014, we observed 46% (16 of 35 birds) of the geolocator-tagged birds at the breeding site. The return rate for the control birds was 45% (10 of 22 birds). There was no difference in return rates between geolocator and control birds (Pearson’s $\chi^2 = 0$, $p = 0.99$), nor in recorded body mass at the time of geolocator deployment and retrieval in the subsequent year (paired t test: $t = 1.25$, $df = 6$, $p = 0.26$).

The retrieved geolocators contained data encompassing three full annual tracks. One device had stopped recording while the bird was still in the non-breeding area (25 March), while two devices had stopped recording during the spring migration, shortly after the birds had left the non-breeding residency sites (20 April, 8 May). The two remaining devices contained no data due to software malfunction.

Geographic positions were calculated using the threshold method. We determined sunrise and sunset times using GeoLocator software (Swiss Ornithological Institute). All data sets were checked and, if necessary, corrected for clock drift. Further analysis concerning determination of stationary periods and calculation of geographic positions were conducted with the R-package ‘‘GeoLight’’ version 1.03 (Lisovski et al. 2012a; Lisovski and Hahn 2012). Ambient light level measurements taken by geolocators suffer from errors caused by habitat, terrain, weather, time of year and bird’s behaviour (Lisovski et al. 2012b). Therefore, we applied double filtering of the outlying sun events using two different techniques. Firstly, the most pronounced outliers of the sunrise and sunset data were filtered with the ‘‘loessFilter’’ function using two interquartile ranges as a threshold. Secondly, we applied a 3-day moving linear regression to the recorded sunrise/ sunset times and filtered sun events differing for more than 40 min from this regression line. This resulted in filtering of 1–45% (mean = 24%) of all sun events among the different datasets. To determine stationary periods, we applied ‘‘changeLight’’ function, with change point probability threshold of 0.9-quantile and a minimum staging period of 3 days. Geographic coordinates for long stationary periods were calculated using sun elevation angles derived from the Hill–Ekstrom calibration. The calibration failed, however, for short stopover periods, and sun elevation angles derived from calibration at the breeding site (in-habitat calibration, Lisovski et al. 2012a) were used instead. Positions in the Southern Hemisphere and above 60°N were discarded. We defined stationary sites as the median position ±25th/75th percentiles within the particular stationary period. Because of the short duration of selected migratory stopover periods and forthcoming equinox times, we were not able to determine geographic positions of all stopover sites.

We also assessed the degree of migratory connectivity of our study population during the non-breeding period. This was measured as the average distance between the individuals during the non-breeding period using nearest-neighbour distances of individuals' median positions.

To evaluate environmental conditions and habitat preferences of the Tawny Pipits during the non-breeding period, we obtained data on monthly precipitation rates at the nonbreeding residency areas. Weather data was obtained via R-package ‘‘RNCEP’’ version 1.0.7 (Kemp et al. 2012) using NCEP/DOE Reanalysis II dataset (Kanamitsu et al. 2002) provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (available at http://www.esrl.noaa.gov/psd/).

Mean values are reported with standard deviations throughout. We used one-tailed Pearson's correlations to test the positive correlation between autumn migration departure time and arrival time at the non-breeding site (Rice and Gaines 1994).

Results

Migration patterns

The median onset of autumn migration of the tracked Tawny Pipits was 10 August (Table 1), and birds followed a general southwest direction. Four of six birds each made two stopovers (6–10 days per stopover), while one bird made only one stopover (13 days). Two birds first stopped at the coast of the Mediterranean Sea near the border of France and Spain before continuing further southwest and making a second stopover in Northern Africa (Fig. 1). One other bird used two stopovers in Northern Africa. Unfortunately, we were not able to estimate geographic positions of stopover sites for the remaining three birds. Longitude estimates during the Sahara Desert crossing indicate that three birds migrated along or near the coastline, while the other three crossed the desert inland. Interestingly, longitude estimates of one individual (CZ-6) during the early stages of the autumn migration indicate a detour along the eastern side of the Alps (Appendix 1 Fig. A1).

The median arrival date at the non-breeding sites was 27 September. There was no significant correlation between the date of departure from the breeding site and arrival at the non-breeding sites (r = 0.65, n = 6, p = 0.08; low statistical power due to small sample size). The mean duration of autumn migration was 52 ± 11.5 days (Table 1).

The median departure date from the non-breeding sites was 23 March (Table 1). Four of five birds had their first stopover of 13.5 ± 4.4 days while still in sub-Saharan Africa. Similar to the patterns found during autumn migration, four of five birds first moved to the coastline before crossing the Sahara whose second non-breeding site was situated approximately 60 km from the coastline, migrated along the coast. All birds stopped over after crossing the Sahara; however, we were not able to estimate geographic positions of all individuals on stopovers (Fig. 1). In total, each bird had one or two stopovers (5–25 days per stopover) before arriving at the breeding site in late April to late May (median 7 May). Note that, similar to the autumn migration, one individual, (CZ-5 in this case) took a detour via the southern Apennine Peninsula and returned to the breeding site along the eastern side of the Alps (Fig. 1; Appendix 1 Fig. A1).

Desert (Appendix 1 Fig. A1), and all birds, including the remaining individual (CZ-2).

For the three birds in which we obtained full annual tracks, the mean duration of spring migration was 45.7 ± 4.0 days, including the first stopover site in sub-Saharan Africa (Table 1). If this stopover site

Table 1. Annual schedules and migration data of the six geolocator-tracked Tawny Pipits.

	CZ-1	CZ-2	CZ-3	CZ-4	CZ-5	CZ-6	Median/ mean
	♂	♂	♂	♂	♂	♀	
Autumn migration							
Departure	30-Aug	18-Aug	12-Aug	9-Aug	6-Aug	24-Jul	10-Aug
Duration (days)	46	43	74	46	48	55	52
Distance (km)	4060	4840	4000	4320	4040	4140	4230
Speed (km/day)	88	113	54	94	84	75	85
Non-breeding period							
Arrival	15-Oct	30-Sep	25-Oct	24-Sep	23-Sep	17-Sep	27-Sep
Changes of site	30-Dec	13-Nov	18-Nov	-	22-Dec	9-Jan	22-Dec
Distance (km)	420	410	620	-	570	340	
Departure	9-Apr	8-Mar	23-Mar	?	18-Mar	20-Apr	23-Mar
Total Duration (days)	176	159	149	>182	176	215	175
Spring migration							
Arrival at breeding site	21-May	22-Apr	?		7-May	?	7-May
Duration (days)	42	45	>15		50	>18	46
Distance (km)	4470	4640	4420	4320	4480	4460	4470
Speed (km/day)	106	103			90		100

In the last column median values for calendar dates and mean values for numbers are provided

was excluded, the mean duration of spring migration was only 30.7 ± 9.1 days.

The average migration speed in autumn was 84.7 ± 19.7 km/day, whereas in spring it was 99.7 ± 8.5 km/day (Table 1).

Non-breeding residency period

Non-breeding sites of the tracked Tawny Pipits were located in extremely dry parts of the Sahel region in western Africa, i.e. Mali, Mauritania and Senegal, and five of six birds utilized two non-breeding residency sites (Fig. 1). On average, the first site was located 592 ± 314 km from the second. After the change in residency sites, the birds were clustered in a small region, residing relatively close to one another: the nearest-neighbour distance of the first non-breeding residency sites was 334 ± 129, and it was 149 ± 102 km for the second non-breeding residence. Average monthly precipitation from November through the end of February at the nonbreeding residency areas was close to zero (dry season in the Sahel). Precipitation patterns of the first and second non-breeding sites were similar (Fig. 1), indicating a year-round preference for dry, sandy habitats.

The switch between the two non-breeding areas the individuals occupied successively occurred between mid-November and early January (median date 22 December). One bird stopped over for a 9-day intermittent period (site latitude unclear) between the non-breeding sites, whereas the others moved without stops. The second non-breeding site in all cases was west of the first, with three of five birds moving southwest (median coordinates ± interquartile range: first site, 17°28′ ± 3°48′N 8°16′ ± 3°22′W; second site, 15°37′ ± 0°56′N 10°56′ ± 4°11′W). On average, the birds spent more time at the second non-breeding area (100.8 ± 11.5 days) than the first (69.6 ± 35.9). The total duration at the non-breeding residency areas for the five birds with complete records was 175 ± 25.2 days on average. Throughout the annual cycle, Tawny Pipits spent on average 48% of time at the non-breeding sites, 27% on migration, and 25% at the breeding site (for individual schedules, see Appendix 1 Fig. A2).

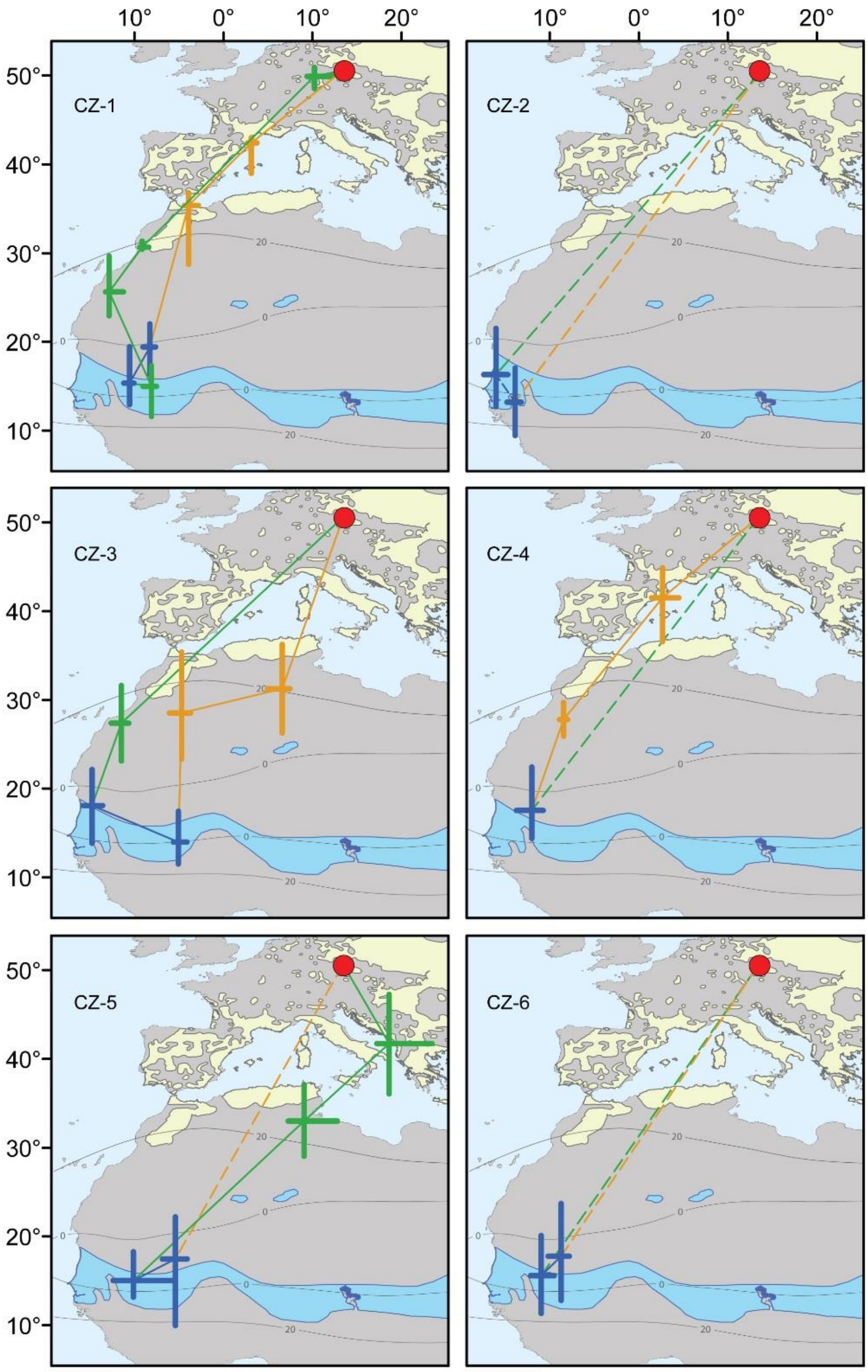

Figure 1. Migration tracks and non-breeding areas of six geolocator-tagged Tawny Pipits. Breeding site (*red dot*), stopover sites longer than 3 days in autumn (*orange*) and in spring (*green*), and non-breeding residency areas (*blue*). All positions are depicted as median ± interquartile range. *Lines* connecting different staging sites do not necessarily show actual migration routes taken. *Solid lines* show movement sequences to and from known staging sites; *dashed lines* connect staging sites with unknown stopovers in-between. Background map shows species breeding range (*yellow*) and non-breeding range (*blue*, BirdLife International and NatureServe 2011). Average monthly precipitation at the non-breeding grounds from 1 November 2013 to 28 February 2014 is given as 0 and 20-mm rainfall isopleths (see ‘‘Methods’’ for details).

Discussion

This study provides the first insight into spatiotemporal organization of the entire annual cycle of a habitat specialist, the Tawny Pipit. The main migration routes of the tracked individuals in both autumn and spring are via the Iberian Peninsula and along the Atlantic coastline. Thus, our study highlights the importance of coastal habitats and the coastline itself in providing stopover sites and landmarks for migratory pathways. The non-breeding residency sites were located in a narrow zone in Western Sahel. We demonstrate that the use of multiple non-breeding residency sites is a common strategy adopted by Tawny Pipits, as five of the six birds utilized two non-breeding residency sites, with the second site located further southwest on average. Tawny Pipits of unknown provenance are known to spend the European winter in the Sahel region throughout Africa (BirdLife International and NatureServe 2011; Cramp 1988); however, to our best knowledge, this is the first study providing details on hitherto unknown connectivity between the European breeding populations and non-breeding residency areas.

Migration strategies

The departure dates and timing of autumn migration of the tracked Tawny Pipits were within the known population limits (Alström and Mild 2003; Jenni and Kéry 2003). The only individual making a detour via the eastern side of the Alps, and thus not following the shortest route (great circle route), was the earliest to depart from the breeding site. The few African ring recoveries of Tawny Pipits breeding in Western Europe coincide with our findings of main migration routes through Spain and Morocco (Bairlein et al. 2014; Keith et al. 1992; Zink 1973). The arrival times of our birds in the Sahel are also in line with southwest passage times recorded in Morocco (Cramp 1988) and field observation data by Gee (Gee 1984). Similarly, the onset of spring migration and passage times of the tracked birds in northern Africa correspond well to the current knowledge of peak migration times from mid-March to April (Smith 1968).

In both seasons birds made long stopovers before crossing the Sahara, suggesting considerable fuelling before crossing the desert (Bairlein 1985). We identified two main strategies for Sahara crossing in autumn: half of the birds (three of six) followed the Atlantic coastline, while the other half crossed the Sahara more inland. In contrast, all birds uniformly migrated along the coast in spring. Field observations from Morocco and Mauritania also indicated considerable movement of Tawny Pipits along the Atlantic coast in both seasons (Gee 1984; Smith 1968); however, similar data from the inner desert is lacking. Crossing the desert along or near the coastline is considered advantageous, as the environmental conditions are better than those of the inner desert (Moreau 1961).

For the three birds with full annual tracks, we found high variability in migration duration in autumn and spring (Table 1), suggesting individually adjusted migration speeds. The overall migration speed of the tracked Tawny Pipits was faster in spring than autumn. This is in line with the general evidence of faster spring migration because of higher pressure for timely arrival at the breeding site (Nilsson et al. 2013).

Non-breeding residency

While the majority of Afro-Palearctic migrants are dependent on the vegetated areas of sub-Saharan Africa (Morrison et al. 2013; Vickery et al. 2014), Tawny Pipits can reside in the most arid parts of the Sahel region (Cramp 1988; Gee 1984; Moreau

1972), therefore occupying a special ecological niche. However, details on population-specific non-breeding areas and associated migratory connectivity are lacking thus far. Most of the birds are found in Western and Eastern Sahel, while very few are observed in the central Sahel (Mali, Niger and Chad, Cramp 1988). Our results now verify that pipits from the central European population near the border of the Czech Republic and Germany migrate to western Africa. Recent bird tracking studies have shown a strong correlation between breeding and non-breeding site longitudes (Hahn et al. 2013; Trierweiler et al. 2014), which suggests that Tawny Pipits breeding further east may be the ones migrating to Eastern Africa. Two of our tracked birds took an eastern detour around the Alps, which with great caution could be viewed as a signal of a mixed genetic background of the population in which westward migration prevails over eastward migration. However, the point at which the migratory divide occurs in the European continent remains unknown.

Moreau (1972) mentions a late influx of Tawny Pipits in Senegal in January, which he infers as the arrival of birds from further north. Our findings indicate that these birds should, in fact, come from further east, as five of the six tracked Tawny Pipits shifted west, which could explain Moreau’s findings. Tawny Pipits start to moult while still in Europe, but some birds interrupt their moult before autumn migration (Stresemann and Stresemann 1968). Moult is usually completed after the arrival in sub-Saharan Africa from October to December, suggesting that the first nonbreeding site is used to complete the interrupted moult. Great Reed Warblers *Acrocephalus arundinaceus* migrating to sub-Saharan Africa are also known to utilize multiple non-breeding residency sites, where the first site is presumably used for moulting (Lemke et al. 2013). On the other hand, this could demonstrate that birds can flexibly adjust to on-site conditions and change their non-breeding residency area in search of more suitable habitats should local conditions deteriorate. The higher degree of migratory connectivity (i.e., shorter nearest-neighbour distances between individuals) of the second non-breeding sites may indicate just this, as the birds gather in areas of suitable habitats.

During the non-breeding periods, all tracked Tawny Pipits were clustered in a small region in Western Sahel, showing a high degree of migratory connectivity. This is in line with the strong connectivity found in Pied Flycatchers *Ficedula hypoleuca* (Ouwehand et al. 2015), Nightingales *Luscinia megarhynchos* (Hahn et al. 2013), and European Rollers *Coracias garrulus* (Finch et al. 2015). However, it contrasts the weak migratory connectivity described in Great Reed Warblers (Lemke et al. 2013), Common Redstarts *Phoenicurus phoenicurus* (Kristensen et al. 2013), and Barn Swallows *Hirundo rustica* (Liechti et al. 2015). Additional studies on breeding populations in the eastern part of the distribution range should reveal further insights on migratory connectivity between Europe and Africa, possibly unveiling the migratory divide in the European breeding population of Tawny Pipits, and thus enabling a better description of alternative strategies adopted during migration and non-breeding periods.

Acknowledgments

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Appendix 1

Supplementary information for Chapter 2

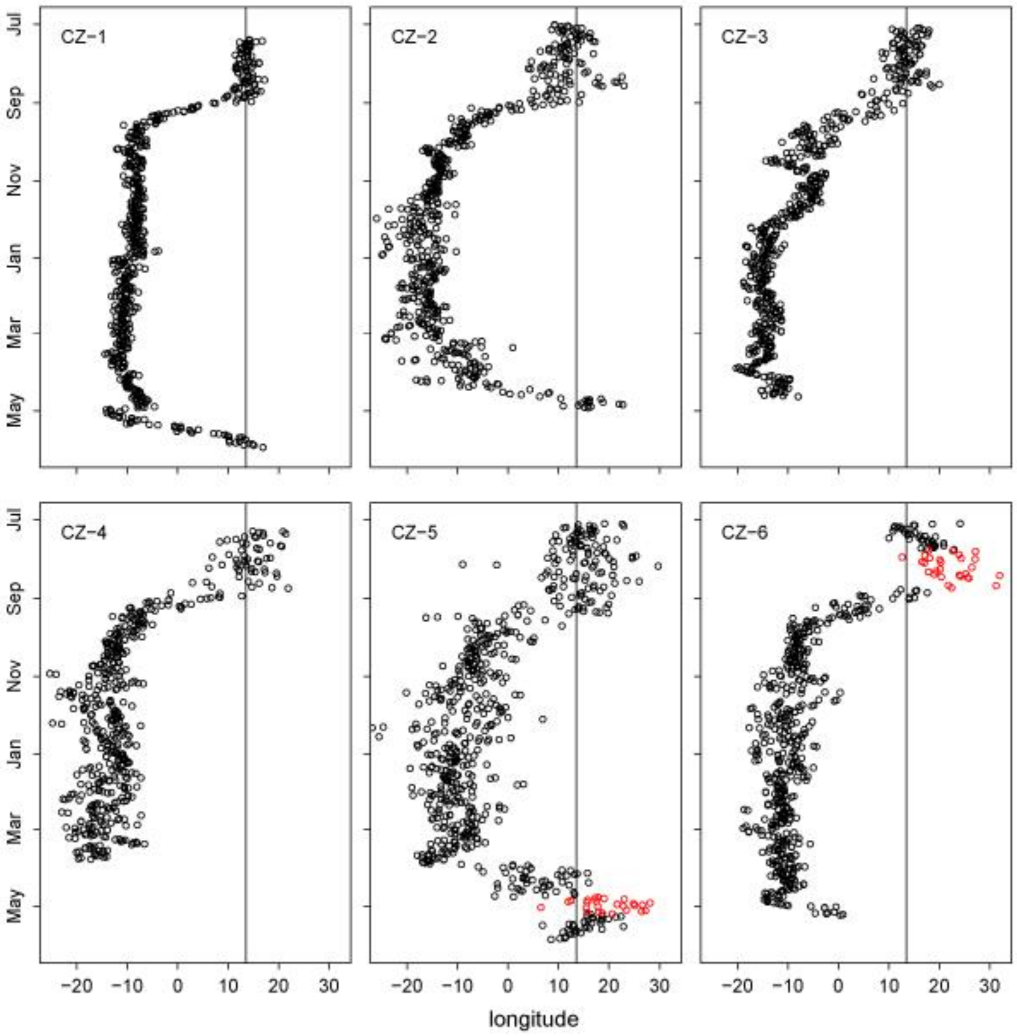

Figure A1. Longitude estimates throughout the annual cycle of the six tracked Tawny Pipits. The identity (ID) of each individual is given in each panel. Note that for three individuals (CZ-3, CZ-4 and CZ-6) the annual tracks are incomplete. *Vertical lines* show breeding site longitude. Longitude estimates suggesting an eastern detour around the Alps are highlighted in *red*.

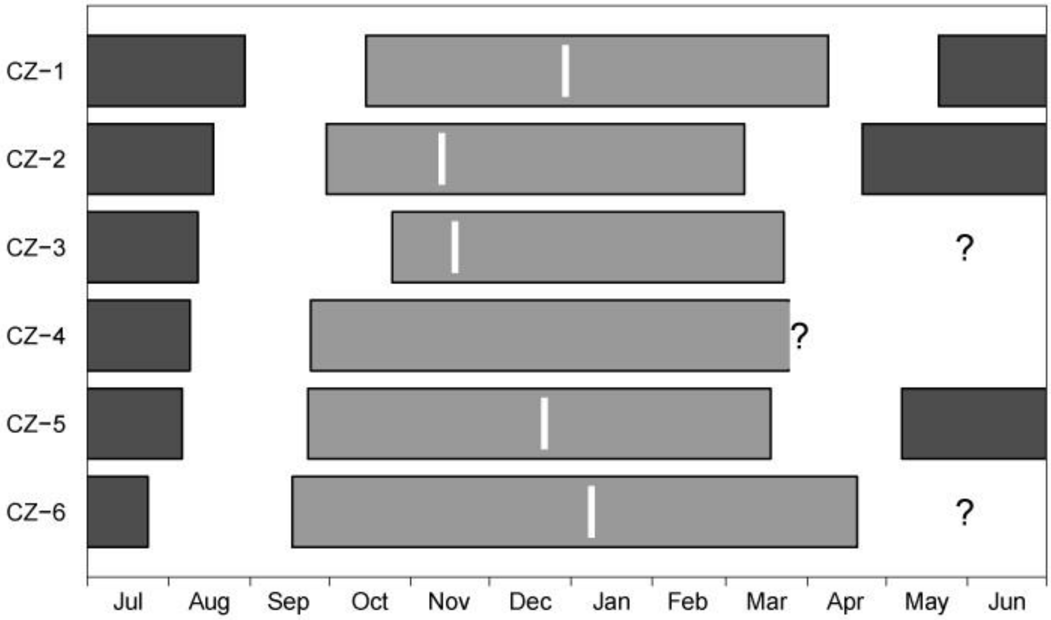

Figure A2. Annual cycle of six, individually tracked Tawny Pipits. Residing at breeding site (*dark grey*), nonbreeding area (*light grey*) and migration periods (*empty*). *White lines* indicate shift between the nonbreeding residency sites. *Question marks* display lack of data due to geolocator failure.

Chapter 3

Year-round spatiotemporal distribution of the enigmatic Semi-collared Flycatcher *Ficedula semitorquata*

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Miroslav Král, Strahil Peev, Peter Adamík

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Abstract

We examined migration routes and nonbreeding sites of a poorly studied long-distance migrant, the Semi-collared Flycatcher *Ficedula semitorquata*, by tracking adult birds with geolocators from an eastern European breeding population across two subsequent years. All 11 birds migrated in a clockwise loop fashion where autumn migration routes lay east from the spring migration routes. Non-breeding sites were located in Eastern-Central Africa, i.e. Uganda, Tanzania, Burundi, Rwanda, and east DR Congo, where birds spent on average 128 days. Non-breeding sites of two birds were located outside of the currently estimated species' non-breeding range.

Keywords: Afro-Palearctic, *Ficedula*, Geolocator, Long-distance migration, Loop migration

Introduction

The three major flyways connecting Palearctic and Africa form the world's largest migratory network with billions of birds undertaking annual cross-continental journeys (Hahn et al. 2009). Using geolocator tracking technology population specific migration routes, stopover areas, and nonbreeding sites of many small Afro-Palearctic migrants are currently being discovered (McKinnon et al. 2013). This is of special importance in the light of recent population declines of many long-distance migrants (Vickery et al. 2014). Currently, for only 60.7% (34/56) of Afro-Palearctic long-distance passerine migrants, the conservation status in Europe has been classified as ''favourable'' (BirdLife International 2004). By revealing population-specific distribution during the non-breeding period, we will be able to assess the main threats outside the breeding range encountered by long-distance migrants and apply appropriate conservation measures.

The Semi-collared Flycatcher *Ficedula semitorquata* is a long-distance migrant breeding in south-east Europe between 35° and 45° latitude from Albania in the west to the Caspian Sea in the east (Cramp and Perrins 1993). During the latest reassessment of the IUCN Red List, its threat status was reclassified from *near threatened* to *least concern*, however, the global population is still declining (IUCN 2015). Until recently the species was considered a subspecies of the well-studied Collared Flycatcher *Ficedula albicollis* (Sætre et al. 2001). Therefore, little is known about the species' ecology, especially migration routes and non-breeding areas. In this study we tracked Semi-collared Flycatchers while on their migration to and from sub-Saharan Africa using light-level geolocators. We were specifically interested in the spatiotemporal patterns of migration and non-breeding residency areas as well as their spatial overlap with the current estimate of the species' non-breeding range (BirdLife International and NatureServe 2011).

Materials and methods

Our study population of Semi-collared Flycatchers is located in east Bulgaria (42°55'N, 27°48'E) where birds breed in open woodland dominated by Hungarian oak *Quercus farnetto* ~120–150 m a.s.l. During the 2013 and 2014 field seasons, we fitted geolocators on 40 (17 males and 23 females) and 49 (27 males and 22 females) adult breeders, respectively. Geolocators [model GDL2.0, Swiss Ornithological Institute, weight including the harness: 0.60 ± 0.01 g (SD)] were fitted on birds' backs using elastic leg-loop silicone harnesses. In 2014 we managed to recapture 11 (27.5%) of the previously tagged birds, however, one bird had lost its geolocator. In 2015 we recaptured and retrieved geolocators from seven (14.3%) birds tagged a year before. Recapture rates for ringed-only control birds were 47.4 and 20.2% in 2014 and 2015, respectively. There was no significant difference between recapture rates of geolocator-tagged and control birds (Pearson's χ^2 test, 2014: $\chi^2 = 1.62$, $p = 0.20$, 2015: $\chi^2 = 0.01$, $p = 0.97$). Due to technical problems experienced by some geolocators we obtained tracks of 11 different individuals: five (including one incomplete track until 18 March 2014) from 2013 to 2014 and six from 2014 to 2015.

We used 'GeoLocator' software (Swiss Ornithological Institute) to obtain sunrise and sunset times from the light-logging data. Further analysis was done using R-package 'GeoLight' v1.03 (Lisovski et al. 2012a). We used the 'loessFilter' function with a threshold of two interquartile ranges to filter outliers from the dataset. Thereafter, we used 'changeLight' function to determine stationary periods of more than 3 days using probability of change $q = 0.8$. We manually checked if the ‘changeLight’ function had detected a change of stationary site at the beginning and end of the migration periods and after the Sahara/Arabian desert crossing [desert crossing times were determined according to the procedure described by Adamík et al. (2016) (see Appendix 2 Fig. A1)]. In cases when movements were not detected, we adjusted the probability of change (q value) in the ‘changeLight’ function.

Daily geographic positions were calculated applying the threshold method (Lisovski and Hahn 2012). To find the appropriate sun-elevation angle for the non-breeding residency period, we applied the Hill-Ekstrom calibration method of minimization of spread of latitudinal positions (Lisovski et al. 2012b). To calculate geographic coordinates for stopover sites known to be north of the Sahara we used the sun-elevation angles derived while the birds were at the breeding site in Europe (in-habitat calibration), while for stopover sites in the sub-Saharan Africa, we used sun-elevation angles derived from the non-breeding residency period (Hill-Ekstrom calibration). Calculated sun elevation angles ranged from +3.5° to +7.5° for in-habitat calibration and from −0.9° to +4° for Hill-Ekstrom calibration. Then we filtered all outlaying positions, which were >10° latitude from the median position, within a particular stationary period. Due to high variability in calculated positions and/or proximity of equinoxes for selected birds, we were not able to obtain geographic coordinates of all stopover sites during the migration periods.

Results

Autumn migration

The median onset of autumn migration was 21 July (for individual schedules see Table 1) and all birds followed a similar route with a predominant southeast direction (average direction: 136.8°). All birds used one long or two shorter stopovers in the eastern Mediterranean basin east of 30° longitude (Fig. 1, see Appendix 2 Fig. A2 for errors of individual position estimates). Birds crossed the Sahara/Arabian desert on 12 August (median date) using a corridor between the River Nile and western part of the Arabian Peninsula, later stopping in Ethiopia (seven out of 11 birds, for four remaining birds, latitude was uncertain but longitude estimates also suggest stopover sites in this region). After the desert crossing, birds remained stationary for prolonged periods of time, on average spending 60 ± 13 days (SD) on stopovers in sub-Saharan Africa before arriving at their respective non-breeding sites. The average autumn migration duration was 84 ± 13 days, and the average migration speed was 70 ± 14 km/day. Autumn migration distance measured as a great circle distance connecting known stopover sites was on average 5775 ± 636 km.

Non-breeding period

Birds arrived at their non-breeding sites from late September until early November (median: 9 October; Table 1). During the non-breeding period, flycatchers clustered in a relatively small region in Eastern-Central Africa near the Equator, i.e., Uganda, Tanzania, Burundi, Rwanda, and east DR Congo (Fig. 1), ~1000–1500 m a.s.l. Median positions of non-breeding residency sites of nine individuals were located within the currently estimated species’ non-breeding range, while two birds resided outside (Fig. 1). Non-breeding residency period on average lasted 128 ± 16 days.

Table 1 Individual migration schedules and non-breeding period data of 11 geolocator tracked Semi-collared Flycatchers from a breeding population in Bulgaria

Birds' ID	Age	Sex	Departure BG	Sahara crossing autumn	Arrival non-breeding site	Departure non-breeding site	Sahara crossing spring	Arrival BG	Autumn migration duration (days)	Autumn migration distance (km)	Autumn migration speed (km/day)	Spring migration duration (days)	Spring migration distance (km)	Spring migration speed (km/day)	Non-breeding residency duration (days)
2013-2014															
9TY	3+	f	30-Jul-13	14-Aug-13	11-Oct-13	21-Feb-14	6-Apr-14	10-Apr-14	73	5119	70	48	5013	104	133
9SY	2	m	21-Jul-13	11-Aug-13	20-Sep-13	22-Feb-14	15-Mar-14	26-Mar-14	61	5706	94	32	5912	185	155
9PH	2	m	24-Jul-13	14-Aug-13	9-Nov-13	7-Feb-14	21-Mar-14	30-Mar-14	108	5315	49	51	5415	106	90
9PE	3+	f	24-Jul-13	26-Aug-13	14-Oct-13	22-Feb-14	30-Mar-14	6-Apr-14	82	6030	74	43	5376	125	131
9OR	2	m	24-Jul-13	8-Aug-13	17-Oct-13	17-Feb-14	17-Mar-14		85	5525	65		5622		123
2014-2015															
11SS	4+	f	9-Jul-14	11-Aug-14	8-Oct-14	20-Feb-15	3-Apr-15	18-Apr-15	91	5066	56	57	5248	92	135
11SR	2	m	12-Jul-14	1-Aug-14	6-Oct-14	18-Feb-15	18-Mar-15	9-Apr-15	86	6903	80	50	5674	113	135
11SN	3+	m	21-Jun-14[a]	6-Aug-14	3-Oct-14	10-Feb-15	16-Mar-15	11-Apr-15	>104[a]	5858	<56[a]	60	5322	89	130
11RZ	2	m	12-Jul-14	16-Aug-14	30-Sep-14	14-Feb-15	20-Mar-15	10-Apr-15	80	6812	85	55	5792	105	137
11RV	2	m	31-Jul-14	23-Aug-14	5-Nov-14	3-Mar-15	7-Apr-15	11-Apr-15	97	6013	62	39	5052	130	118
11RU	4+	f	20-Jul-14	12-Aug-14	9-Oct-14	10-Feb-15	28-Mar-15	9-Apr-15	81	5181	64	58	5325	92	124
Median/average[b]			21-Jul	12-Aug	9-Oct	18-Feb	21-Mar	9-Apr	85	5775	70	49	5432	114	128

In one case (bird ID – 9OR) the geolocator stopped working during spring migration before the bird arrived back at the breeding site

*Bird left the breeding site before the geolocator started recording data on 21 June

**Only tracks with full data are included in the averages/medians

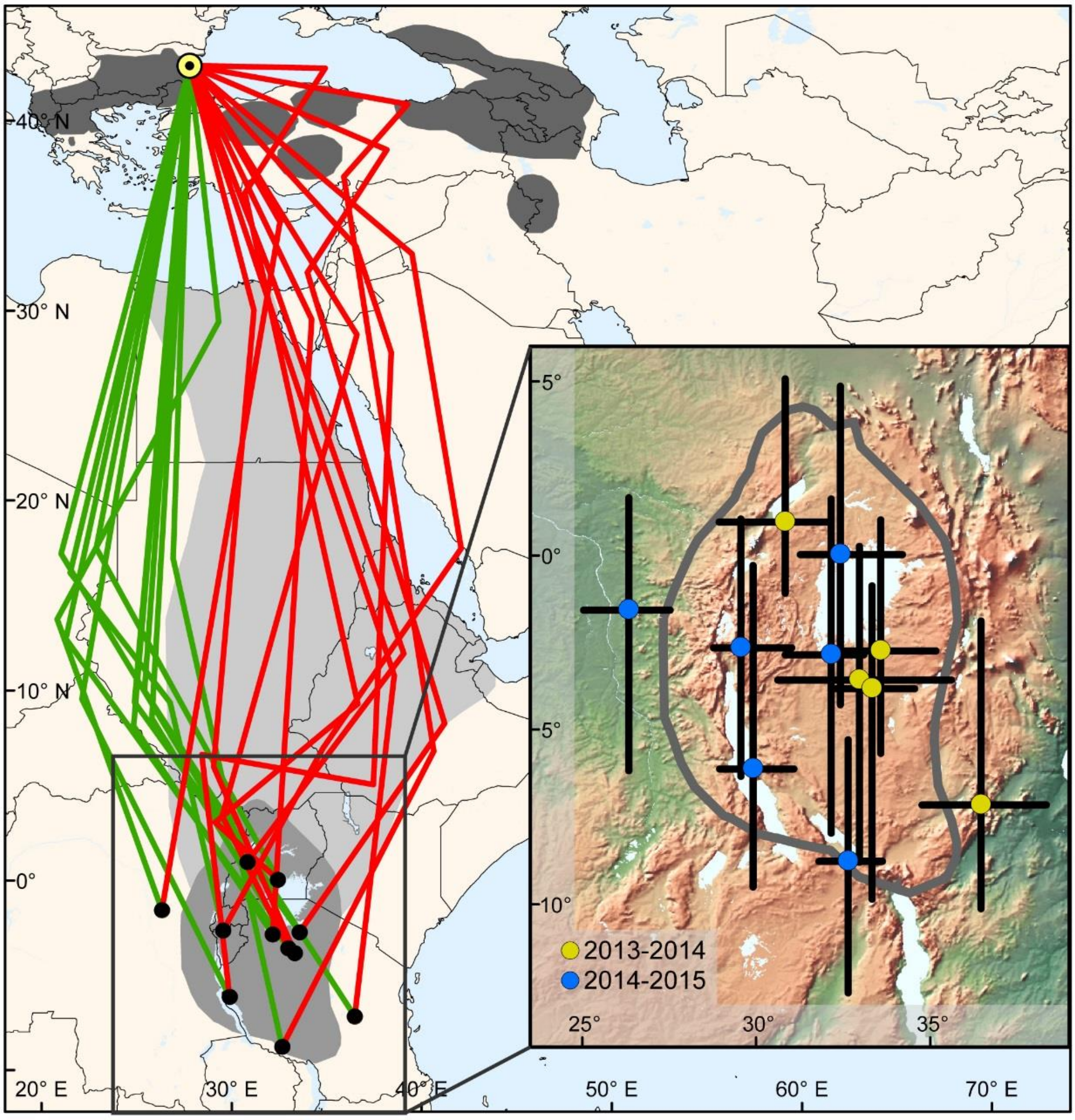

Figure 1. Migration of Semi-collared Flycatchers from an eastern European breeding population (*yellow dot*) from 2013 to 2014 (n = 5) and 2014–2015 (n = 6). *Lines* connect stopover sites to illustrate the seasonally different migration corridors (*red*—autumn, *green*—spring) but do not necessarily depict the exact migration pathways. Main non-breeding sites are shown as *black dots*. Background map gives the estimated distribution range [*dark grey*—breeding, medium *grey*—non-breeding, *light grey*—migration; (BirdLife International and NatureServe 2011)]. The inset shows detailed non-breeding sites with median position ± interquartile ranges (*yellow*—2013–2014, *blue*—2014–2015). The *grey line* encircles the currently known non-breeding range.

Spring migration

The median onset of spring migration was 18 February and all tracked flycatchers stopped over for 34 ± 9 days in a previously unknown staging area between 20° and 27°E (Fig. 1) before crossing the Sahara desert (median: 21 March, Table 1). Sahara crossing times encircle the vernal equinox, therefore, in all but one late migrating bird (11SN), we were not able to estimate the latitude of stopover sites after the desert crossing. Birds arrived at the breeding site from late March until mid-April with the median arrival date on 9 April.

The average spring migration duration was 49 ± 9 days, and the average migration speed was 114 ± 28 km/day (Table 1). The average spring migration distance was 5432 ± 289 km.

All birds migrated in a clockwise loop fashion when carrying out their annual migratory journeys. Tracked birds spent on average 104 days (28.5% of a year) at the breeding site, 133 days (36.4%) on migration and 128 days (35.1%) at the non-breeding site. The total amount of time spent in sub-Saharan Africa comprises 222 ± 7 days (60.8%, Appendix 2 Fig. A3).

Discussion

Our results provide the first insight into the spatiotemporal patterns of the entire annual cycle of one of Europe’s least studied songbirds, the Semi-collared Flycatcher. Adult birds from a breeding population in eastern Bulgaria performed a clockwise loop migration with non-breeding sites in Eastern-Central Africa. The recorded non-breeding residency sites of all, but two, individuals were located within the known species’ non-breeding range (Fig. 1, BirdLife International and NatureServe 2011). Tracked flycatchers were distributed across the small non-breeding range, suggesting that birds of different breeding origins may congregate during the non-breeding period (Fig. 1, *inset*).

In our tracked flycatchers, duration of spring migration was shorter and showed less variation than autumn migration supporting expectations of short optimal arrival period at the eastern European breeding site (Nilsson et al. 2013). However, the average migration distance was smaller in spring, possibly accounting for some of the observed differences in duration and speed.

When favorable foraging habitats, flight conditions (e.g., favorable wind) or potential hazards are distributed differently in autumn and spring, differences between the seasonal migration routes can arise resulting in a loop-migration system (Klaassen et al. 2010). Under such circumstances birds may aggregate at favorable locations in large numbers. Tracked Semi-collared Flycatchers congregated at stopover areas north and south of the Sahara desert highlighting the importance of selected stopover regions prior to and after the flight across large barriers. Such strong preference for particular stopover regions can increase vulnerability of this species since habitat degradation at such sites can affect many spatially separated breeding populations (Cresswell 2014). This, along with the relatively small non-breeding range and declining global population, showcases the conservation status of this poorly-studied passerine bird.

Acknowledgments

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Appendix 2

Supplementary information for Chapter 3

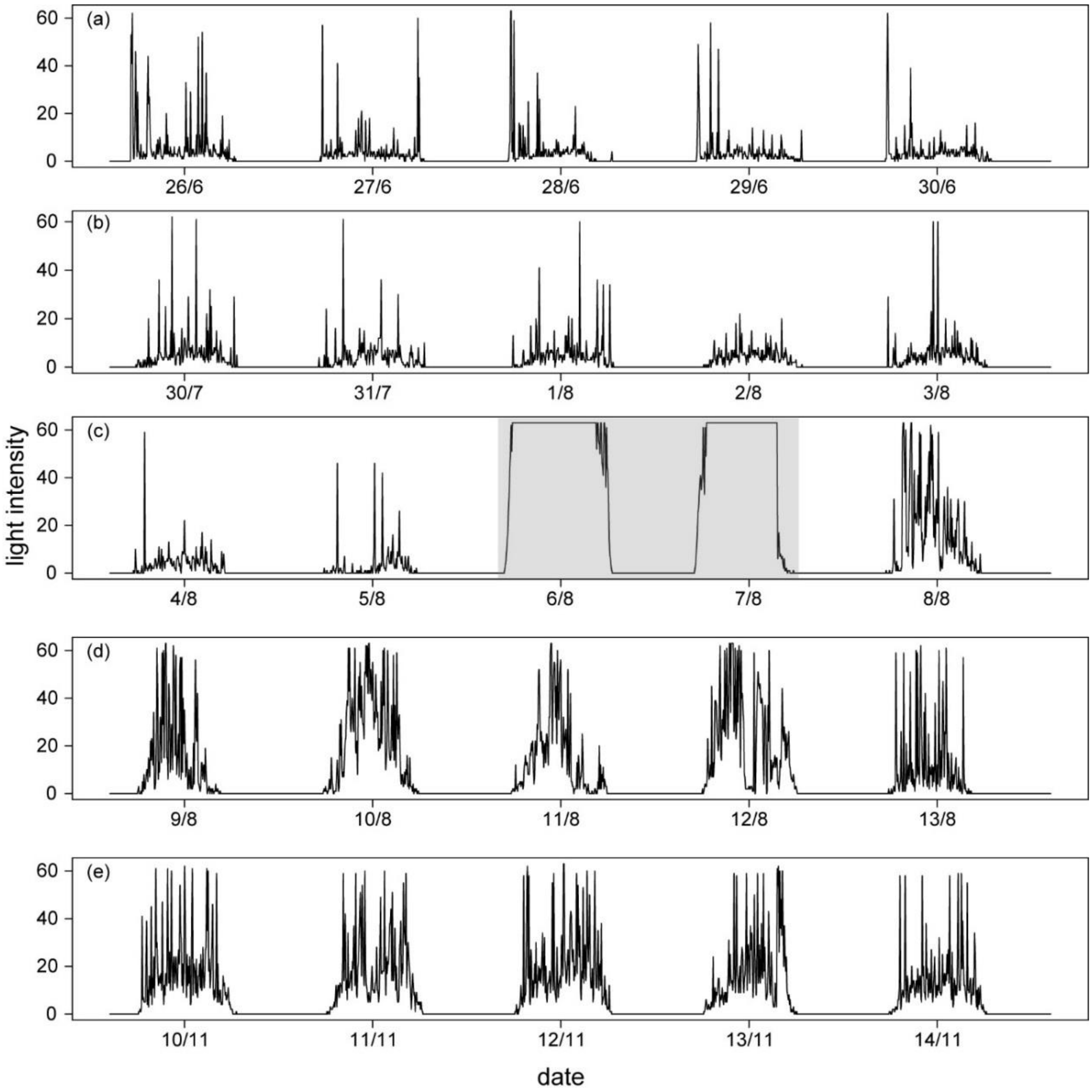

Figure A1. Daily patterns of raw light intensity data recorded by the geolocator 11SN during the time when the bird was (a) at the breeding site, (b) at a stopover site north of the Sahara-Arabian deserts, (c) when crossing the Sahara desert (*highlighted*), (d) at a stopover site south of the Sahara-Arabian deserts, (e) at the non-breeding residency site.

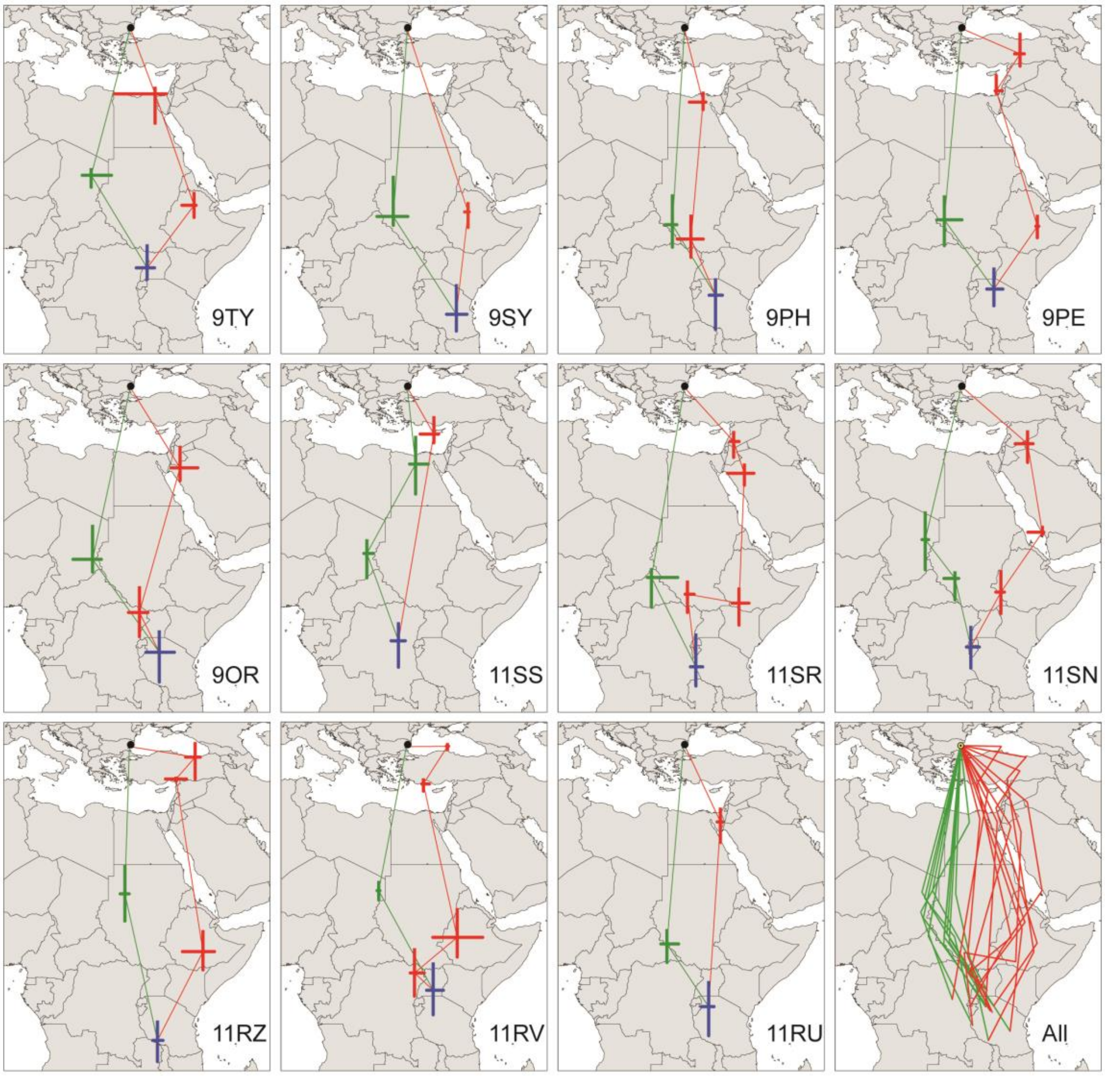

Figure A2. Individual tracks of 11 geolocator tagged Semi-collared Flycatchers from a breeding population in eastern Bulgaria (*black dot*). Location estimates are shown as median coordinates ± interquartile ranges. Autumn stopovers (*red*), non-breeding sites (*blue*) and spring stopovers (*green*). *Lines* are connecting stationary sites and indicate utilized migratory flyway in a broader sense but do not necessarily depict exact migration pathways taken. The bottom right panel shows all migration tracks.

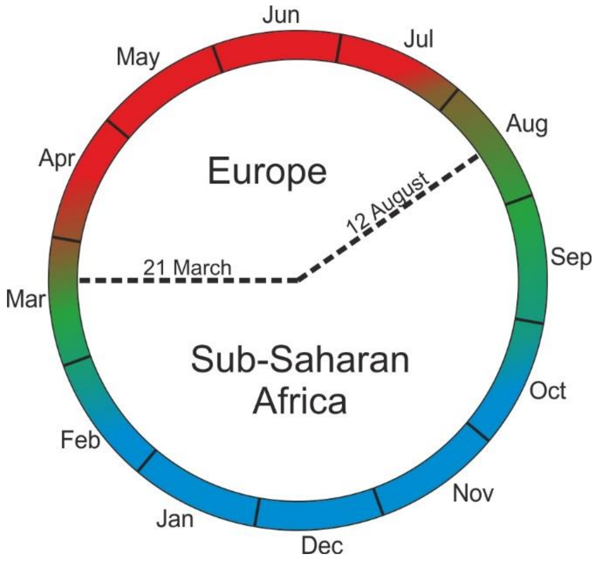

Figure A3. The annual cycle of Semi-collared Flycatcher. Time spent at breeding site (*red*), on migration (*green*) and at non-breeding residency area (*blue*). *Dashed lines* represent median Sahara crossing date obtained from geolocation data.

Chapter 4

Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant

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(Editor's choice)

Abstract

The temporal and spatial organization of the annual cycle according to local conditions is of crucial importance for individuals' fitness. Moreover, which sites and when particular sites are used can have profound consequences especially for migratory animals, because the two factors shape interactions within and between populations, as well as between animal and the environment. Here, we compare spatial and temporal patterns of two latitudinally separated breeding populations of a trans-Equatorial passerine migrant, the collared flycatcher *Ficedula albicollis*, throughout the annual cycle. We found that migration routes and non-breeding residency areas of the two populations largely overlapped. Due to climatic constraints, however, the onset of breeding in the northern population was approximately two weeks later than that of the southern population. We demonstrate that this temporal offset between the populations carries-over from breeding to the entire annual cycle. The northern population was consistently later in timing of all subsequent annual events – autumn migration, non-breeding residence period, spring migration and the following breeding. Such year-round spatiotemporal patterns suggest that annual schedules are endogenously controlled with breeding latitude as the decisive element pre-determining the timing of annual events in our study populations.

Introduction

In birds, different events in the annual cycle like reproduction, migration, and moult are linked both physiologically and ecologically in a unified sequence, where one event can have downstream consequences for the others (Harrison et al. 2011). For instance, sub-optimal timing of a particular annual event or a spatial disadvantage (e.g. residency in suboptimal habitat) often results in reduced body condition and performance, which can impact on subsequent events and ultimately – individual fitness (Marra et al. 1998, McKinnon et al. 2015). Optimizing spatiotemporal patterns throughout the annual cycle is, therefore, of vital importance on the individual and population scale, especially for migratory animals, where different populations may adapt their annual cycles differently (Alerstam 2011). Comparative studies including full annual cycles have hitherto been underrepresented in animal ecology and, thus, ask for further investigation (Marra et al. 2015).

Earlier attempts to link breeding latitude (and breeding time) with other parts of the annual cycle have mostly used ring recoveries (Both 2010) or migratory passage dates (Sokolov et al. 1999, Hedlund et al. 2014). These methods, however, lack information on the entire annual cycle of individual birds or particular populations. Recent studies linking annual events have focused on migratory connectivity and migration routes of single (Schmaljohann et al. 2012, Tøttrup et al. 2012a, b) or longitudinally separated populations (Hahn et al. 2013, Trierweiler et al. 2014). Further, multi-population studies on annual cycles of migratory birds using tracking data (Ouwehand et al. 2015, Stanley et al. 2015), stable isotopes (Arizaga et al. 2015), and genetic markers (Ruegg et al. 2014) have showed that spatiotemporal organization of the annual cycle may strongly depend on breeding site location.

In temperate climate zones latitude is a good broad scale indicator of phenology in plants and animals, i.e. onset of the growing season (Rötzer and Chmielewski 2001), migratory bird arrival (Kölzsch et al. 2015) and onset of breeding (Lack 1950). Recent, year-round tracking of bar-tailed godwits *Limosa lapponica baueri*, an arctic breeding shorebird, revealed how annual schedules are shaped by individuals breeding latitudes (Conklin et al. 2010). Birds spending the non-breeding period at the same location showed individually adapted migration schedules, fine-tuned according to breeding site phenology. Similarly, different subspecies of red knot *Calidris canutus* breeding at different locations in the Arctic have differently adapted migration schedules (Buehler and Piersma 2008). Furthermore, Fraser et al. (2013) verified that purple martins *Progne subis* with different breeding origins differ in spring migration schedules, with southern populations starting their spring migration earlier compared to northern populations.

In this study we compared the annual cycle of a long-distance trans-Equatorial Passerine migrant, the collared flycatcher *Ficedula albicollis*, from two geographically distant populations. We were interested in both spatial and temporal aspects of the annual cycle particularly regarding overlap and/or differences in the non-breeding residency periods, migration routes and the timing of key life history events. The two study populations differ in their breeding site latitude while longitude is similar. Due to their latitudinally separate breeding sites, we hypothesize that 1) the northern breeding population spends the non-breeding period further south (leap-frog migration; Alerstam and Högstedt 1980), 2) the timing of breeding is the main factor shaping the annual schedules and that 3) differences in annual schedules between the populations persist throughout the entire annual cycle.

Materials and methods

The southern study population of collared flycatchers breeds in deciduous (mainly beech–oak) woodland between 300–500 m a.s.l in the Czech Republic (49°50′N, 17°13′E). The northern population on the Baltic island of Gotland, Sweden (57°01′N, 18°16′E) breeds in deciduous (mainly ash-oak-hazel) woodland at approximately 15 m a.s.l. The latitudinal distance between the two populations is 835 km, while the difference in longitude is 74–88 km. Both populations breed in nest boxes and nearly all birds are marked with aluminium rings.

In 2013 we fitted 69 breeding birds (33 males, 36 females) with geolocators at the southern study site. At the northern study site 50 breeders (30 males, 20 females) were fitted with geolocators in 2012 and 49 (31 males, 18 females) in 2013 (Appendix 3.1). In all cases we used SOI-GDL2.0 geolocators (Swiss Ornithological Inst.), which were attached on bird's back using a silicon leg-loop harness. The geolocator including the harness weighed 0.6 ± 0.04 g which represents less than 5% of the body mass of the tagged birds (mean ± SD, northern population: males = 13.2 ± 0.5 g, n = 59; females = 13.7 ± 0.7 g, n = 40; southern population: males = 12.9 ± 0.6 g, n = 33; females = 13.2 ± 0.6 g, n = 36).

We acquired nine full tracks (2012: 6 males and 3 females) and seven incomplete tracks (2012: 1 male and 2 females; 2013: 2 males and 2 females) from the northern population and nine full (2013: 5 males and 4 females) and six incomplete tracks (2013: 3 males and 3 females) from the southern population.

Data analysis

To calculate geographic positions we used the threshold method (Lisovski et al. 2012). Sunrise and sunset times were determined using GeoLocator software (Swiss Ornithological Inst.) and all data sets were corrected for clock drift. Sunrise and sunset data were filtered using loessFilter function of the R-package 'GeoLight' ver. 1.03, using two interquartile ranges as a threshold before saying that a particular sun event is an outlier. Stationary periods were determined by the changeLight function (probability of change = 0.85, minimal staging period = 3 d; Lisovski and Hahn 2012). Geographic positions of the individual non-breeding areas were calculated using sun-elevation angles derived from the Hill–Ekstrom calibration. The resulting sun elevation angles ranged between 8.6 and −0.7. We determined population specific non-breeding areas by applying kernel density analysis to the estimated positions (ArcMap 10.1; ESRI; search radius 300 km, 70% of maximum density). Additionally, we determined time of the Sahara crossing by inspecting the raw ambient light recordings according to the procedure described by Adamík et al. (2016).

Since we did not observe differences between sexes in timing of annual events in neither of the two study populations (northern population: autumn: W = 41, p = 0.34, spring: W = 23.5, p = 42; southern population: autumn: W = 30.5, p = 0.82, spring: W = 25, p = 0.77), we pooled data on annual schedules of males and females. Onset of breeding for each individual was determined as first egg's-laying date.

As oak trees provide primary feeding habitat during the breeding season (Adamík and Bureš 2007, Veen et al. 2010), we used the phenophase beginning of English oak *Quercus robur* leaf unfolding as a proxy of vegetation development for the two sites. This data were available from the national phenological networks for the sites Grötlingbo, Sweden and Sobotín, Czech Republic (4 and 20 km from our study sites, respectively).

Data available upon request from the MoveBank data repository (project ID 166151488).

Results

Spatial organization

Autumn migration route differed slightly between the two study populations. Birds from the southern breeding population crossed the Mediterranean Sea via southern Italy, while birds from the northern population migrated mainly via Greece (Fig. 1).

Non-breeding residency areas of both populations were located in southern and central Africa, i.e. Angola, Botswana, Democratic Republic of the Congo, Zambia (Fig. 1; see Appendix 3.2 Fig. A1 for data on individual birds) and largely overlapped (Wilcoxon test; latitudes: W = 66, p = 0.24, longitudes: W = 77, p = 0.52) with the southern population birds residing slightly further north (coordinates of max kernel density, northern population: 13°47′S, 23°56′E; southern population: 16°30′S, 23°38′E). The great circle distance between the breeding and non-breeding sites were 8190 km for the northern population and 7104 km for the southern population.

During spring both populations migrated along the same flyway crossing the Sahara Desert at ca 14°–20° E and continuing via Greece to cross the Mediterranean Sea (Fig. 1). The southern populations performed a counter-clockwise migration to and from the non-breeding areas, whereas the spatial difference between the seasonal migration routes was minimal for the northern population.

Annual schedules

During the three years covered by this study the average onset of oak tree leaf unfolding at the southern study site was 27 April (range: 22 April–1 May). At the northern study site leaf unfolding started on average three weeks later – 17 May (range 14–20 May).

In the year of geolocator deployment the median onset of egg laying for the southern population was 4 May (range: 29 April–28 May; Fig. 2). The northern population began egg laying significantly later – median date 21 May (14 May–19 June, Wilcoxon test: W = 211.5, p < 0.001). Thus, both populations bred in the same phenological environment in relation to oak tree phenology. The between-population differences in timing persisted throughout the entire annual cycle (Fig. 1, 2). The southern population underwent both, autumn and spring migration, earlier and returned to their respective breeding site two to three weeks before the northern population.

Median departure date from the breeding area for the southern population was 26 July (15 July–8 August), with Sahara crossing on 4 September (21 August–15 September) and arrival at the non-breeding site on 25 September (18 September–11 October). The northern birds were 2–4 weeks later in their autumn migration schedule leaving their breeding site on 19 August (6–30 August; W = 1, p < 0.001), crossing the Sahara on 17 September (7–22 September; W = 19, p < 0.001) and arriving at their respective nonbreeding sites on 24 October (6 October–5 November; W = 3.5, p < 0.001).

Median spring departure date from the non-breeding areas for the southern population was 3 March (11 February–20 March) with Sahara crossing on 9 April (6–17 April) and arrival at the breeding site on 22 April (19–25 April). As in autumn, the northern population was consistently later in their spring migration schedule when compared to the southern population.

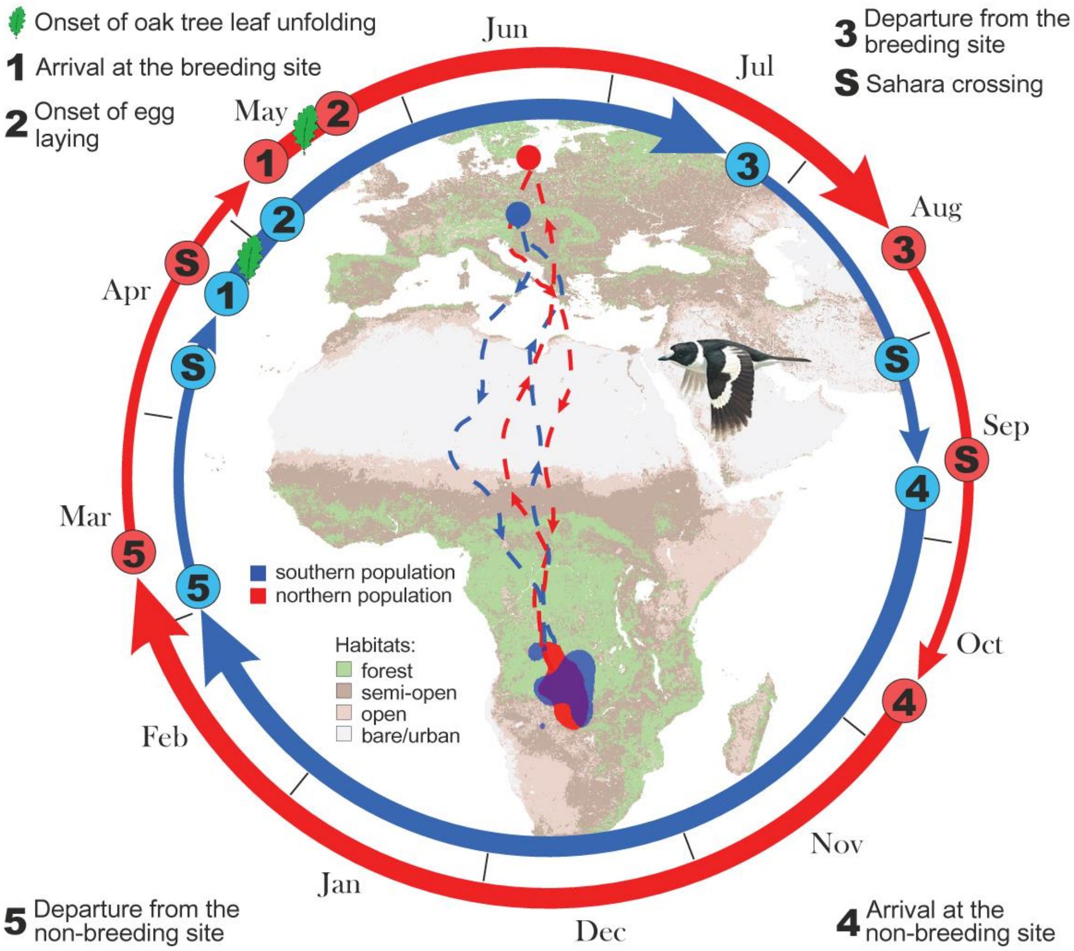

Figure 1. Spatiotemporal organization of the annual cycle of the northern (red) and southern (blue) breeding populations of a trans-Equatorial migrant, the collared flycatcher. Breeding sites (dots), migration routes (population median routes expressed as changes in observed longitude in respect to time elapsed since departure) and non-breeding residency areas (70% kernel density isopleths). Northsouth and east-west on the map correspond to summer-winter solstices and vernal-autumnal equinoxes on the time axis. Thick circular arrows on the time axis represent stationary periods, thin – migration periods. The base map shows terrestrial habitats of land cover data from GLC2000 database, European Commission Joint Research Centre (available at <http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php >). The collared flycatcher illustration © Copyright Birds of Armenia Project.

Median departure date for the northern birds was 9 March (23 February–21 March, W = 42, p = 0.24) with Sahara crossing on 22 April (6 April–2 May; W = 20.5, p = 0.02) and arrival at the breeding site on 10 May (5–16 May; W = 0, p < 0.001).

For the southern population the median onset of breeding in the following spring was 2 May (29 April–13 May). As in the previous breeding season, the median onset of breeding in the northern population was more than two weeks later – 20 May (14 May–26 May, W = 0, p < 0.001).

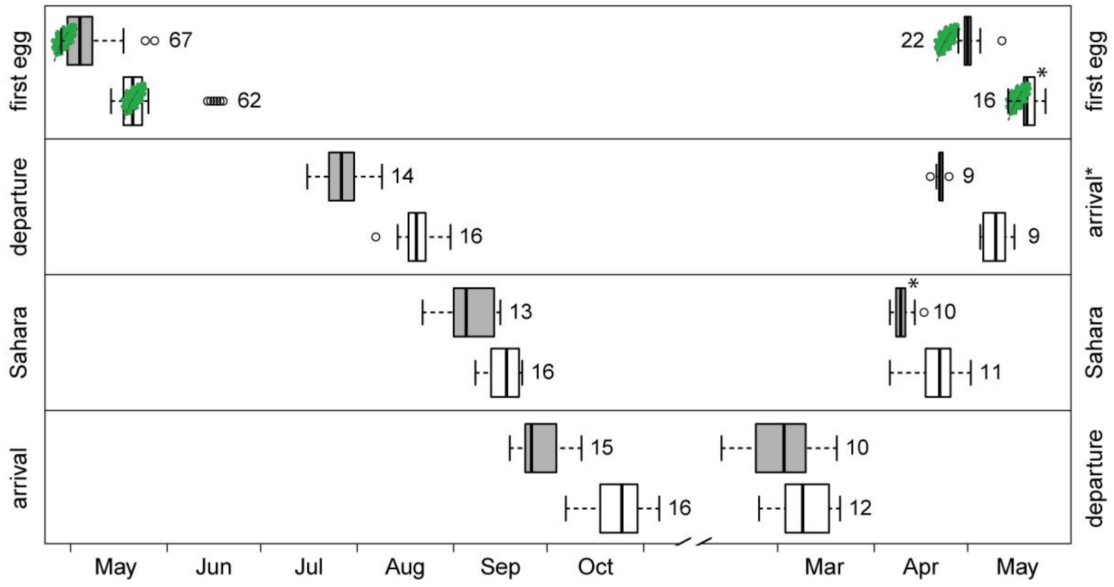

Figure 2. Timing of major events over the collared flycatcher's annual cycle (first egg laid, migratory departure, Sahara crossing and arrival) from the southern (grey box plots) and the northern breeding populations (white box plots). Only geolocator-tagged birds are considered. Sample size for each stage of the annual cycle is indicated beside each box plot. Oak leaf symbols indicate oak tree leaf unfolding dates at the respective breeding locations. Stars (*) denote significant changes ($p < 0.05$) in temporal scatter of data within population compared to the preceding event (next to box plots) and between populations (next to axis labels).

Temporal variation of annual events between and within populations

Variation in timing of annual events between the populations did not differ throughout autumn migration and onset of spring migration but was significantly different at the breeding site arrival (Levene's test: $F = 14.3$, $p < 0.01$; Fig. 2, Appendix 3.2 Table A1). Variation within population decreased from the non-breeding site departure to breeding site arrival (southern population: $F = 16.1$, $p < 0.001$; northern population: $F = 7.6$, $p < 0.05$), but the variation increased again at the onset of egg laying for the northern population ($F = 4.5$, $p < 0.05$).

Duration of key annual phases

The median duration of autumn migration for the southern birds was 64.5 d (range: 58–85), the stationary non-breeding period – 157.5 d (range: 126–175), and the spring migration – 50 d (range: 34–69). Similarly, the median duration of autumn migration of the northern birds was 66 d (range: 45–98), stationary non-breeding period – 141.5 d (range: 123–193), and spring migration – 48 d (range: 16–65). The length of autumn migration ($W = 98$, $p = 0.78$) and spring migration ($W = 41.5$, $p = 0.96$) did not differ between the two populations, but duration of the stationary nonbreeding period was significantly shorter in the northern population ($W = 90.5$, $p < 0.05$).

Discussion

Our study presents an insight into the spatiotemporal organization of the complete annual cycle of two latitudinally distant breeding populations of a trans-Equatorial migrant bird. We demonstrate different temporal schedules for spatially similar non-breeding periods of the two populations in which the northern breeding population is always later than the southern population. This might suggest that climatic constraints at different breeding latitudes could be the determining factor for the temporal differences between the populations.

The remarkably similar spatial organization of the annual cycle contradicted our expectation of a leap-frog migration pattern. Furthermore, the non-breeding sites of both populations lie west of the previously known non-breeding range (BirdLife International and NatureServe 2011). Several recent studies have highlighted strong migratory connectivity between breeding and non-breeding longitudes (Hahn et al. 2013, Ouwehand et al. 2015), and might help explain our findings as both studied populations are located on the western edge of the species breeding range. The observed differences in autumn migration routes fit the pattern of autumn ring recoveries from southern Europe (Hölzinger 1993), whereas very little is known about spring migration routes.

Recent tracking studies have also demonstrated different migration schedules of latitudinally separated breeding populations (Fraser et al. 2013, Stanley et al. 2015). In the temperate climate zone breeding sites along the latitudinal gradient are successively occupied in accordance with the advancing spring (Lack 1950). Conklin et al. (2010) demonstrated this in a non-passerine bird, the bar-tailed godwit, where individuals from a non-breeding site in New Zealand were tracked back and forth to their breeding grounds. Similar to our findings, godwits of different breeding origins spent the non-breeding period in the same locations, therefore experiencing the same ambient conditions. The onset of spring migration, however, differed among individuals with southern breeders departing first and completing all stages of the onward and return migratory journeys earlier when compared to more northerly breeding individuals. The temporal pattern between the populations of our tracked flycatchers was not significantly different at the onset of spring migration but increased gradually throughout the annual cycle (Fig. 1, 2). Due to the overlapping non-breeding sites, this might indicate that environmental signals are involved in triggering spring migration.

Occupation and passage of the same sites at different times can have various implications because food availability, parasite abundances or potential hazards vary temporarily (Bauer et al. 2016). Therefore, we argue that analyzing temporal patterns is of similar importance as analyzing spatial patterns for understanding the consequences of different annual cycles.

Spatiotemporal patterns of occupancy of specific sites by migratory birds and phenology of these sites often vary annually (Tøttrup et al. 2012b) and shift in the long-term (Hedenström et al. 2007). The majority of our geolocation data for the northern population come from the 2012/2013 season, while all data for the southern population are from 2013/2014. Different study years are unlikely to affect the choice of the final non-breeding residency areas, but the variation of migration patterns is less clear. Overall, temporal patterns during long-distance migration seem relatively consistent between years (Battley 2006, Stanley et al. 2012), with exceptions occurring under extreme weather conditions (Tøttrup et al. 2012b) or adaptation to long-term climate change (Both 2010). Individual migration routes, on the other hand, seems to vary to a higher degree (Stanley et al. 2012, López-López et al. 2014).

The evident similarity between the two populations regarding individual variation in timing of annual events (Fig. 2) suggests similar seasonal selection pressures in both populations. The difference in breeding site arrival between the northern and southern population could be explained by the unusually warm spring in 2014 at the southern study site when most birds arrived during a single large influx early in the season. Consistent with our findings Lindström et al. (2015) found the smallest temporal variation among individuals for breeding site arrival. This implies strong selection pressure at this stage of the annual cycle, while timing of other parts might be more relaxed.

Our findings emphasize the importance of climatic constraints at breeding latitude (and in turn breeding time) as a primary factor shaping the annual schedules in our two study populations. We suggest that the annual schedules are largely endogenously controlled by mechanisms adapted to the environmental conditions at the breeding site to maximize breeding output. Experiments on collared flycatchers exposed to photoperiods of various latitudes have revealed that timing of migratory restlessness at the end of autumn and it's onset in spring is fixed irrespective of the photoperiod (Gwinner 1989). Further studies suggest that migration schedules of long-distance migrants are endogenously controlled (Berthold 1991, Gwinner 1996), with breeding site latitude as the main driver for temporal variation on a broad geographic scale (Conklin et al. 2010). Thus, breeding and its timing could be considered a key life history event shaping the annual schedule at least in single-brooded long-distance migratory species, while other events might be subordinated.

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Appendix 3

Supplementary information for Chapter 4

Appendix 3.1. Materials and methods

Return rates

From the 50 birds fitted with geolocators in 2012 in the northern population we recaptured 12 (6 males and 6 females) individuals – 11 in 2013 and one in 2014. From the geolocator series deployed in this population in 2013 we retrieved 12 (7 males and 5 females) out of the 49 devices. At the southern population 28 (14 males and 14 females) of 69 geolocator birds were recaptured in 2014. Birds ringed only with aluminum rings were used as a control group to account for recapture rates. The between-years return rates of the geolocator tagged birds from the northern population were 22.0% and 24.5% (control group: 40% and 39%) in 2013 and 2014, respectively. For the southern population the return rate was 40.6% (control group: 45.5%). The differences in the return rates of tagged and control group birds were significant in the northern but not in the southern population (Pearson's χ^2-test, northern population 2012: $\chi^2 = 6.1$, $p = 0.013$, 2013: $\chi^2 = 4.5$, $p = 0.035$, southern population 2013: $\chi^2 = 0.09$, $p = 0.76$).

Additionally, we observed difference in return rates among early and late breeding individuals, with the latter having lower return rates. This might explain lower return rates in the northern population as proportionally more late breeding birds were tagged. Moreover, the slightly longer migration distance and crossing of an extra barrier (the Baltic Sea) might co-affect the return rates observed in the geolocator-tagged flycatchers from the northern population.

Calculating migration routes

We were not able to determine any stopover sites during migration. This was due to (i) irregular shading of the sensor causing large errors in positioning for short stationary periods and (ii) migration close to equinox periods (more pronounced in autumn) when latitude assignments are not possible. Longitude estimations, however, are always possible, because they are derived from midday and midnight times (Hill 1994). Thus, we used total migration time and longitude estimates to describe migration routes, considering continuous movement at a steady pace throughout migration. First, longitude and latitude at the beginning of migration give the start point (e.g. known breeding site for autumn migration) and population specific median longitude and latitude at the end of migration period was set as end point (e.g., respective non-breeding site). Since we assume continuous movement between start and end, a percentage of migration time corresponds to the same percentage of migration distance, e.g. when 25% of total migration time has passed 25% of total migration distance had been covered and thus refers to relative latitude. The longitude readings are derived from geolocator records at each time point (see also Hahn et al. 2014).

Annual variation in breeding time

Although, the majority of the geolocation data for the northern population come from 2012/13, while for the southern population all data are from 2013/14, the data are comparable since the annual variation in the onset of egg-laying is minimal. In 2012 the median first egg-laying date for the northern population was 18 May (n = 114) while in 2013 it was 20 May (n = 118). For the southern population egg-laying date was 5 May (n = 112) in 2012 and 8 May (n = 118) in 2013.

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Appendix 3.2. Supplementary figures and tables

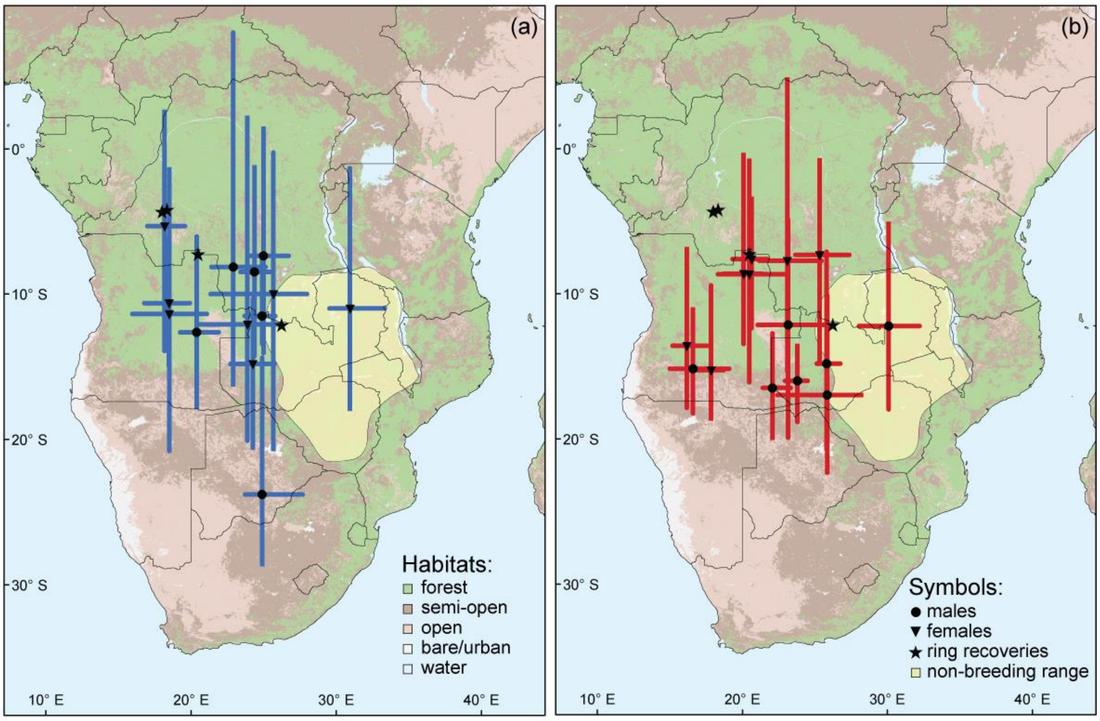

Figure A1. Non-breeding residency sites of individually tracked Collared Flycatchers from the southern breeding population in the Czech Republic (a, n = 13) and the northern breeding population in Sweden (b, n = 14) depicted as median positions (● – males, ▼ – females) and interquartile ranges (lines). Stars represent sub-Saharan ring recoveries of Collared Flycatchers according to EURING database. The currently estimated non-breeding range is outlined in yellow (BirdLife International and NatureServe 2011). The base map shows terrestrial habitats of reclassified land cover data from GLC2000 database, European Commission Joint Research Centre (available at http://bioval.jrc.ec.europa.eu/ products/glc2000/glc2000.php).

Table A1. Results of Levene's test of variation between and within (between consecutive events) populations in timing of key stages in the annual cycle, including breeding (Breeding I), departure from the breeding site (BS departure), Sahara crossing in autumn (Sahara autumn), arrival at the non-breeding site (Non-BS arrival), departure from the non-breeding site (Non-BS departure), Sahara crossing in spring (Sahara spring), arrival at the breeding site (BS arrival), and breeding the following year (Breeding II), of Collared Flycatchers. Significant values are highlighted in bold font.

Stage	Between populations		Between events – southern population (Czech Republic)		Between events – northern population (Sweden)	
	F	p-value	F	p-value	F	p-value
Breeding I	1.794	0.183				
BS departure	0.238	0.629	0.001	0.970	1.029	0.314
Sahara autumn	1.981	0.171	0.688	0.415	0.003	0.959
Non-BS arrival	0.373	0.546	0.092	0.764	2.687	0.112
Non-BS departure	0.930	0.346	2.781	0.109	0.119	0.733
Sahara spring	3.518	0.076	**12.111**	**0.003**	0.453	0.508
BS arrival	**14.297**	**0.002**	2.015	0.174	1.368	0.258
Breeding II	0.001	0.981	1.100	0.303	**4.454**	**0.046**

Chapter 5

Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy

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Abstract

Over decades it has been unclear how individual migratory songbirds cross large ecological barriers such as seas or deserts. By deploying light-level geolocators on four songbird species weighing only about 12 g, we found that these otherwise mainly nocturnal migrants seem to regularly extend their nocturnal flights into the day when crossing the Sahara Desert and the Mediterranean Sea. The proportion of the proposed diurnally flying birds gradually declined over the day with similar landing patterns in autumn and spring. The prolonged flights were slightly more frequent in spring than in autumn, suggesting tighter migratory schedules when returning to breeding sites. Often we found several patterns for barrier crossing for the same individual in autumn compared to the spring journey. As only a small proportion of the birds flew strictly during the night and even some individuals might have flown nonstop, we suggest that prolonged endurance flights are not an exception even in small migratory species. We emphasise an individual's ability to perform both diurnal and nocturnal migration when facing the challenge of crossing a large ecological barrier to successfully complete a migratory journey.

Introduction

Twice a year billions of birds undertake a migratory journey of several thousand kilometres to their non-breeding sites and back. The Palearctic-African flyway represents probably the largest avian migration system on earth[1]. An estimated 2.1 billion songbirds and near-passerines move from Europe to Africa each autumn[2]. At some point in time, nearly all of them have to cross a major ecological barrier, the 1500–2000 km wide Sahara Desert.

A crucial, and to date debated, issue is which migratory strategy individual songbirds use to reach their destination. In his seminal work, Moreau[3] suggested "it does seem that an ability to maintain flight for 50–60 hours without food or water is essential for those birds which regularly migrate across the Sahara". However, since the 1980s, an accumulating number of studies brought evidence in favour of the alternative intermittent migratory strategy[4–7]. In this scenario songbirds cross the Sahara in small steps: flying at night and resting and/or refuelling during the day. The picture, however, seems to be complex, as radar studies from various sites across the globe have brought evidence of nocturnal migrants regularly prolonging flight into the day when crossing large-scale barriers[8–11]. The proportion of diurnal migratory traffic in these studies was just a fraction of typical night-time migration, suggesting that landing occurs shortly around sunrise and that only some birds are capable of prolonged daytime flights. This means that some individuals show flexible migratory behaviour and they can switch from nocturnal to partially diurnal migration. In general, nocturnal migration is the prevailing pattern in small birds within the Palaearctic African migration system[12]. With our own survey we estimate that about 63% of species (44 out of 70 trans-Saharan migrants for which we have collated data; Appendix 4 Table S1) are expected to migrate during the night when crossing continental Europe. Another 16% migrate solely during the daytime, so the pool of individuals that might theoretically switch to temporary daytime migration is considerable. While we already know that daytime migration and prolonged flights across vast barriers do happen in small songbirds[13], the magnitude, temporal and seasonal (spring vs. autumn passage) effects at the individual and species level remain little known for the large barriers between Europe and Africa.

Recent technical development of satellite transmitters and small light intensity data loggers (geolocators) has enabled research showing that at least in some larger migratory species, extreme endurance flights of several thousands of kilometres are possible[14–16]. Here we tracked several small songbird species, weighing about 12 g, and for the first time investigated their individual migratory patterns while crossing the Sahara Desert and the Mediterranean Sea. By the analysis of anomalies in the light patterns recorded during barrier crossing periods we aim to evaluate i) the occurrence and the timing of prolonged flights into the day by typical nocturnal migrants, ii) the day-to-day diversity in migratory patterns, and iii) to compare autumn and spring migration periods.

Results

Spatial organization

All four species in this study, i.e. the collared flycatcher *Ficedula albicollis*, pied flycatcher *Ficedula hypoleuca*, Eurasian reed warbler *Acrocephalus scirpaceus* and aquatic warbler *Acrocephalus paludicola* (see Appendix 4 Table S2 for details) are widely thought to migrate at night and rest during daytime. This behaviour is reflected in geolocator data with a zigzagging light pattern during the day, caused by variable exposure of the light sensor during foraging, preening, resting and moving through vegetation (Fig. 1). In both spring and autumn migration periods, however, there was a noticeable pattern of continuous full light intensity (full light pattern; FLP) during the daytime in all four species, i.e. the sensor recorded maximum light levels for uninterrupted periods of several hours (for an overview of FLP anomalies see Fig. 2). This FLP anomaly lasted for 1–3 days. In the collared flycatcher it occurred in 12 out of 13 birds in autumn and in all birds in spring (11 individuals for which data have been recorded until spring). All pied flycatchers showed FLP in both autumn and spring (4 and 2 individuals, respectively). Similarly, all aquatic warblers had FLP (5 and 2 individuals). In reed warblers FLP occurred in 4 out of 12 birds in autumn and in all 8 birds tracked in spring. Summarising across species, all individuals showed FLP in spring and the absence of FLP was observed in autumn only (9 out of 34 tracked individuals). Seven of 9 birds without FLP still had a distinct zigzag pattern of increased light intensities.

In all four species the occurrence of FLP coincides with the migration time between Europe and Africa (Appendix 4 Table S2). The majority of the stopover sites preceding and following FLPs are located North and South of the Sahara (Fig. 3), demonstrating that FLP occurred while the birds were crossing the Sahara and/or the Mediterranean Sea.

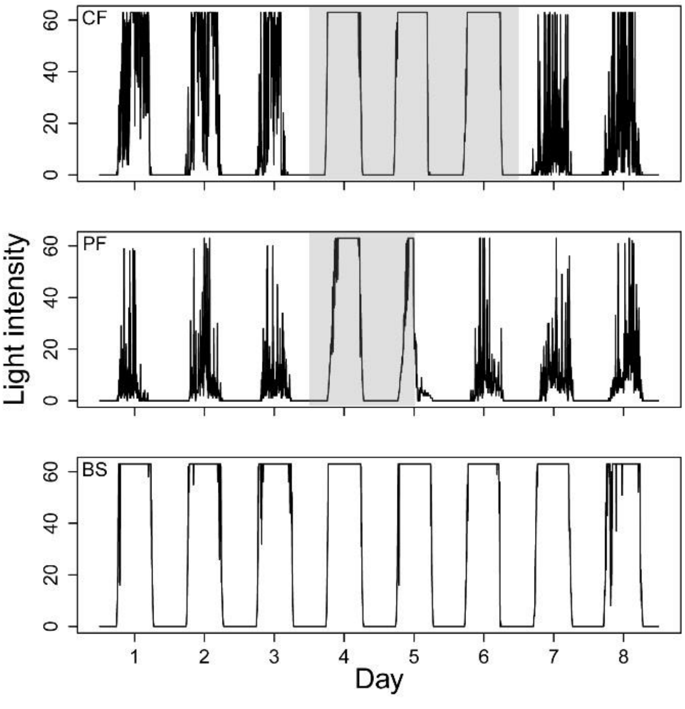


Figure 1. Representative examples of full light pattern anomalies (FLP, grey area) in a collared flycatcher (CF), pied flycatcher (PF) and barn swallow (BS) recorded by light-level geolocators on days while crossing the Sahara desert. The middle plot (PF) depicts an example of FLP that abruptly ends on the second day at 12:00 UTC. Tick marks on x-axis denote noon. The zigzag light pattern (shading caused by habitat and bird behaviour) a few days before and after the full light pattern in collared and pied flycatchers represents typical geolocator data for most birds throughout their annual cycle. The barn swallow data represent typical geolocator data for an aerial forager.

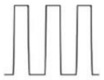
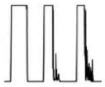
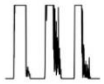
Light pattern		Occurrence in		Description	Interpretation	
		Autumn	Spring			
	No FLP	26.5% (9)	-	Shaded sensor during the day	Bird stays in habitat, no diurnal migration	**A**
	Perfect FLP	26.5% (9)	34.8% (8)	No sensor shading during the day	Diurnal movement or resting in sun-exposed habitat	**B**
	FLP with abrupt ending on the last day	29.4% (10)	43.5% (10)	No shading during first days and/or shading in the last day	Diurnal movement or resting in sun-exposed habitat during first days, extending flight into the last day with arrival in dense habitat or shelter	**C**
	FLP with abrupt ending on the last two days	2.9% (1)	4.3% (1)	No shading on the first day, strong shading at the end of last two days	As above but last two days prolonged flights into the day	**D**
	FLP with abrupt ending on all days	5.9% (2)	8.7% (2)	Sudden strong shading at the end of all days	Regularly prolonging nocturnal flights into the day	**E**
	FLP with abrupt ending and perfect FLP in-between	2.9% (1)	-	A combination of the above cases	A combination of prolonged flights into the day with diurnal movement or resting in sun-exposed habitat	**F**
	FLP with shaded day in-between and abrupt FLP ending	2.9% (1)	8.7% (2)	First no sensor shading, later heavy sensor shading + sudden shading during the last day	Prolonging flights into the day on the first and last day with 1 day stopover in between	**G**
	Outlier: shaded start in the morning followed by FLP	2.9% (1)	-	Heavy sensor shading in the morning only	Sudden departure from shelter/habitat later during the daytime	**H**

Figure 2. Detailed seasonal overview of daytime light pattern anomalies (FLP) recorded by geolocators while the birds were crossing the Sahara Desert. Each category is accompanied by a representative figure of recorded light intensities, % of occurrence (numbers of individuals are in parentheses), description of the anomaly and our most plausible interpretation (categories A–H).

The estimated flight duration between stationary sites before and after the FLP was positively related to the estimated travel distance that the birds had to cross (b = 0.033 ± 0.009 SE, t = 3.9, P = 0.004; Fig. 4), while controlling for the non-significant effect of season (t = 1.5, P = 0.129; model means ± SE: autumn 52.1 ± 7.7 h, spring 47.7 ± 7.6 h; random effects variance: bird identity 49.3 (7.0 SD), species 170.4 (13.1 SD), residual variance 67.6 (8.2 SD)).

Strategies of barrier crossing

In both seasons FLPs often ended abruptly during daytime on the last day of the presumed Sahara crossing (see middle plot of Fig. 1). We interpret this as prolonged flight into the day and the sudden change in light intensities as landing time (Fig. 2). In autumn FLP occurred in 73.5% (25 out of 34) of tracked birds and 47.1% (16) had an abrupt ending of FLP. Abrupt FLP endings mostly occurred on the last day and for the remaining birds various patterns were detected (Fig. 2). In spring all 23 tracked birds had FLP and abrupt ending occurred in 65.2% (15) of individuals, and as in autumn, the abrupt FLP ending occurred often on the last day (Fig. 2). We found no statistical difference in the number of FLPs occurring in autumn compared to spring (Chi-squared test with Yates' correction $\chi^2 = 0.34$, df = 1, P = 0.561). Eight individuals prolonged their flights into the day during the two- or three-day period of barrier crossing but the durations of diurnal flights within individuals varied considerably (Fig. 2 and Appendix 4 Table S2). Four out of 22 birds tracked during both migratory periods showed the same pattern of barrier crossing (Appendix 4 Table S3). If we consider categories B and C (Fig. 2) as a variation on the same pattern, then 9 out of 22 birds showed the same pattern.

Consistent with radar measurements (Fig. 5b [6]) we found FLP with $T_{max} < 92$ min (threshold time it took for each sunrise event to reach the maximum light intensity) and abrupt FLP endings to occur up to 12 hours after sunrise. The frequency of prolonged flights into the day (i.e. the number of FLPs with abrupt endings during daytime) was higher in spring (50% out of 28 cases) than in autumn (39.5% out of 38 cases; Fig. 5a) but this difference is not statistically significant (Kolmogorov-Smirnov test, D = 0.402, P = 0.31). The flights into the day ceased on average 5.8 ± 3.0 (SD) hours (n = 15 cases) after sunrise in autumn and 6.8 ± 2.1 hours (n = 14 cases) after sunrise in spring.

FLP without abrupt ending or any gaps by shading occurred in 26.5% (9) birds in autumn and 34.8% (8) birds in spring. Among them only one bird had perfect FLP and a low T_{max} on both FLP days in autumn (i.e. 2.9% of 34 checked individuals; pied flycatcher, $T_{max} = 61$ and 53 min) and another bird had perfect FLP for one day in spring (i.e. 4.3% of 23 individuals; aquatic warbler, $T_{max} = 34$ min). All remaining birds showed a combination of perfect FLP and gaps by shading.

Our simulation approach showed that, depending on the assumed flight speeds, between 20–80% of individuals fly into the day, to cover the distance for crossing the Sahara desert (Appendix 4 Fig. S3). The simulation shows that for spring migration a slightly higher percentage of daytime flights are necessary for crossing the desert (Appendix 4 Fig. S3).

Discussion

High light intensities are typically recorded by geolocators in aerial foragers such as martins or swallows that stay airborne during large parts of the day (Fig. 1). In these "classic" diurnal migrants the light sensor is consistently exposed to the sun during the day. As a result, FLP is recorded regularly. We show here that four songbird species, which have been considered to be mainly nocturnal migrants, also show FLP during a limited migration period that coincides with their crossing of the Sahara desert. We suggest that migratory birds can flexibly switch from typical nocturnal migration to a prolonged flight into the day when facing the task of crossing a major ecological barrier. We found, however, that in three individuals (one aquatic warbler and two collared flycatchers) FLP was also detected outside the main migratory period (Appendix 4 Table

S2). In two birds it occurred in November–December in sub-Saharan Africa (presumably effect of open habitat or perching behaviour) and in one bird at the breeding site in open habitat (marshes). Hence, at the moment we do not have any evidence for diurnal movements north of the Mediterranean.

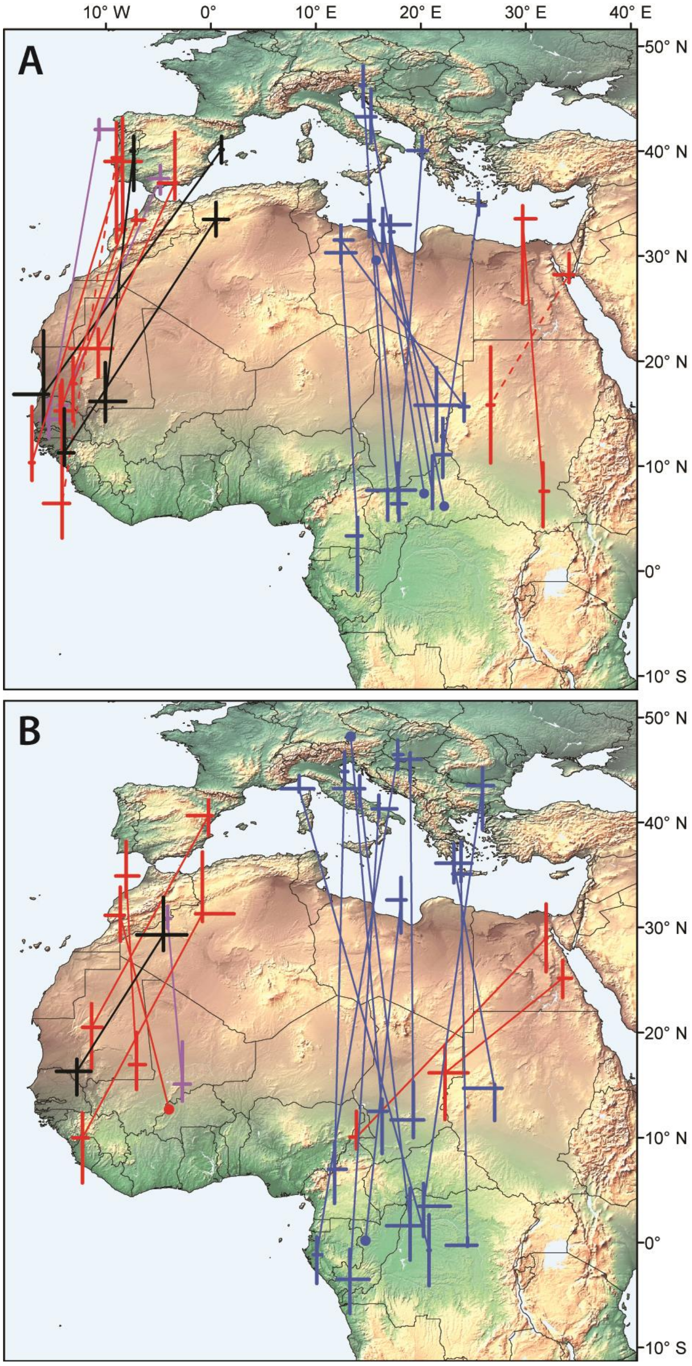


Figure 3. Autumn (A) and spring (B) stationary sites of birds (median ± 25th and 75th percentiles of location estimates) just prior and after the occurrence of the full light pattern (blue = collared flycatcher, black = pied flycatcher, red = Eurasian reed warbler, purple = aquatic warbler). The two dashed lines connect stationary sites for birds without FLP. The background map was made with Natural Earth public domain free vector and raster map data@naturalearthdata.com. The stationary sites were depicted in ArcGIS.

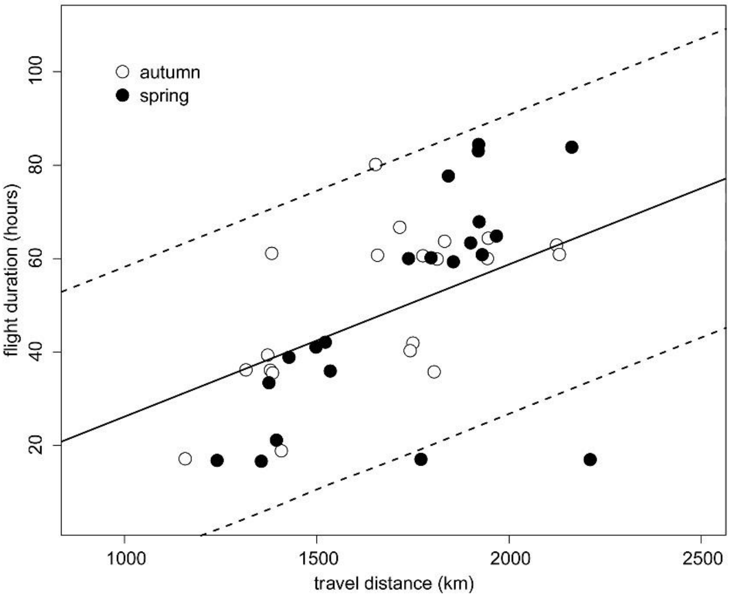


Figure 4. Relationship between travel distance (width of the Sahara desert on the individual crossing course) and the estimated duration of flight based on cumulative length of FLP (including night lengths). Fitted line ± 95% CI (dashed lines) is from a linear mixed-effect model. Note that there was no seasonal effect in the relationship (see Results). The point in the lower right corner was excluded as an outlier.

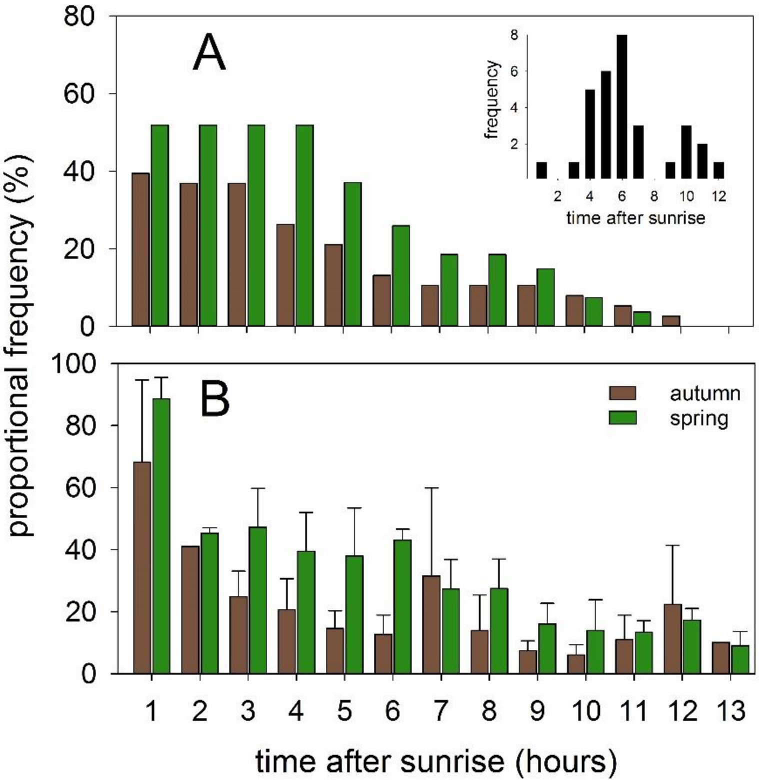


Figure 5. Estimates of proportions of birds with diurnal flights while crossing the Sahara desert and their timing of landing (inset in the upper right corner). The upper plot (A) shows frequencies of migratory flights into the day estimated from this study (excluding cases when $T_{max} > 92$ min) and the lower panel (B) those (mean ± SD) recalculated from a radar field study in the Mauritanian Sahara[6].

In 9 individuals we did not find FLP while crossing the Sahara in autumn but for 7 of them we could still observe elevated light intensities that were above the average of typical light data recorded at times prior and after the desert crossing. We suggest that these birds behaved as typical nocturnal migrants that landed before dawn and rested during the day. In contrast, very few individuals (one in autumn and one in spring) showed perfect FLP either during the entire period of the Sahara crossing (or at least on some of the days needed for the crossing). Our very conservative suggestion is that these might be the non-stop flying individuals. An alternative view would be that the birds were resting on the ground without hiding in the shade. This seems unlikely, however, as the majority of observations of grounded birds show that they were actively hiding during daytime hours[17]. In addition, our simulation approach showed that the birds would have to fly at extreme speeds to cross the recorded distances by nocturnal flight only. Finally the diverse patterns of FLPs (Fig. 2) emphasise that birds are able to perform both diurnal and nocturnal migration even within one and the same journey.

The duration of FLP (i.e. the sum of nocturnal and diurnal periods) was positively related to the distance we calculated that the birds have to fly over the Sahara. For birds that crossed longer distances over the Sahara, multiple and/or longer durations of FLP were recorded. In contrast, birds that crossed the Sahara at its narrowest points had FLP usually only on one day. Interestingly, spring and autumn desert crossing times were similar. Hence it seems that desert crossing is optimized independently from seasonal time pressures; crossing the inhospitable region as fast as possible might be the main aim for every individual. And indeed, currently available geolocator studies showed fast crossing of the Sahara desert[7,18,19].

Earlier field studies demonstrated that nocturnally migrating birds of unknown provenience prolong their flights into the day[3,11,20,21]. It was generally believed that these prolonged flights had just a very short duration and most birds tended to land shortly after dawn[6,11,22] (but see[10]). Based on abrupt endings of the FLP during daytime, we found that the birds on average prolong the flights until noon during both autumn and spring migration. Our estimates of diurnal flights (as estimated from the durations of FLPs and $T_{max} < 92$ min) showed a gradual decline over the day. This pattern was remarkably similar to the one derived from the radar study in the western Sahara[6] (recalculated in Fig. 5b). In spring, however, a higher proportion of tracked birds (i.e. with FLP and abrupt ending) prolonged their flights into the day than in autumn. Similarly, this seasonal pattern strongly resembled findings of the radar study by Schmaljohann et al.[6]. In addition, we found slightly higher occurrence of FLP in spring (25 out of 34 birds in autumn, while in all 23 individuals in spring). These two facts, however, do not match with estimates of desert crossing times which were similar for the two periods (see above). Faster total migration in spring is the general pattern across bird species[23] but our data indicate that this might not be the case during desert crossing. That we found slightly more FLPs in spring might result from frequent tailwinds which prevail at higher flight altitudes at this time of the year[24]. Tailwinds are similar in autumn but at lower flight altitudes, in hotter and dry air[24], which might explain the lower proportion of flights into the day. Accordingly, more birds prolonged their migration into the day under tailwind conditions as shown by radar[11]. Our data suggest that landing or searching for shade can occur nearly at any time of the day, most probably depending on when the bird reaches a suitable destination. This suggests an individually flexible prolongation of nocturnal migration into the day based on the bird’s needs and environmental conditions.

Another striking pattern we found was that the prolonged flights into day occurred most frequently on the last day of barrier crossing. Abrupt FLP endings were followed by much lower and variable light levels (i.e. a typical zigzag pattern) for the rest of the daytime than was typically observed on regular days without FLP. Field observations from the Sahara show that grounded fat birds (i.e. those that do not need to stop for refuelling) were often found resting in shade (e.g. single rocks, wadis, depressions or mountain ridges[4,17]) and our data seem to be in line with this. By simulation we estimated that depending on the flight speed between 20–80% of birds extended their nocturnal flights into the day in order to travel the distance they did.

To summarise, earlier studies detected diurnal flights of nocturnal migrants[3,9,10] but were supposing that a small number of birds were doing so and that landing occurred shortly after dawn[6]. Here we emphasise that, at least in the four songbird species studied, prolonging flights into the day may be a common migratory pattern during barrier crossing. Such flights might be more common also in other barrier crossing systems, as has been recently shown for blackpoll warblers[13]. Based on the diverse patterns of FLP and its absence in some individuals, we emphasise the ability of birds to appropriately switch between diurnal and nocturnal migration when facing the challenge of crossing a large ecological barrier. There is accumulating evidence in larger-sized birds of considerable spatial but low temporal variability in migratory behaviour[25–27]. Often we found the same individuals to show different patterns of barrier crossing in autumn compared to spring journeys. This might be in line with the hypothesis of individually optimized migration schedules[28]. Such an assessment should be possible in the future by using larger data sets containing data from both sexes and repeated tracks of individuals across several migratory seasons.

Methods

Study species and the detection of light anomalies

From 2011 to 2012 individuals of four songbird species were equipped with geolocators (SOI-GDL 2.0, weight approx. 0.6 g, manufactured by the Swiss Ornithological Institute) at their European breeding grounds. After a year we retrieved 34 functional loggers: 13 from collared flycatchers, 4 from pied flycatchers, 12 from Eurasian reed warblers and 5 from aquatic warblers (Appendix 4 Table S2). The geolocators used an SMD photodiode EPD-470-1-0.9-1 (EPIGAP Optoelektronik, Germany) for light intensity measurements with a sensor wave length between 380 to 555 nm and a maximum range of about 3500 lux (corresponding to 63 arbitrary units). The SOI-GDL 2.0 geolocators recorded ambient light intensity in 5 min intervals.

The geolocators, conventionally used for positioning of migratory birds are also suitable for documenting changes in behaviour over the annual cycle[29–32]. When inspecting geolocator data in the four focal species we detected an obvious pattern of continuous full light intensity (hereafter full light pattern–FLP) with regular occurrence twice a year at times that coincide with the migratory period in many species (Fig. 1). We classified FLP as an uninterrupted period of > 5 h (or > 1 h on days with abrupt FLP ending, see below) during daytime where maximum light intensity (63 in arbitrary scale) was recorded.

An overview of individual FLP cases is given in Appendix 4 Table S2. The FLPs were classified into several categories in two steps based on a) the amount of shade of the daily light curves and b) time (T_{max}) it took for each FLP sunrise event to reach the maximum light intensity (i.e. from 0/1 to 63 units). In the first step we fitted quadratic regressions to the sunrise data (delimited by the time of sunrise using the software Geolocator (SOI, Sempach) and the first consecutive data point which reached maximum light intensity) and sunset data (delimited by the last data point which reached maximum light intensity and sunset determined by the R-package GeoLight, version 1.03[33]) and summed up the absolute residuals. For the daytime period (delimited by the first and the last data point which reached maximum light intensity) we summed up all deviations from the maximal light intensity. These sums were used to assign every sunrise, day and sunset to the following categories: 1) perfect FLP, virtually no shading; 2) slight shading; 3) substantial shading. Additionally we assigned category 4 to FLPs with an abrupt start or end (Appendix 4 Fig. S1). In the second step, we calculated the T_{max} for each sunrise FLP event. We assumed that during the flight the bird was at an unknown height above ground. This implies no shading by vegetation or by folded wings occasionally covering the light sensor and thus a rapid increase in the recorded light intensity from 0 at twilight to maximum values. To extract sunrises for potential flights prolonged into the day from other sunrises, we compared the data to the sunrise pattern recorded by a typical diurnal migrant and aerial forager. We used light-level logger data of barn swallows *Hirundo rustica* breeding in southern Switzerland and migrating along the central European-African flyway[34]. We selected 6 days during autumn (n = 10 birds) and spring (n = 7 birds) migration, when the birds moved between 16° and 35°N (southern borders of the Sahel and the Mediterranean Sea) and *vice versa*. This was at periods between 12–30 Sept and 10 March–17 April. The maximum T_{max} value and its 95th percentile in barn swallows were 127 min and 91 min, respectively (Appendix 4 Fig. S2). The latter was used as a threshold for our conservative estimates of prolonged flights into the day. Hence, unless otherwise stated, for further analyses of flight into the day we considered only those FLP cases when $T_{max} < 92$ min (68 FLP events, 27 excluded) and the FLP was classified as 1, 2 or 4.

Determining stationary periods

Data from autumn and spring were analysed independently using January 1 as a separator. We calculated stationary periods prior and after the occurrence of FLP using the changeLight function of the R-package GeoLight with minimum staging period set at 3 days. We filtered outlying positions that were > 800 km from the median latitude of a given stationary site. We defined a stationary site to be the median of the geographic coordinates ± their 25th/75th percentiles within the particular stationary period. The same number of interquartile ranges (k = 2) of the loessFilter function was used for all individuals of the same species except for one bird (7OY, k = 1.1). To determine the first stationary period before and after the FLP the probability threshold of the changeLight function was adjusted for each bird individually. For autumn, geographic positions of the stationary periods before and after the FLP were calculated using sun-elevation angles derived from the in-habitat calibration in the breeding areas or Hill-Ekstrom calibration from data of the respective stationary period[35]. When one of the calibration techniques was not applicable or failed, the other was used instead. Please note that we were not able to determine stationary sites for all birds (available estimates are for 22 birds in autumn and 19 in spring). An example of light data profile used to determine the stationary periods before and after crossing the barrier is provided in Appendix 4 Fig. S4.

Duration of light anomalies

We considered two scenarios for estimating the duration of potential flight over the Sahara Desert at times when FLP occurred: nocturnal flight only or including prolonged flight into the daytime. When FLP ended abruptly during daytime, we took that abrupt change (accuracy to 5 min) as a termination of FLP and the assumed prolonged flight. We estimated the theoretical duration of the prolonged flight as nocturnal flight plus FLP. We assumed that the bird took off for the flight within an hour after sunset the day preceding the occurrence of FLP[36–38]. For cases when there were two or more periods of FLP separated by days without FLP, we excluded the daytime non-FLP period from the estimates of flight times. In those cases when an abrupt end of FLP occurred during the day, we added the time period between sunrise and the moment of abrupt decline of light data to the nocturnal flight duration. For cases without an abrupt end of FLP, landing time was estimated to be within an hour before the sunrise on the day that followed the FLP day[11]. Duration of nocturnal flights only was estimated as a sum of night lengths before, during and after the FLP.

We compared the frequency of potential flights into day based on abrupt FLP endings with those found in an empirical study provided by[6]. We recalculated the migration traffic rates from their original dataset by setting nocturnal migration traffic rates to 100 and calculated the declining proportion of traffic rates binned to hours after sunrise in autumn and spring.

Flight range estimates during FLP times

Distance between stationary sites was measured as the loxodromic distance between median positions of the last stationary site before the FLP and the first thereafter. For an approximation of barrier crossing distances, we estimated the width of the Sahara desert (minimum travel distance) at points where the bird presumably entered and exited the desert on the loxodromic line that connects the stationary sites just before and after the FLP. Northern and southern desert borders were derived from the land cover map from the GLC2000 database, European Commission Joint Research Centre, http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php. We hypothesized that the duration of FLP was driven by the width of the desert and the barrier-crossing strategy of an individual. The relationship between travel distance and the estimated duration of flight during FLP was assessed by a linear mixed-effect model in the R-package lme4. We ran a model with flight duration as response variable that included our estimates of summed time for both nocturnal and diurnal migration (n = 40 cases after excluding one case, a reed warbler where a distance of 2211 km in 17 h was considered as an outlier, see Fig. 4. This individual would have to fly at speed of ca 130 km h^{-1} which is very unlikely). The fixed effect was travel distance, while season (autumn, spring) was taken as a covariate. Individual identity nested within species was entered as a random effect. We obtained similar results (not shown) when we ran the same analysis with travel distances between the stationary sites. All data analyses were conducted in R version 3.0.1[39].

Ethical note

The field work was carried out in accordance with the current laws of Belarus, Czech Republic, Finland, Germany, Sweden and Ukraine. The procedures used to handle and fit the birds with geolocators were approved by Academy of Sciences of the Czech Republic (#38/2011), Varsinais-Suomi Centre for Economic Development, Transport and the Environment (#LOS-2009-L-308-259), Landratsamt Saale-Orla-Kreis (#16.075.364.622.0 SC/12), Landkreis

Leipzig (364.620/15/7/4), Stockholms södra djurförsöksetiska nand (#S55-11), Ukrainian Ministry of Ecology and Natural Resources (1/2011) and by ethical committees of Palacký University and Czech Ministry of Education (#1/2011, licence #CZ00231).

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Author contributions

P.A., T.E., M.B. and S.H. conceived the study design, collected data, performed data analyses, wrote the manuscript. L.G., I.H., M.K., T.L., F.L., P.P. and V.S. contributed with data, commented on the manuscript. All authors approved the manuscript.

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Appendix 4

Supplementary information for Chapter 5

Table S1. Classification of long-distance migratory birds according to their migratory strategy: either nocturnal (N; birds rest during the day and fly at night) or diurnal (D; resting during the night and flying at daytime). When mixed strategies exist the less prevalent strategy is given in parentheses. Listed are species for which at least a part of European breeding population winters S of the Sahara Desert. This non-exhaustive compilation includes only species with reliable information and it relies mainly on expert knowledge, basic handbook sources and information from a long-term ringing monitoring in the Alps (Col de Bretolet) run by the Swiss Ornithological Institute.

Common name	**Scientific name**	**Migratory strategy**
Great Reed Warbler	*Acrocephalus arundinaceus*	N
Aquatic Warbler	*Acrocephalus paludicola*	N
Marsh Warbler	*Acrocephalus palustris*	N
Sedge Warbler	*Acrocephalus schoenobaenus*	N
Eurasian Reed Warbler	*Acrocephalus scirpaceus*	N
Tawny Pipit	*Anthus campestris*	D & N
Red-throated Pipit	*Anthus cervinus*	D
Tree Pipit	*Anthus trivialis*	D & N
Common Swift	*Apus apus*	D & N
Alpine Swift	*Apus melba*	D & N
Pallid Swift	*Apus pallidus*	D & N
Greater Short-toed Lark	*Calandrella brachydactyla*	D & N
European Nightjar	*Caprimulgus europaeus*	N
Red-rumped Swallow	*Cecropis daurica*	D
Rufous-tailed Scrub Robin	*Cercotrichas galactotes*	N
Great Spotted Cuckoo	*Clamator glandarius*	D & N
European Roller	*Coracias garrulus*	D
Common Quail	*Coturnix coturnix*	N
Common Cuckoo	*Cuculus canorus*	(D) & N
Cream-colored Courser	*Cursorius cursor*	D
Common House Martin	*Delichon urbicum*	D
Ortolan Bunting	*Emberiza hortulana*	D & N
Collared Flycatcher	*Ficedula albicollis*	N
European Pied Flycatcher	*Ficedula hypoleuca*	N
Semi-collared Flycatcher	*Ficedula semitorquata*	N
Black-winged Pratincole	*Glareola nordmanni*	D
Collared Pratincole	*Glareola pratincola*	D
Icterine Warbler	*Hippolais icterina*	N
Melodious Warbler	*Hippolais polyglotta*	N
Barn Swallow	*Hirundo rustica*	D
White-throated Robin	*Irania gutturalis*	N
Red-backed Shrike	*Lanius collurio*	N
Isabelline Shrike	*Lanius isabellinus*	N

Lesser Grey Shrike	*Lanius minor*	N
Woodchat Shrike	*Lanius senator*	N
River Warbler	*Locustella fluviatilis*	N
Savi's Warbler	*Locustella luscinioides*	N
Common Grasshopper Warbler	*Locustella naevia*	N
Thrush Nightingale	*Luscinia luscinia*	N
Common Nightingale	*Luscinia megarhynchos*	N
Bluethroat	*Luscinia svecica*	N
European Bee-eater	*Merops apiaster*	D & N
Rufous-tailed Rock Thrush	*Monticola saxatilis*	N
Blue Rock Thrush	*Monticola solitarius*	N
White Wagtail	*Motacilla alba*	D & N
Grey Wagtail	*Motacilla cinerea*	D
Western Yellow Wagtail	*Motacilla flava*	D & N
Spotted Flycatcher	*Muscicapa striata*	N
Desert Wheatear	*Oenanthe deserti*	N
Black-eared Wheatear	*Oenanthe hispanica*	N
Northern Wheatear	*Oenanthe oenanthe*	N
Eurasian Golden Oriole	*Oriolus oriolus*	(D) & N
Common Redstart	*Phoenicurus phoenicurus*	N
Western Bonelli's Warbler	*Phylloscopus bonelli*	N
Common Chiffchaff	*Phylloscopus collybita*	D & N
Iberian Chiffchaff	*Phylloscopus ibericus*	N
Wood Warbler	*Phylloscopus sibilatrix*	N
Willow Warbler	*Phylloscopus trochilus*	N
Eurasian Crag Martin	*Ptyonoprogne rupestris*	D
Sand Martin	*Riparia riparia*	D
Whinchat	*Saxicola rubetra*	N
Eurasian Stonechat	*Saxicola torquatus*	N
Eurasian Blackcap	*Sylvia atricapilla*	N
Garden Warbler	*Sylvia borin*	N
Subalpine Warbler	*Sylvia cantillans*	N
Common Whitethroat	*Sylvia communis*	N
Lesser Whitethroat	*Sylvia curruca*	N
Orphean Warbler	*Sylvia hortensis*	N
Barred Warbler	*Sylvia nisoria*	N
Eurasian Hoopoe	*Upupa epops*	D & (N)

Table S2. Patterns of occurrence of FLP during autumn and spring migration. Breeding population gives the European breeding site locations, Migratory period refers whether FLP occurred in spring or autumn, Dates of light anomaly (FLP) listed are days when a distinct light pattern occurred that could be interpreted as FLP or as a strong zigzagging pattern potentially indicating that the bird was in the desert but resting in shelter during the daytime, # days with FLP gives the number of days with FLP, Abrupt FLP ending (yes or no) reports for each case whether FLP ended abruptly during the daytime, Elapsed time gives the time in hours between sunrise and the abrupt end of FLP during the daytime, i.e. the duration of prolonged flight into the day. T_{max} gives the time (in minutes) it took to reach the maximum light intensities. Values that were over the threshold of 91 min are in bold. Note that spring and autumn tracks are not available for all individuals as in several cases the geolocator battery life span was less than a year. In three individuals (7EN, 7HO and 7JA) light anomalies (> 5h of max light intensities) were also recorded on several occasions outside of the main migration period, see remarks at the bottom of the table.

Species	Logger ID	Breeding population	Migratory period	Dates of FLP	# days with FLP	Abrupt FLP ending	Elapsed time	T_{max}
Reed Warbler	7QN	Germany	autumn	7-11 October 2012***	0			
Reed Warbler	7RY	Germany	autumn	8 October 2012	1	yes	6.4	42
Reed Warbler	7RJ	Germany	autumn	26-28 September 2012***	0			
Reed Warbler	7QK	Germany	autumn	-	0			
Reed Warbler	9CI	Germany	autumn	13 September 2012	1	yes	5.5	62
Reed Warbler	7QG	Germany	autumn	-	0			
Reed Warbler	9BI	Czech Republic	autumn	22-24 September 2012***	0			
Reed Warbler	7SF	Czech Republic	autumn	31 Aug, 18-19 Sept 2012***	0			
Reed Warbler	7SC	Czech Republic	autumn	14-15 September 2012***	0			
Reed Warbler	9BL	Czech Republic	autumn	10 September 2012	1			73
Reed Warbler	9AZ	Czech Republic	autumn	1 September 2012	1	yes**		**347**
Reed Warbler	9BV	Czech Republic	autumn	12 September 2012***	0			
Reed Warbler	7QN	Germany	spring	13-14 April 2013	2	yes, yes	9.8, 6.6	43, 47
Reed Warbler	7QK	Germany	spring	18 May 2013	1	yes	6.1	91
Reed Warbler	9CI	Germany	spring	11-12 April 2013	2	yes, yes	10.2, 5.2	42, 52
Reed Warbler	7QG	Germany	spring	3 May, 5 May 2013	1+0+1	yes, yes	6.8, 3.6	62, 82
Reed Warbler	9BI	Czech Republic	spring	15 May 2013	1	yes	6.3	85
Reed Warbler	7SC	Czech Republic	spring	13 May 2013	1	yes	10.5	47
Reed Warbler	9AZ	Czech Republic	spring	14 March 2013	1	yes	4.8	58
Reed Warbler	9BV	Czech Republic	spring	25 March 2013	1	yes	5.5	**137**

Reed Warbler	9BV	Czech Republic	spring	25 March 2013	1	yes	5.5	**137**
Pied Flycatcher	3GS	Finland	autumn	16-17 September 2011	2	yes	5.5	**167, 202**
Pied Flycatcher	3JE	Finland	autumn	30 Sept-1 October 2011	2			61, 53
Pied Flycatcher	3OX	Finland	autumn	5-6 October 2011	2			**127, 98**
Pied Flycatcher	3PG	Finland	autumn	5-6, 8 October 2011	2+0+1	no, yes	7.3	74, 73, **92**
Pied Flycatcher	3GS	Finland	spring	11 April 2012	1	yes	7.9	**212**
Pied Flycatcher	3JE	Finland	spring	17-18 April 2012	2	yes	5.1	64, 78
Collared Flycatcher	3AE	Czech Republic	autumn	29-30 August 2011	2			38, 63
Collared Flycatcher	3EU	Czech Republic	autumn	7-9 September 2011	3	yes	3.6	53, 37, 42
Collared Flycatcher	7HA	Sweden	autumn	9-10 September 2012	2	yes	5.4	**203, 132**
Collared Flycatcher	7HN	Sweden	autumn	8-9 September 2012	2			**123**, 81
Collared Flycatcher	7HO	Sweden	autumn	18-20 September 2012	3	yes	4.1	52, 32, 37
Collared Flycatcher	7IB	Sweden	autumn	16-17 September 2012	2			57, 54
Collared Flycatcher	7IG	Sweden	autumn	22-23 September 2012***	0			
Collared Flycatcher	7JA	Sweden	autumn	7-8 September 2012	2			62, 42
Collared Flycatcher	7JB	Sweden	autumn	22-23 September 2012	2	yes	8.3	**127, 127**
Collared Flycatcher	7JI	Sweden	autumn	21-23 September 2012	3	yes, yes	6.9, 6.0	40, 39, 37
Collared Flycatcher	7JJ	Sweden	autumn	21-23 September 2012	3	yes, yes	5.5, 3.8	**112**, 55, 62
Collared Flycatcher	7LA	Sweden	autumn	19-20 September 2012	2	yes	4.8	57, 62
Collared Flycatcher	7LH	Sweden	autumn	18-19 September 2012	2			**147**, 69
Collared Flycatcher	3EU	Czech Republic	spring	25-27 April 2012	3			58, 85, **93**
Collared Flycatcher	7HN	Sweden	spring	6-8 April 2013	3	yes	4.5	74, 73, **93**
Collared Flycatcher	7HO	Sweden	spring	7-9 April 2013	3			77, 74, 57
Collared Flycatcher	7IB	Sweden	spring	13-14, 16 April 2013	2+0+1	no, yes	5.2	57, 62, 52
Collared Flycatcher	7IG	Sweden	spring	11-13 April 2013	3	yes, yes	7.9, 9.2	82, 72, **157**
Collared Flycatcher	7JA	Sweden	spring	25-27 April 2013	3			43, **93**, 69
Collared Flycatcher	7JB	Sweden	spring	22-23 April 2013	2			82, **142**
Collared Flycatcher	7JI	Sweden	spring	23-24 April 2013	2			**147, 132**
Collared Flycatcher	7JJ	Sweden	spring	22-23 April 2013	2			72, 88
Collared Flycatcher	7LA	Sweden	spring	1-3 May 2013	3	yes	8.2	**119**, 78, **102**
Collared Flycatcher	7LH	Sweden	spring	22-23 April 2013	2			**172, 143**

Aquatic Warbler	7EN	Belarus	autumn	multiple periods over the annual cycle	*			
Aquatic Warbler	7OY	Ukraine	autumn	26-27 August 2012	1+1	yes, yes	11.6, 2.5	38, 47
Aquatic Warbler	7PE	Belarus	autumn	21 Aug, 29-30 Aug 2012	1+0+2	no, yes	10.4	**107**, 32, 39
Aquatic Warbler	7PO	Ukraine	autumn	23-24 August 2012	2	yes	1.0	38, 44
Aquatic Warbler	7HK	Belarus	autumn	18-19 August 2012	1+1	yes, yes	11.1, 4.4	47, 43
Aquatic Warbler	7EN	Belarus	spring	9 March 2013	1			34
Aquatic Warbler	7OY	Ukraine	spring	26 March 2013	1	yes	5.7	62

* a case that cannot be clearly interpreted as FLP occurred multiple times but we could not estimate the stationary sites around those FLP days; ** unusual FLP pattern when low light intensities occurred in the morning followed by FLP for the rest of the day; *** in these cases FLP was absent but on those days we could still observe elevated but zigzagged light recordings during daytime.

Light anomalies were detected in three individuals also during other times when they were presumably not crossing any barriers: 7HO – on 16 Nov 2012 and 22 Nov 2012, both cases with FLP only for several hours during the middle of the day and with considerable shading effect, 7JA – 6 cases of FLP between 15 Nov and 4 Dec 2012, 7EN – a series of 11 days with FLP of various quality between 15 August 2012 and 23 Sept 2012 (we assume that some of them were during barrier crossing but we fail to estimate stationary sites around the FLP days) and another series with 8 FLPs days of various quality between 11 May 2013 and 19 May 2013.

Table S3. A comparison of autumn and spring migratory strategies used by individual birds that were tracked during the entire annual cycle. Strategies, listed by capital letters, are from Fig. 2. Note that categories C and B are from the perspective of barrier crossing likely identical.

		Category of light pattern	
Species	**Logger ID**	Autumn	Spring
Pied Flycatcher	3GS	C*	C
Pied Flycatcher	3JE	B	C
Collared Flycatcher	3EU	C	B
Collared Flycatcher	7HN	B	C
Collared Flycatcher	7HO	C	B
Collared Flycatcher	7IB	B	G
Collared Flycatcher	7IG	A	D
Collared Flycatcher	7JA	B	B
Collared Flycatcher	7JB	C	B
Collared Flycatcher	7JI	D	B
Collared Flycatcher	7JJ	F	B
Collared Flycatcher	7LA	C	C
Collared Flycatcher	7LH	B	B
Aquatic Warbler	7OY	E	C
Aquatic Warbler	7EN	not interpretable	B
Reed Warbler	7QG	A	G
Reed Warbler	7QK	A	C*
Reed Warbler	7QN	A	E
Reed Warbler	7SC	A	C*
Reed Warbler	9AZ	H	C*
Reed Warbler	9BI	A	C*
Reed Warbler	9BV	A	C*
Reed Warbler	9CI	C*	E

* cases when FLP occurred during one day only and the bird landed during the daytime

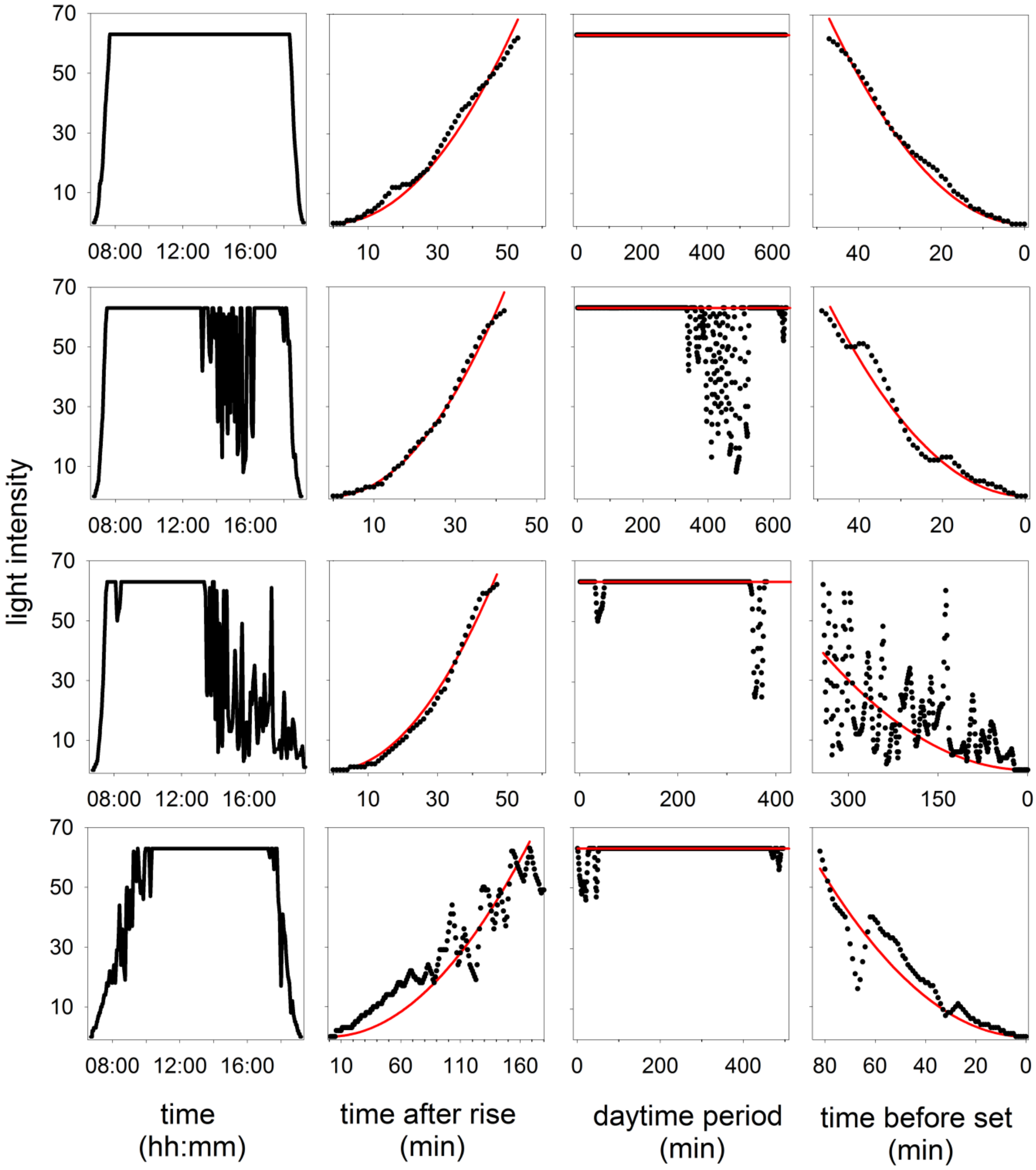

Figure S1. Illustrative examples of FLP classification based on shadiness. From the whole FLP (first left column) the sunrise (second column) and sunset (fourth column) have been classified using the sums of the absolute residuals from a fitted quadratic regression when light (y-axis) is plotted against time (x-axis, red line). The daytime period (third column) was classified using the sum of all deviations from the maximum light intensity (red line = 63 units). The bottom row shows data with considerable shading early in the morning. Such FLP cases were excluded from our interpretation as flights into the day.

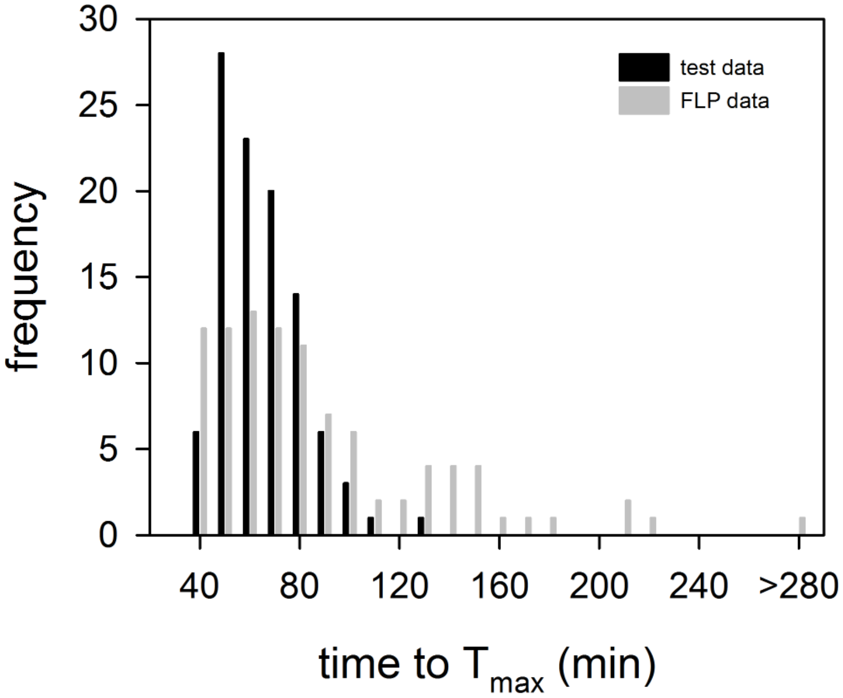

Figure S2. Distribution of T_{max} values for barn swallows (black bars – test data) and our four focal species (grey bars – FLP data).

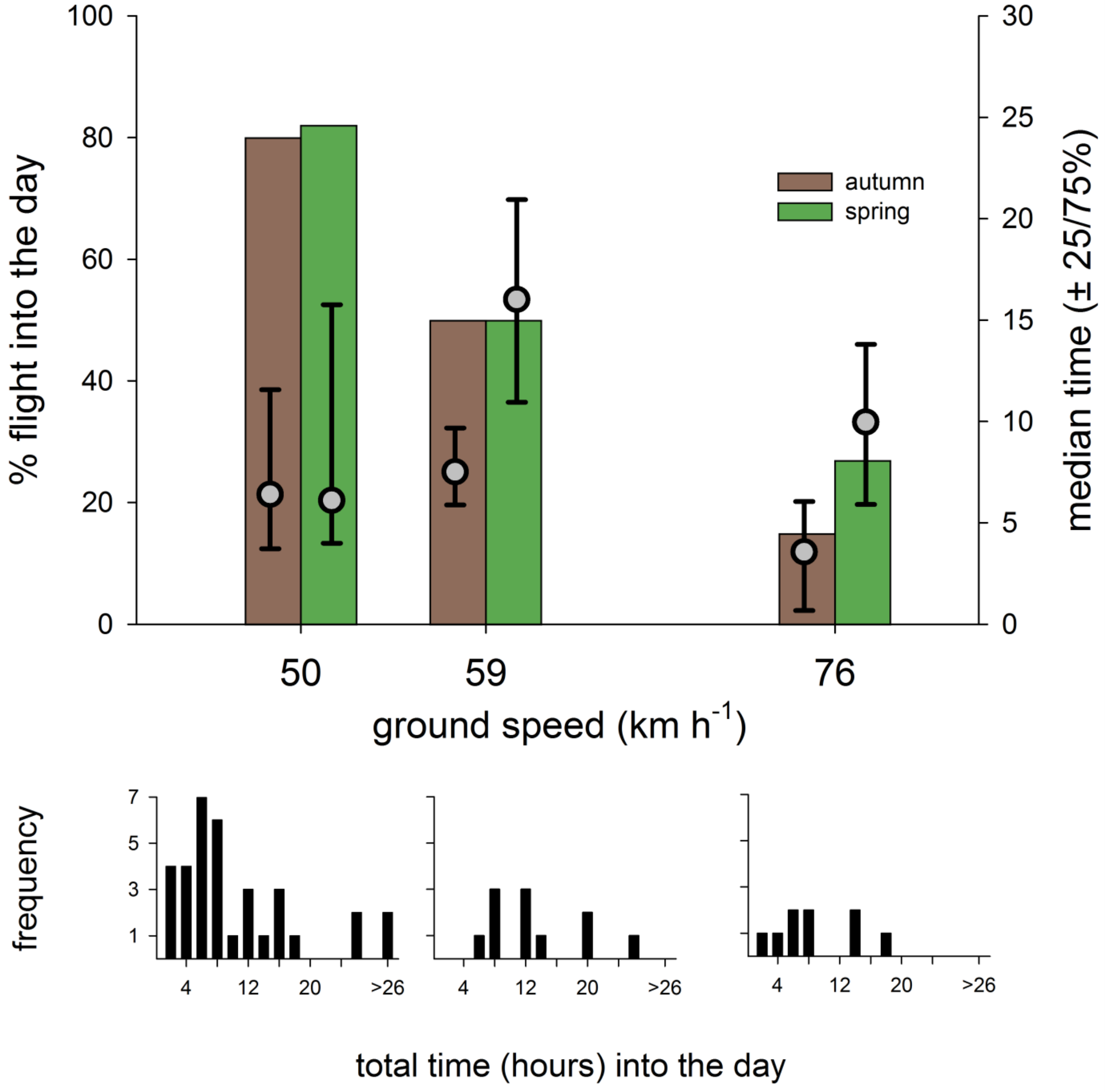

Figure S3. Simulation (separately for autumn and spring data) of how many individuals (bars in %) in our study had to fly at least partly into the day in order to be able to cross the desert under three empirically measured flight speeds. The average ground speeds were taken as 50 km h^{-1} (Schmaljohann, Liechti, and Bruderer 2007), 59 km h^{-1} (Salewski, Schmaljohann, and Liechti 2010) and 76 km h^{-1} (Biebach et al. 2000). We used these speeds and the travel distance (the width of the Sahara each individual had to cross – see Methods) to calculate the time the bird must be aloft. Then we compared this time estimate with the summed nocturnal flight times from the night preceding the FLP, all nights between FLP days and the night after the last FLP day if we did not find an abrupt ending. Total time (summed during FLP; circles in hours on right vertical axis) of expected flight into the day ranged between 6h at 50 km h^{-1} to max 16h for the spring model at 59 km h^{-1} speed (median ± 25/75 percentiles). The lower panel gives the frequencies of total flight times into the day (binned to 2 hours), which decreased with higher ground speeds.

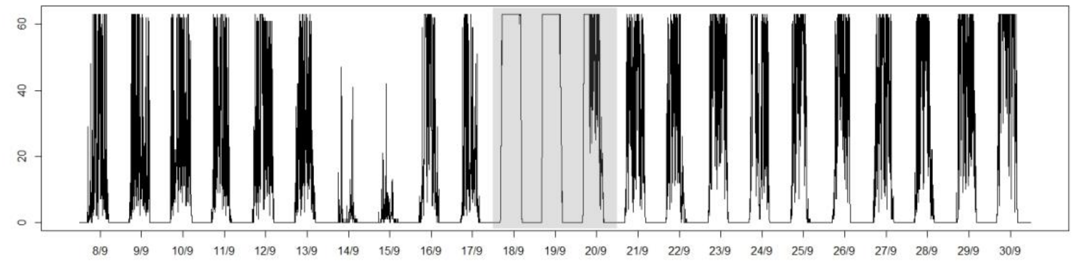

Figure S4. A representative example of light data profile (collared flycatcher #7HO during autumn migration) used to determine the stationary periods before and after crossing the barrier. The FLP anomaly is in grey area.

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Chapter 6

Cold spell *en route* delays spring arrival and decreases apparent survival in a long-distance migratory songbird

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Abstract

Background: Adjusting the timing of annual events to gradual changes in environmental conditions is necessary for population viability. However, adaptations to weather extremes are poorly documented in migratory species. Due to their vast seasonal movements, long-distance migrants face unique challenges in responding to changes as they rely on an endogenous circannual rhythm to cue the timing of their migration. Furthermore, the exact mechanisms that explain how environmental factors shape the migration schedules of long-distance migrants are often unknown.

Results: Here we show that long-distance migrating semi-collared flycatchers *Ficedula semitorquata* delayed the last phase of their spring migration and the population suffered low return rates to breeding sites while enduring a severe cold spell *en route*. We found that the onset of spring migration in Africa and the timing of Sahara crossing were consistent between early and late springs while the arrival at the breeding site depended on spring phenology at stopover areas in each particular year.

Conclusion: Understanding how environmental stimuli and endogenous circannual rhythms interact can improve predictions of the consequences of climate changes on migratory animals.

Keywords: Circannual rhythm, Climate change, Geolocator, Long-distance migrant, Phenology, Weather extremes

Background

Over the course of the 20th century, the Earth's near-surface temperature has increased, [1] and many species have advanced their phenology as a response to this climate warming [2]. Among those, various migratory birds have advanced their spring migration and breeding schedules [3], with stronger responses in short-distance compared to long-distance migrants [4].

Long-distance migrants spend the non-breeding period in the areas where they often have limited possibilities to assess the climatic conditions at their distant breeding grounds, thus limiting their ability to time the spring migration accordingly. Current theory suggests that long-distance migratory birds depend on endogenously controlled circannual rhythms to cue their spring migration [5, 6]. Photoperiod and environmental factors may serve as *Zeitgeber* to fine-tune the timing of departure [7–9]. While the mechanisms regulating the onset of spring migration are not yet fully understood, even less is known about the processes modifying migration rates and decision making *en route* [10]. Thus, the specific factors that determine the observed advances in spring arrival of long-distance migrants remain unknown.

The understanding how animals respond to the changing environment is of special importance with respect to increasing frequency of extreme weather events [11]. Inability to respond to a rapidly changing environment can have severe consequences on population demography and viability. If long-distance migrants rely solely on endogenous signals to time the entire spring migration, this could result in suboptimal arrivals at the breeding sites, possibly leading to mismatches of food peak availability and food demand [12].

Here we examine how long-distance migrating semicollared flycatchers *Ficedula semitorquata* respond to contrasting climatological conditions encountered in two consecutive spring migrations. Flycatchers' peak arrival period at their breeding range extends from the end of March to the beginning of April [13]. In Southeastern Europe in 2014, this period was the warmest on record since 2000, followed by an exceptional cold spring in 2015 with temperatures well below the long-term average (Fig. 1). Such extreme and opposing conditions present an ideal opportunity to study phenotypic plasticity in a natural setting. We were particularly interested to test whether this obligatory long-distance migrant is capable of adjusting its migration rate based on environmental cues *en route* to fine-tune arrival at the breeding site.

Methods

Study site and geolocators

Our study site is located in eastern Bulgaria (42°55′N, 27°48′E) approximately 8 km from the Black Sea coast at 120–150 masl. Habitat at the breeding site is oak woodland dominated by Hungarian oak *Quercus frainetto* with very little undergrowth. A population of approximately 100 pairs of semi-collared flycatchers breeds in nest boxes.

During the breeding season of 2013 and 2014 we equipped 40 (17 males, 23 females) and 49 (27 males, 22 females) adults with geolocators (GDL2.0, Swiss Ornithological Institute; weight including the harness: 0.6 g) which were fitted on birds' backs using elastic leg-loop silicone harnesses. The geolocators on average constituted 4.6 ± 0.3% (SD) of the bird's body mass. There was no difference in the average load of the geolocator between the birds that returned and those that did not return (average ± SD; returned: 4.7 ± 0.3%, n = 18; not returned: 4.6 ± 0.3%, n = 71; t test: $t_{87} = -1.19$, $p = 0.25$).

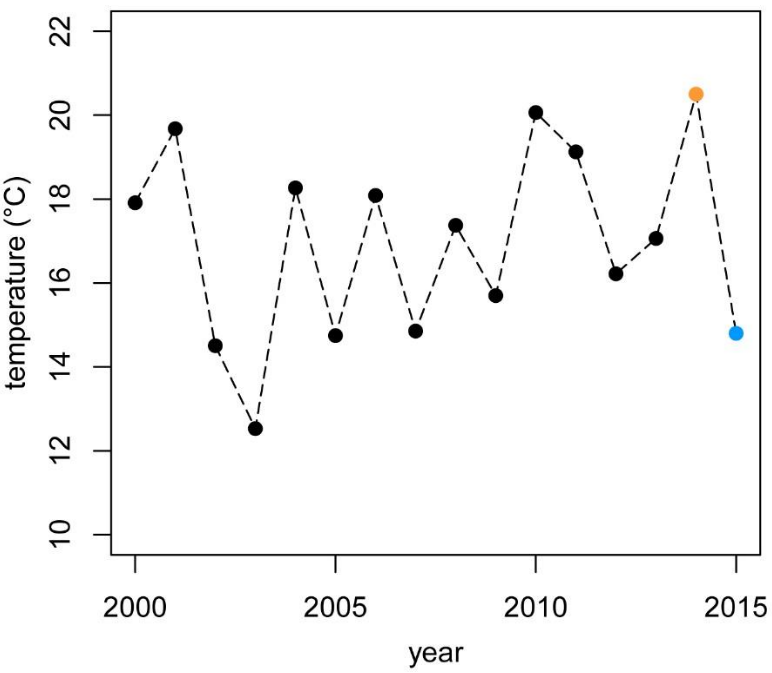


Figure 1. Average land surface temperature in Bulgaria, Greece and Turkey from 22 March to 7 April from 2000 to 2015 [Data available from the U.S. Geological Survey (http://www.usgs.gov/)].

We did an extensive recapturing of the tagged birds upon their arrival at the breeding site. Birds were captured using mist-nets and traps inside the nest boxes before the initiation of nest building. All adult breeders were captured later in the season when feeding nestlings, allowing for additional geolocator retrieval from the birds not captured earlier. In total we recovered 18 geolocators (2014: n = 11, 2015: n = 7); however, due to technical problems, we obtained spring migration data from only 5 [2 females, 3 males (1 incomplete)] and 6 (2 females, 4 males) devices in 2014 and 2015, respectively.

In addition, we acquired spring migration passage dates of flycatchers from the Antikythira Bird Observatory, Greece (35°51′N, 23°18′E, [14]) from 2007 to 2015.

Data analyses

We processed the light recording data using the R-package ‘GeoLight’ v2.0 [15], having determined sunrise and sunset times with ‘Geolocator’ software (Swiss Ornithological Institute) beforehand. We filtered the datasets for outlaying sun events using the ‘loessFilter’ function (k value = 2). We determined departure from the nonbreeding site and arrival at the breeding site using the ‘changeLight’ function (probability of change q = 0.8). Minimum stationary period duration was set to 3 days. We determined Sahara crossing time according to the procedure described by Adamík et al. [16]. In short, during the Sahara crossing days geolocator’s light sensor records uninterrupted maximal light intensities throughout the day, suggesting that birds cross the ecological barrier with a non-stop flight or at least prolonging the typical nocturnal flight for several hours into the following day. We adjusted the probability of change in the ‘changeLight’ function for each individual starting from q = 0.8, so that the function detects Sahara crossing time as a movement period. Annual timing of key migration phases are given as median date plus interquartile range (IQR) throughout.

To test for differences in apparent local survival rates between 2013–2014 and 2014–2015, we used a Chi-squared goodness-of-fit test without Yates correction.

Weather data acquisition

We obtained land surface temperature data (data set: MOD11A2) and leaf area index (MOD15A2) data during the spring migration period (10 February–7 April) from MODIS terra and aqua satellites, accessed from the Land Processes Distributed Active Archive Center (LP DAAC) at the US Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (https://lpdaac.usgs.gov/). We obtained wind data for the 850 mb pressure level (approximately 1500 masl) from the National Center for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) Reanalysis dataset [17] using R-package 'RNCEP' [18]. Data were gathered across a 2.5° grid for every 6 h period in 2014, 2015 and annually averaged across the whole spring migration period (10 February–7 April). Winds at the 850 m bar pressure level are largely free of orographic distortion and, thus, are frequently used for describing wind patterns experienced by migratory birds [19].

Results

Weather patterns

The average land surface temperature during the spring migration period across Bulgaria, Greece and Turkey—countries on the species flyway—from 22 March–7 April was 20.5 °C in 2014, while in 2015 it was only 14.8 °C (Fig. 2a, b). This was the largest such difference in air temperature for over a decade (Fig. 1). Plant phenology, measured by leaf development, was delayed by approximately 29 days in 2015 compared to 2014 (Fig. 2c). Along other parts of the flycatchers' migratory flyway of the flycatchers, the prevailing winds and temperatures were similar between the two study years (Fig. 3).

Responses of migrants

During both years, flycatchers departed from their nonbreeding grounds in Eastern-Central Africa in the second half of February {median date 2014: 21 February [interquartile range (IQR) = 17–22 Feb], 2015: 16 February (11–19 Feb), Fig. 2c} and crossed the Sahara desert in late March [2014: 23 March (17–30 Mar), 2015: 27 March (21 Mar–5 Apr)]. After crossing the Sahara, the birds stayed in the Mediterranean Basin for 5 days (3.5–7.1) in 2014 before arriving at the breeding site on 2 April (29 Mar–7 Apr). In 2015 birds spent three times longer (mean 15 days, IQR 9.8–19.5) in the Mediterranean Basin and arrived at the breeding site on 10 April (9–11 Apr, see Online Additional file 1). We found a negative relationship between the time spent in the Mediterranean Basin and leaf development at the breeding site (Pearson's one-tailed correlation: $r = -0.82$, $n = 10$, $p = 0.002$; Fig. 2d). The median spring migration passage times of flycatchers at Antikythira Bird Observatory in 2014 and 2015 were within the species' typical long-term passage period (2014: 17 Apr; 2015: 14 Apr; 2007 2015: 15 Apr, IQR = 12–18 Apr).

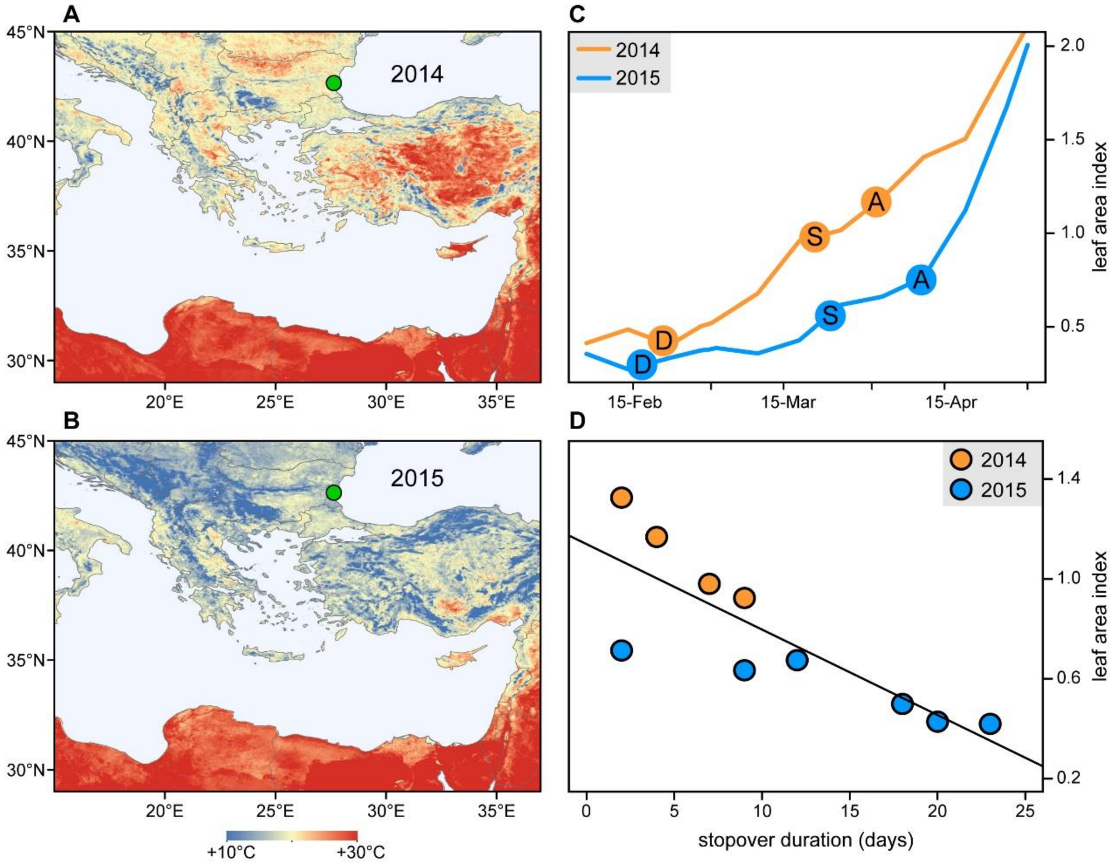


Figure 2. Annual differences in weather conditions and the corresponding migration phenology of semi-collared flycatchers. Land surface temperatures (°C) from 22 March–7 April in a 2014 and b 2015. c Leaf area index (m2 of leaf area per m2 ground area) progression from 6 February–1 May at the flycatcher's breeding site in 2014 (orange) and 2015 (blue) and the related flycatcher migration phenology in each year, including (D) departure from the non-breeding site, (S) Sahara crossing, and (A) arrival at the breeding site. d Stopover duration north of the Sahara in relation to leaf area index at the breeding site at the time of Sahara crossing [The background maps in a and b made were made from data available from the U.S. Geological Survey (http://www.usgs.gov/); maps were created in ArcMap 10.1 (http://www.esri.com/)].

The cold spell of 2015 also had severe consequences on apparent local survival. Return rates of geolocator-tagged and ringed-only control birds were approximately two times lower in 2015 (Table 1), with males and older individuals (more than 3 years old) affected more severely.

Discussion

Our findings show that a cold spell encountered *en route* delayed spring arrival and decreased local apparent survival in a trans-Equatorial migrant. After reaching the temperate climatic zone where environmental cues of spring phenology become available, tracked semi-collared flycatchers flexibly adjusted their migration rate and advanced (in the warm spring of 2014) or delayed (in the cold spring of 2015) their arrival at the breeding site depending on local conditions (e.g. temperature and leaf development).

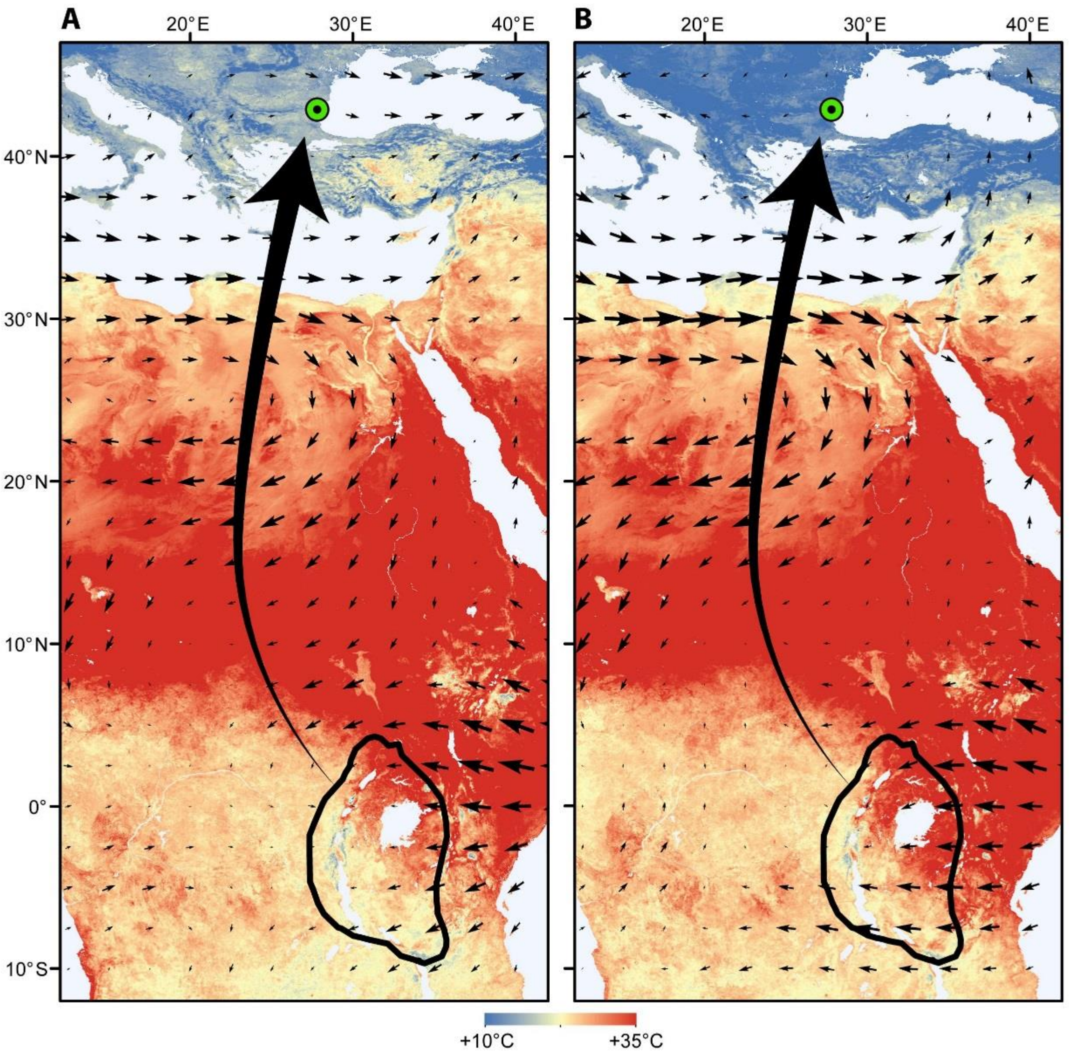


Figure 3. Average land surface temperature (background map) and wind patterns at 850 kPa pressure level (small arrows) during semi-collared flycatcher spring migration from 10 February to 7 April in a 2014 and b 2015. Black shape outlines semi-collared flycatcher non-breeding range (BirdLife International and NatureServe 2011) and large arrows indicate spring migration routes [Temperature data available from the U.S. Geological Survey (http://www.usgs.gov/); wind data available from National Oceanic and Atmospheric Administration (http://www.noaa.gov/). Maps were created in ArcMap 10.1 (http://www.esri.com/)].

The typical passage times of semi-collared flycatchers at Antikythira Bird Observatory range from the end of March to the end of April [14], with most birds passing in the second decade of April. Median passage times in the second decade of April may imply that the flyway through Antikythira do not pass there until after the prolonged stopovers of our tracked birds in 2015. Indeed in 2014, birds from our study population arrival at the breeding site earlier than the median passage time at Antikythira, supporting this idea.

So far, contrasting results have been reported in long-distance migrants regarding their ability to use environmental signals to cue spring migration [5]. Nearctic-Neotropical long-distance migrants have been shown to use environmental cues to some extent to adjust their migration rate in spring [20, 21]. On the contrary, pied flycatchers *Ficedula hypoleuca* were not able

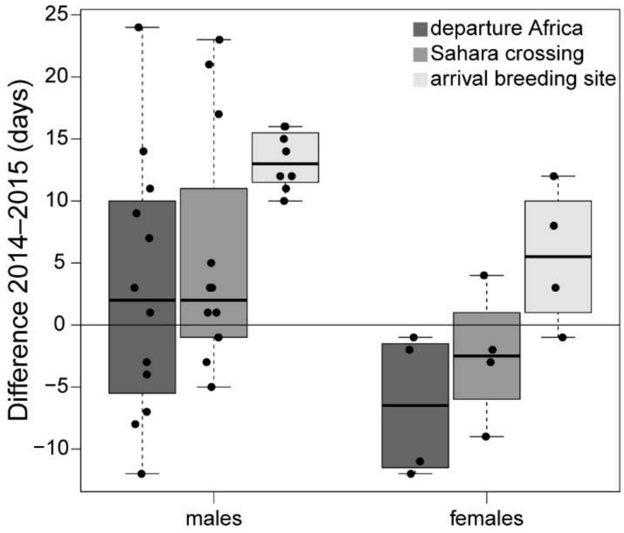
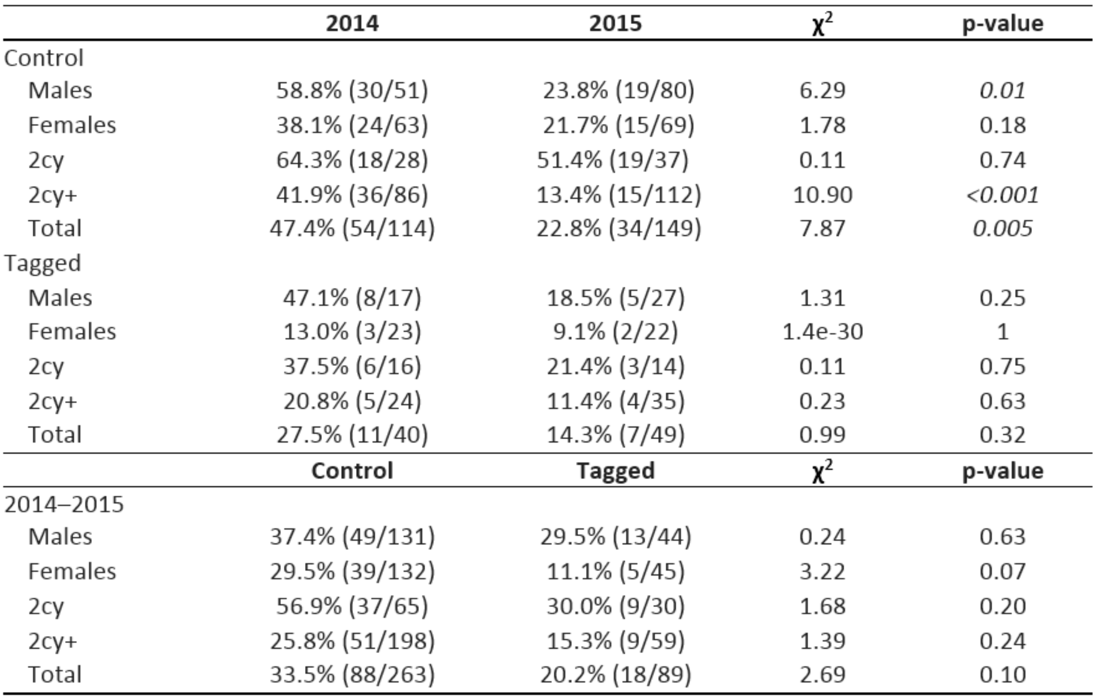


Figure 4. Sex-specific difference in individual migration schedules between a cold (2015) and a warm spring (2014). The delay in arrival is larger for the earlier migrating males than for later migrating females. Individual data points represent difference between every possible pair of two individuals tracked in different years.

to adjust the arrival time proportionally to the increasing spring temperatures suggesting a tight endogenous routine controlling phenology of spring migration in that population [22]. Recent tracking studies confirm these findings, showing that breeding site arrival date in pied flycatchers largely depends on the onset of spring migration, rather than birds making adjustments *en route* [23]. In the closely related collared flycatcher *F. albicollis*, spring arrival at different breeding sites is related to local phenology, and timing of the onset of spring migration seems to be less important [24]. This coincides with our findings in semi-collared flycatchers. The differences between these three *Ficedula* species may be related to the migratory flyway they use during the spring migration. Resource availability and ecological barriers encountered *en route* can influence on the rate and timing of bird migration [25, 26]. Species that encounter ecological barriers along the migratory flyway and have larger migratory distance show a greater degree of variation in their migratory behaviour and ability to adjust migration rate in response to the environment. In spring, pied flycatchers migrate along the western Afro-Palearctic flyway, while collared and semi-collared flycatchers migrate along the central Afro-Palearctic flyway. Migrants using the central Afro-Palearctic flyway encounter larger ecological barriers (e.g. the distance to cross the Sahara Desert is larger) and harsher conditions compared to the species using the western Afro-Palearctic flyway.

To date there seems to be no general consensus on where along a migration route the changing conditions should have the largest effect on the timing of bird arrival [10]. Tøttrup et al. [27] demonstrated that drought in the Horn of Africa delayed spring arrival of Afro-Palearctic migrants, as birds prolonged their stopovers in this area. This, when considered with our results suggests that prolonged stopovers due to adverse weather conditions could occur at any place along the migratory route (in the tropics and temperate regions alike), and can cause delayed arrival at the breeding sites.

Table 1. Differences in return rates of semi-collared flycatchers between 2014 and 2015, and between control group and geolocator-tagged group.



	2014	**2015**	**χ^2**	**p-value**
Control				
Males	58.8% (30/51)	23.8% (19/80)	6.29	*0.01*
Females	38.1% (24/63)	21.7% (15/69)	1.78	0.18
2cy	64.3% (18/28)	51.4% (19/37)	0.11	0.74
2cy+	41.9% (36/86)	13.4% (15/112)	10.90	*<0.001*
Total	47.4% (54/114)	22.8% (34/149)	7.87	*0.005*
Tagged				
Males	47.1% (8/17)	18.5% (5/27)	1.31	0.25
Females	13.0% (3/23)	9.1% (2/22)	1.4e-30	1
2cy	37.5% (6/16)	21.4% (3/14)	0.11	0.75
2cy+	20.8% (5/24)	11.4% (4/35)	0.23	0.63
Total	27.5% (11/40)	14.3% (7/49)	0.99	0.32
	Control	**Tagged**	**χ^2**	**p-value**
2014–2015				
Males	37.4% (49/131)	29.5% (13/44)	0.24	0.63
Females	29.5% (39/132)	11.1% (5/45)	3.22	0.07
2cy	56.9% (37/65)	30.0% (9/30)	1.68	0.20
2cy+	25.8% (51/198)	15.3% (9/59)	1.39	0.24
Total	33.5% (88/263)	20.2% (18/89)	2.69	0.10

Significant differences are given in italics

As a consequence of adverse weather, increased mortality rates have previously been reported across different taxa [28]. Our finding of low apparent survival of flycatchers in a year with adverse weather conditions likely indicates increased mortality. Alternatively, birds may have acted opportunistically and settled for breeding elsewhere along the migratory route or exhibited a higher degree of breeding dispersal compared to the previous year. In our study, males showed lower return rates than females in the colder spring of 2015. By arriving earlier, males are exposed to a more hostile environment, including lower food availability, than later arriving females. Similarly, older flycatchers usually arrive at the breeding site earlier than younger ones and would therefore undergo similar consequences to those of males versus females. In cliff swallows *Petrochelidon pyrrhonota* higher mortality of older individuals was found as a result of a cold spell, coinciding with our findings of low return rates [29].

Geolocator attachment has been shown to negatively affect return rates of birds [30]. However the recent evidence is ambiguous, with a number of studies showing no apparent effect on return rates of the tagged birds [e.g. 31, 32], while some report negative influence [33] including delayed breeding site arrival time and decreased breeding success in the year following the geolocator deployment [34]. Furthermore, the differences in return rates between tagged and control birds seem to vary among sites within the same species [24, 35]. Therefore, having a control group of ringed only individuals within a study population is recommended in order to evaluate the impact of the attached devices on the animals. It may be that the limited sample size of tagged birds restricted our ability to detect a significant negative effect on individual apparent survival associated with carrying the geolocator, despite the fact that return rates of the geolocator-tagged individuals in our study were lower than for ringed only birds (see Table 1). However, we have no reason to believe that the extra weight of the geolocators influenced the migration speed and stopover behaviour of our study birds, as our field observations show simultaneous arrival of the tagged and ringed-only birds.

Conclusions

Our tracked flycatchers prolonged their stopovers in the Mediterranean region when confronting a cold spell, while the population as a whole suffered increased mortality. One must keep in mind that tracking by geolocator only provides data from recaptured, surviving individuals. Individuals differ in their response to abiotic stressors [36], and those not returning may have died due to an inappropriate response strategy. Because of spatial and temporal differences in climate change [1], long-distance migrants might be particularly challenged in their responses. For migratory birds the ability to combine external and internal stimuli appears to be essential for successful organization of the annual cycle. Understanding how species, populations, and even individuals respond to the changing climate and its associated weather extremes can help to predict the consequences for their population dynamics. Large phenotypic plasticity is likely to play a crucial role for population viability under the rapidly changing environment.

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Online additional files

Additional file 1. Video of semi-collared flycatcher spring migration progression tracked by light-level geolocators in relation to temperature anomalies in 2014 and 2015.

Additional file 2. Raw sunrise and sunset data recorded by the geolocators.

Authors' contributions

MB and PA carried out field work. MB analysed the data and was a major contributor in writing the manuscript. All authors actively commented during the writing of the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Experiments were approved by the Ministry of Environment and Water of Bulgaria.

Availability of data and materials

Summary statistics of data supporting the conclusions of this article has previously been published [13] and raw data are also included in the additional information files (Online Additional file 2) of this published article.

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Chapter 7

Linking events throughout the annual cycle in a migratory bird – carry-over effects of parental investment and non-breeding habitat conditions alter annual schedules

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Submitted manuscript

Abstract

Annual cycles of animals consist of various life history phases linked in a unified sequence, and processes taking place in one season can influence an individual's success in the consecutive seasons via carry-over effects. Here we link summer–winter–summer events in long-distance migratory collared flycatchers *Ficedula albicollis* using breeding data, individual-based tracking and signatures of stable hydrogen isotopes in winter-grown feathers to unravel connections between different phases of the full annual cycle. To disentangle true carry-over effects from individuals' intrinsic quality we experimentally manipulated the brood size of geolocator-tracked birds prior to tracking. We did not find unambiguous differences in annual schedules between individuals of reduced and increased broods; however, the latter were earlier with Sahara crossing in spring and arrival at the breeding grounds. Annual schedules depended on both the absolute parental investment expressed as the total number of fledglings (irrespective of experimental treatment) and conditions at the non-breeding areas (inferred from feather δ2H). Individuals with higher absolute parental investment delayed their autumn migration, had shorter non-breeding residency period and advanced spring migration compared to individuals with lower breeding effort. The conditions at the non-breeding areas rather than previous parental investment, better explained the timing of spring evens, particularly the onset of breeding. While on migration, collared flycatchers showed a pronounced "domino effect" which weakened with increasing timespan between events. Our results demonstrate the tight links between spatially- and temporally-distinct phases of the annual cycles of migrants which can have a significant implication for population dynamics.

Key-words: deuterium, geolocator, phenology, seasonal interactions, stable isotope

Introduction

Annual cycles of migratory animals consist of various spatially- and temporally-distinct episodes, like reproduction, moult, migration, and non-breeding residency. Nevertheless, these events are linked to each other physiologically and ecologically, and preceding events may have profound consequences on the following life history phases (Harrison et al. 2011). For long-distance migratory birds this means that experiences at their tropical non-breeding grounds may carry over across seasons and continents to influence events taking place at their temperate breeding grounds and *vice versa*. For instance, residing in sub-optimal habitat at non-breeding areas can result in delayed spring migration, consequently negatively affecting breeding performance the following season (Marra et al. 1998; Norris et al. 2004). Such events and processes taking place in one season which result in individuals making the transition between seasons in different physical conditions and ultimately affecting their performance are defined as carry-over effects (Norris and Marra 2007; Harrison et al. 2011). Habitat quality, social status, population density and breeding effort have been identified among the main drivers of carry-over effects (Harrison et al. 2011). Carry-over effects are described by an individual surviving the transition between the seasons with its fitness components altered. Thus, differences in individuals' intrinsic quality, seasonal compensation and developmental effects are not considered true carry-over effects. To disentangle true carry-over effects from individuals' intrinsic quality, an experimental approach may be required.

Reproduction is arguably one of the most costly processes in an animal's annual cycle in terms of energy expenditure (Svensson 1988). As found in great tits *Parus major*, increased breeding effort results in increased mortality, demonstrating the potentially high costs of parental care (Stearns 1992). Thus, finding balance in energy expenditure across seasons is crucial, particularly for migratory animals, among which the highest mortality often occurs during migration and the non-breeding period (Sillett and Holmes 2002; Lok et al. 2015). Carry-over effects can influence individual condition not only in the following season but also across years. For example, successful breeding in one year can negatively influence breeding probability and fecundity in the following year (Gustafsson and Sutherland 1988; Inger et al. 2010). Furthermore, parental investment can affect migration timing as well as the geographical distribution of individuals during the non-breeding season. In Cory's shearwaters *Calonectris diomedea*, birds with experimentally reduced breeding effort started autumn and the following spring migration earlier and were more likely to engage in long-distance migration than their conspecifics which had naturally higher breeding effort (Catry et al. 2013). This suggests that energetic and time-dependent costs of reproduction can influence subsequent migration episodes via carry-over effects. However, we still lack a comprehensive assessment of how strong the impact is on different parts of the full annual cycle.

Just as parental effort influences migration and the non-breeding period, experiences at non-breeding areas have consequences for the following spring migration and breeding season. Non-breeding habitat quality is known to influence spring migration phenology and individual fitness. Individuals residing in better quality habitats arrive at the breeding sites earlier and in better condition (Marra et al. 1998). For such studies, stable isotope ratios of winter-grown tissues have been increasingly used to evaluate the local conditions individual birds experience at their distant non-breeding areas. Thus far, stable carbon isotope (δ13C) signatures have been used most often to discriminate between higher quality (i.e., mesic) and lower quality (i.e., xeric) habitats (Bearhop et al. 2004; Norris et al. 2004; Procházka et al. 2008) as δ13C values allow for the discrimination between habitats with C3 and C4 plants. Nonetheless, other stable isotopes like nitrogen (δ15N), oxygen (δ18O), and hydrogen (δ2H) also have great potential for inferring conditions at non-breeding areas. For example, feather δ2H values reflect conditions at the areas where the feathers were grown allowing for the differentiation between regions of high (low δ2H values) and low (high δ2H values) precipitation, as there is a strong, mechanistic relationship between precipitation and stable hydrogen isotopes in biological tissue (Bowen et al. 2005).

Negative consequences of carry-over effects are often exhibited as delays in timing of annual events (Harrison et al. 2011). In annual migrations it has often been shown that delays in one phase of migration (i.e., onset of migration) translate into delays in the following migration phases (i.e., end of migration) – a so-called “domino effect” (Piersma 1987). Such patterns can have significant consequences for individual fitness and population dynamics revealing links between different parts of the annual cycle (Bauer et al. 2015). Several studies have shown that advanced spring migration yields increased breeding performance and fitness (Norris et al. 2004; Paxton and Moore 2015); thus, migratory birds should optimize their spring migration for early arrival.

Protandry is a widely-known phenomenon in animals when males appear at the breeding areas earlier in the season than females (Morbey and Ydenberg 2001). It has been especially well-observed in migratory birds (Rubolini et al. 2004; Tøttrup and Thorup 2008; Saino et al. 2010). Early arriving individuals gain an advantage over the later arriving conspecifics by securing territories of superior quality which in-turn increases their fitness (Kokko 1999). However, less is known about scheduling autumn migration and arrival time at the non-breeding sites, where pressure for early arrival might be more relaxed (Briedis et al. 2016; Lindström et al. 2016).

Collared flycatchers *Ficedula albicollis* are long-distance Afro-Palearctic migrants which breed across large areas of the Western Palearctic and migrate to Southern-Central Africa during winter in the Northern Hemisphere (Briedis et al. 2016). During their annual cycle, flycatchers spend about three months at breeding sites where birds reproduce and undergo a complete body moult before departing for autumn migration (Cramp and Perrins 1993). For the greater part of the year birds reside in sub-Saharan Africa, where approximately five months are spent at the non-breeding residency sites (Briedis et al. 2016). During the non-breeding period the species is known to feed solely on invertebrates, but little is known about habitat use and preferences (Cramp and Perrins 1993). However, we might expect that inhabiting mesic habitats should be advantageous over residing in xeric habitats as the former offer better feeding opportunities (Studds and Marra 2007).

With this study we aim to narrow the gap in our understanding of full annual cycles in animal ecology (Marra et al. 2015) by linking summer–winter–summer events in a long-distance migratory bird. We couple an experimental approach with observational data to unravel the links between different parts of the annual cycle by combining breeding monitoring, tracking by light-level geolocators and stable isotope analyses of winter-grown tissues. By doing so, we are able to follow individual passerine birds throughout the full annual cycle and asses the magnitude of carry-over effects from the breeding season to autumn migration, the non-breeding period, spring migration, and the following breeding period as well as from the non-breeding season to spring migration and the subsequent breeding season. As the non-breeding period in collared flycatchers is supposedly less time-constrained (Briedis et al. 2016), we predict that (i) parental investment will affect autumn migration schedules via carry-over effects, but the costs of breeding may be overcome during the non-breeding residency, rather than accumulate further (Senner et al. 2014). Therefore, (ii) spring migration schedules and the consecutive breeding period will be more dependent on the non-breeding habitat conditions, rather than the previous parental investment.

Methods

We studied collared flycatchers at two localities in the Czech Republic approximately 30 km apart (site Dlouhá Loučka: 49°50′N, 17°13′E, site Kosíř: 49°32′N, 17°04′E). In spring flycatchers arrive starting from the second decade of April (Briedis et al. 2016) and the earliest clutches are initiated in late April or early May. At both sites birds breed in nest boxes situated mainly in mixed deciduous woodlands. Nest boxes were regularly monitored throughout the breeding season and nearly all breeding birds were captured and marked with aluminium rings while feeding the nestlings. Site Dlouhá Loučka is under heavy predation pressure by edible dormouse Glis glis; therefore, we protected the nest boxes by applying plastic foil, approximately 50 cm wide, around the trees roughly 50 cm above and below the nest boxes.

Geolocator deployment and retrieval

Field work was carried out during three breeding seasons from 2013–2015. In 2013 and 2014 we attached geolocators (model GDL2.0, Swiss Ornithological Institute) to the backs of adult birds using flexible 24 mm long leg-loop harnesses made from 1 mm thick silicone or neoprene cords. Geolocators measured ambient light intensity every minute and stored maximum values in 5 min intervals. To reduce potential shading of the light sensor by birds' feathers, all devices were equipped with a 7 mm long light stalk. Each device weighted approximately 0.6 g including the harness and light stalk (i.e. < 5% of the body mass of collared flycatchers).

In 2013 at Dlouhá Loučka we deployed a total of 69 geolocators on breeding birds (33 males, 36 females) during late stages of their respective breeding cycles (last days of feeding nestlings in the nest boxes). In 2014 we deployed a total of 165 geolocators (157 males, 8 females) at Kosíř where birds were captured and equipped with the devices upon their arrival at the site before the onset of breeding (n = 139) and during nestling provisioning (n = 26).

In the years following the deployment of the devices, we conducted extensive re-trappings of the returning birds before and during the breeding season. In 2014 at Dlouhá Loučka we recovered 28 (40.5%, 14 males, 14 females) of the 69 deployed geolocators. One additional device (male) was recovered in 2015 accounting for a total recovery rate of 42%. In 2015 at Kosíř we recovered 29 geolocators (17.6%, all males) and one additional device from a male was recovered in 2016 (total recovery rate: 18.2%). The relatively low recovery rate at Kosíř may at least partly be explained by the deployment of devices on birds before the onset of breeding, as not all birds that were fitted with geolocators bred in the nest boxes in 2014 and/or 2015. Since all captured males were fitted with geolocators at Kosíř in 2014, we were not able to compare return rates of tagged and untagged birds. At Dlouhá Loučka the geolocators had no apparent effect on return rates of the tagged individuals compared to the control group of ringed-only birds (return rate of untagged individuals = 45.5%, $\chi^2 = 0.09$, $p = 0.76$).

Brood size manipulation

To disentangle true carry-over effects from the intrinsic quality of individuals, during the 2014 field season at Kosíř we conducted a brood size manipulation experiment by adding or subtracting one chick to/from the initial brood. Nests with the same hatching date were treated in pairs by randomly moving one chick from one nest to another. The manipulation took place on day two or three after the eggs had hatched. In total, 104 nests (52 pairs) were experimentally manipulated. Adult males were equipped with geolocators at 46 nests with increased brood size and 44 nests with decreased brood size. However, this represents only 86 individuals, since four of those males were polygynous and caught on two nests. We obtained migration and non-breeding residency data from the geolocation data of seven individuals with reduced broods (8/7 chicks = 1 case, 7/6 = 1, 6/5 = 1, 5/4 = 1, 4/3 = 2, 3/2 = 1) and nine individuals with increased brood size (5/6 chicks = 2 cases, 6/7 = 7, including one polygynous male that also took care of another nest with increased brood size 3/4).

Assessment of non-breeding conditions

Upon geolocator retrieval we collected feather samples from all previously tagged birds. We used stable isotope ratios of non-exchangeable hydrogen (δ2H) measured from tertial feathers moulted at the non-breeding sites (Svensson 1992) to assess the non-breeding conditions. Low δ2H values should indicate that during the non-breeding period birds resided and moulted feathers at regions with high precipitation (Hobson et al. 2012). Such areas of high water availability are known to accommodate increased quantities of invertebrates (Studds and Marra 2007), thus providing better feeding opportunities.

Feather samples were cleaned of surface oils and contaminants using a 2:1 chloroform–methanol solution and then dried in a drying oven over 24 h at 50 °C. From each feather sample, we placed a subsample of 1 mg (± 0.1 mg) in a silver foil capsule (IVA Analysetechnik e.K. Meerbusch, Germany) and then analysed the samples as described in Popa-Lisseanu et al. (2012) and Voigt et al. (2012). Briefly, feather samples were placed in the autosampler (Zero Blank autosampler; Costech Analytical Technologies Inc., Italy) of the elemental analyser (HT Elementaranalysator HEKAtech GmbH, Wegberg, Germany). Before combustion, samples were flushed in the autosampler for at least 1 h with chemically pure helium (Linde, Leuna, Germany). We used a Delta V Advantage isotope ratio mass spectrometer (ThermoFischer Scientific, Bremen, Germany) that was connected via an interface (Finnigan Conflo III, ThermoFisher Scientific, Bremen, Germany) with the elemental analyser. Using laboratory keratin standards with known stable isotope ratios of the nonexchangeable portion of hydrogen, we were able to report only stable isotope ratios of the non-exchangeable hydrogen in feather keratin (Popa-Lisseanu et al. 2012). The keratin standards used were cross-validated and referenced to keratin standards from Wassenaar & Hobson, i.e. we analysed our laboratory standards in the Stable Isotope Laboratory of Environment Canada, Saskatoon, using the offline steam equilibration method as described in detail in Wassenaar & Hobson (Wassenaar and Hobson 2000; Wassenaar and Hobson 2003). Analytical precision based on the repeated analyses of laboratory keratin standards was always better than 1.26 ‰ (one standard deviation of mean ratios).

Data analyses

We determined sunrise and sunset times within the recorded geolocator light data using 'GeoLocator' software (Swiss Ornithological Institute). Non-breeding sites and migratory departure and arrival times were determined with R-package 'GeoLight' v 1.03 following the standard procedures outlined by Lisovski & Hahn (2012) setting the 'changeLight' function parameters to q = 0.85, days = 3. Time of Sahara crossing was determined by carefully inspecting daily patterns of raw light recordings and searching for days with periods of uninterrupted maximal light intensities throughout the day, which indicate non-stop diurnal flight, characteristic of a desert crossing (Adamík et al. 2016). Migration distance for each individual was measured as a great circle (orthodromic) distance between the respective breeding and non-breeding sites (using the median position within the non-breeding residency site).

We used general linear models to identify if there was an effect of study year (and accordingly study site), birds' age and sex on the timing of annual events (e.g. breeding, onset of migration, Sahara crossing, etc.). Analyses revealed that study year was a significant predictor for timing of breeding, departure from the breeding site, arrival at the non-breeding site, and breeding the following year (Appendix 5 Table S1), while age was a significant predictor only for the timing of breeding in the first year. Sex had no effect on the dependent variables (i.e., no protandry) therefore, we pooled male and female data. For further analyses we centred the timing of annual events relative to the average first egg's laying date in each year (2013: 10 May, SD = 8.53, n = 115, 2014: 4 May, SD = 7.33, n = 125), thus compensating for the year effect on the consecutive parts of the annual cycle. Only the first clutch of each individual was considered, omitting any replacement clutches.

To test for carry-over effects of breeding effort on the timing of consecutive parts of the annual cycle we categorized all birds according to their breeding performance. This was done due to the relatively low variation in the number of fledged nestlings, which did not allow us to fully explore the costs associated with rearing a high or low number of young (but see Appendix 5 Figure S1 for regression analyses of the number of fledglings against the annual schedule variables). Each individual was assigned to one of the two groups depending on the number of nestlings fledged – above or below the average (5.4 ± 1.4 SD fledged nestlings, n = 30). Further analyses on how breeding effort influenced the timing of consecutive parts of the annual cycle were done using these two categories. We excluded all individuals that fledged zero nestlings due to adverse weather or predation as the nest losses may have happened at different stages of the breeding season and the further whereabouts of these individuals were unknown. Some individuals may have attempted to have a replacement clutch (e.g., outside of our nest boxes) while others may not, thus not allowing for the accurate evaluation of their breeding effort.

Sample sizes of timing data for different stages of the annual cycle differed due to technical issues with the geolocators (typically lower sample sizes for spring events due to limitations of the geolocators' batteries' life span) or the inability to determine the timing of certain events due to high noise in the recorded light data (n = 2 cases).

Statistical tests were performed in R version 3.3.1 (R Core Team 2016). We assessed the timing of spring events in relation to the non-breeding conditions (δ2H values) and previous parental investment using general linear models. We calculated the unbiased Cohen's d values and their confidence intervals according to Nakagawa

& Cuthill (2007) accounting for small sample sizes.

Results

Brood size manipulation

The comparison of annual migration schedules of experimentally manipulated birds revealed no significant differences in timing at any stage of the annual cycle between the males whose brood size was increased (average fledged: 6.1 ± 0.9 SD, n = 9) and those with reduced broods (averaged fledged: 4.1 ± 1.9 SD, n = 7; t-test: $t_8 = 2.56$, $p = 0.03$; Table 1). Nor did we find a statistically significant difference between the two treatment groups regarding migration durations in autumn or spring, non-breeding residency duration or total migration distance. However, the high Cohen’s d effect size values for timing of the Sahara crossing in spring (d = 1.42, 95% CI [−0.43, 3.27]), arrival at the breeding site (d = 1.27; 95% CI [−0.54, 3.08]) and non-breeding residency duration (d = 0.94, 95% CI [−0.80, 2.68]) suggest that birds with increased brood sizes spent less time at the non-breeding sites and migrated earlier in spring.

Absolute parental investment

When looking at the absolute fledgling numbers (not considering brood manipulation) as a proxy for parental investment, we found that individuals that fledged a higher number of nestlings (average: 6.3 ± 0.5 SD, n = 18) underwent all stages of autumn migration later than those fledging fewer nestlings (average: 4.0 ± 1.0 SD, n = 12; t-test: $t_{14} = 7.24$, $p < 0.001$; Table 2). The timing difference between the two groups was significant for arrival at the non-breeding site ($p = 0.007$) with birds fledging more young arriving on average 10 days later. The opposite was observed regarding the timing of spring migration – birds that

Table 1. Differences in migration and non-breeding parameters between collared flycatcher males whose brood sizes were experimentally manipulated before tracked migration. Values are given as average ± SD with sample sizes in parentheses. The presented dates were back-calculated from within-year deviations from mean laying date.

Seasonal variable	-1 chick	+1 chick	F	df	p	Cohens’s d [95% CI]
Departure breeding site	8 Aug ± 13 d (7)	6 Aug ± 9 d (9)	0.082	1, 14	0.778	0.14 [−1.02, 1.29]
Sahara crossing autumn	9 Sep ± 10 d (7)	5 Sep ± 10 d (9)	0.667	1, 14	0.428	0.39 [−0.77, 1.51]
Arrival non-breeding site	2 Oct ± 11 d (7)	6 Oct ± 10 d (9)	0.573	1, 14	0.462	−0.36 [−1.52, 0.80]
Mig. duration autumn	55.9 ± 12.4 d (7)	61.3 ± 10.7 d (9)	0.897	1, 14	0.360	−0.45 [−1.62, 0.72]
Non-breeding residency	156.7 ± 10.6 d (3)	145.1 ± 11.2 d (7)	2.278	1, 8	0.170	0.94 [−0.80, 2.68]
δ^2H of winter-grown feathers	−51.8 ± 10.8 (6)	−48.2 ± 6.5 (9)	0.664	1, 13	0.430	−0.39 [−1.55, 0.78]
Migration distance	7372 ± 588 km (7)	7075 ± 502 km (9)	1.075	1, 14	0.317	0.49 [−0.68, 1.66]
Departure non-breeding site	8 Mar ± 10 d (3)	3 Mar ± 9 d (7)	0.637	1, 8	0.448	0.50 [−1.18, 2.18]
Sahara crossing spring	19 Apr ± 15 d (3)	6 Apr ± 4 d (7)	5.216	1, 8	0.052	1.42 [−0.43, 3.27]
Arrival breeding site	3 May ± 9 d (3)	23 Apr ± 6 d (7)	4.137	1, 8	0.077	1.27 [−0.54, 3.08]
Mig. duration spring	55.7 ± 13.2 d (3)	51 ± 9.4 d (7)	0.417	1, 8	0.536	0.40 [−1.27, 2.07]

Table 2. Differences in migration and non-breeding parameters between individuals whose fledgling numbers were below and above the study average of 5.4. Values are given as average ± SD with sample sizes in parentheses. The presented dates were back-calculated from within-year deviations from mean laying date (see Methods for more details). Significant values are given in bold font.

Seasonal variable	Fledged – below 5.4	Fledged – above 5.4	F	df	p	Cohens's d [95% CI]
Departure breeding site	30 Jul ± 10 d (11)	7 Aug ± 13 d (18)	2.97	1, 27	0.096	−0.64 [−1.45, 0.17]
Sahara crossing autumn	5 Sep ± 8 d (12)	11 Sep ± 10 d (18)	2.95	1, 28	0.097	−0.62 [−1.41, 0.16]
Arrival non-breeding site	28 Sep ± 7 d (12)	8 Oct ± 10 d (18)	8.46	1, 28	**0.007**	−1.05 [−1.87, −0.24]
Mig. duration autumn	59.8 ± 12.2 d (11)	62 ± 9.0 d (18)	0.31	1, 27	0.584	−0.21 [−1.00, 0.58]
Non-breeding residency	163.6 ± 10.9 d (5)	149.2± 10.2 d (13)	6.88	1, 16	**0.018**	1.31 [0.14, 2.49]
δ^2H of winter-grown feathers	−49.4 ± 10.4 (11)	−53.1 ± 5.9 (17)	1.44	1, 26	0.241	0.46 [−0.33, 1.24]
Migration distance	7089 ± 624 km (11)	6986 ± 468km (17)	0.24	1, 26	0.629	0.18 [−0.61, 0.98]
Departure non-breeding site	10 Mar ± 10 d (5)	7 Mar ± 10 d (14)	0.28	1, 17	0.604	0.26 [−0.77, 1.30]
Sahara crossing spring	19 Apr ± 11 d (5)	10 Apr ± 4 d (14)	8.37	1, 17	**0.010**	1.44 [0.28, 2.60]
Arrival breeding site	30 Apr ± 10 d (5)	25 Apr ± 5 d (14)	0.70	1, 17	0.416	0.42 [−0.63, 1.46]
Mig. duration spring	50.8 ± 12.9 d (5)	51.5 ± 8.4 d (13)	0.02	1, 15	0.899	−0.06 [−1.13, 1.01]

fledged more young in the previous year underwent all stages of the spring migration earlier with a significant difference in timing of the Sahara crossing ($p = 0.01$). We did not find significant differences in migration durations in autumn or spring, nor in total migration distance. However, birds that fledged more young spent on average 14 days fewer at the non-breeding residency areas ($p = 0.018$, Table 2) allowing for their advanced spring migration. Furthermore, Cohen's d effect size values (Table 2) suggest a moderate to high difference between the two groups in timing of all key annual migration stages, except for departure from the non-breeding sites. Individual schedules are summarized in Figure 1.

Regression analyses between the timing of different annual events (centred to each year's mean laying date) revealed no significant correlation between breeding time and the timing of any of the further stages throughout the annual cycle, nor the timing of breeding the next year (Fig. 2). When not considering the breeding time, there was a positive relationship between the timing of previous and all following stages of the annual cycle with positive slopes in all but two cases (arrival at the non-breeding site – Sahara crossing in spring, breeding site departure – Sahara crossing in spring, Fig. 2). These relationships were statistically significant ($p < 0.05$) in 9 out of 21 cases (Fig. 2). The results were very similar when the timing of each event was centred to the annual mean of that event instead of to the annual mean laying date (see Appendix 5 Figure S1). Furthermore, we found a pronounced "domino effect" where the timing of each annual stage had the strongest impact on the timing of the following one and the interactions got weaker with increasing timespan between the events ($F_{1,26} = 11.48$, $r^2 = 0.28$, $p = 0.002$, Figure 2 *inset*). Thus, there was a stronger relationship of timing between intra-seasonal events than between inter-seasonal events.

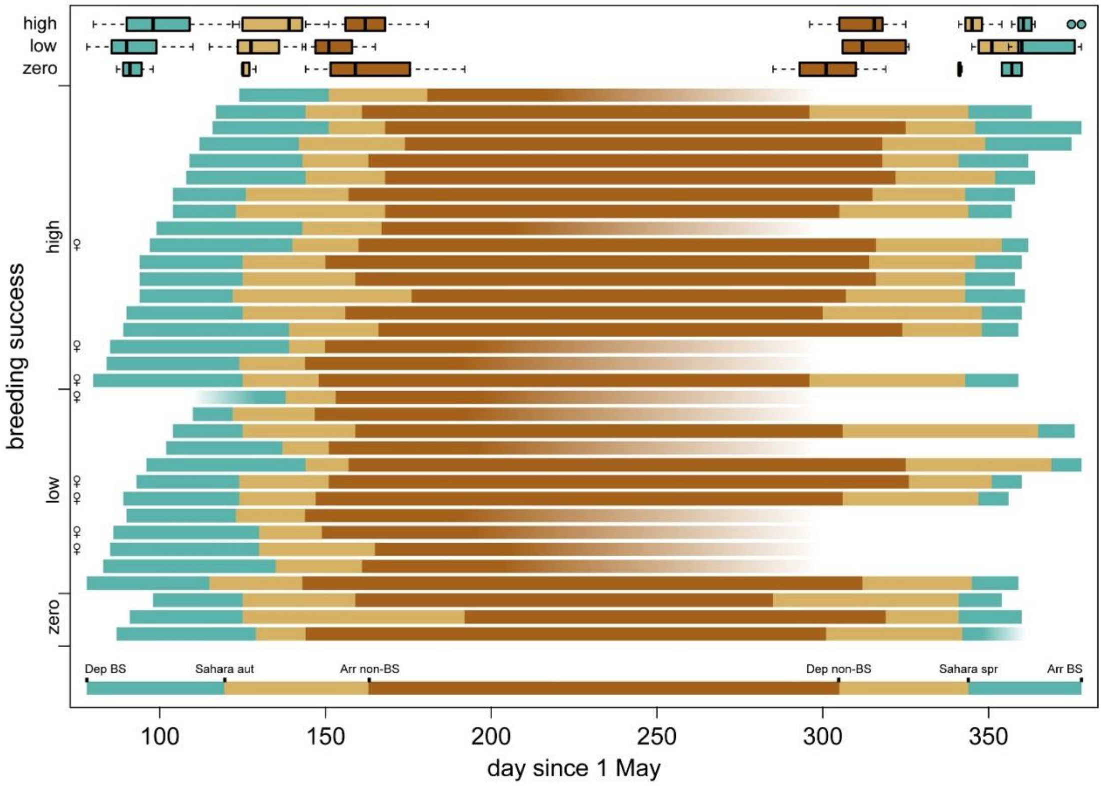

Figure 1. Migration schedules of the 33 geolocator-tracked collared flycatchers according to their breeding effort (number of fledglings below or above the average). Individual level (solid lines) and pooled category level (boxplots) data are presented. Migration schedules include departure from the breeding site (Dep BS), Sahara crossing in autumn (Sahara aut), arrival at the non-breeding site (Arr non-BS), departure from the non-breeding site (Dep non-BS), Sahara crossing in spring (Sahara spr) and arrival at the breeding site (Arr BS). Faded lines indicate lack of data due to failure of the geolocator's battery or uncertainty of the timing of a particular event. Only individuals with known fledgling numbers are shown.

Stable isotopes

Overall, we found no difference in spring migration departure time between individuals residing at drier or wetter non-breeding areas (respectively, high and low δ2H values; Fig. 3a). However, at each consecutive step of the spring migration and the following onset of breeding, collared flycatchers from wetter habitats were more advanced when compared to individuals of drier non-breeding habitats (Fig. 3a–d, Table 3a–d). Furthermore, we found that the time interval between the spring migration departure and onset of egg laying was significantly longer for individuals originating from drier non-breeding sites (Fig. 3f, Table 3f). This pattern was largely caused by the shorter time it took to prepare for breeding and start egg laying after arrival for the individuals originating from non-breeding areas of more depleted δ2H values (Fig. 3e, Table 3e). The impact of the previous parental investment on the timing of the following breeding period was marginal, and the onset of breeding was more dependent on the amount of precipitation at non-breeding areas (inferred from feather δ2H values).

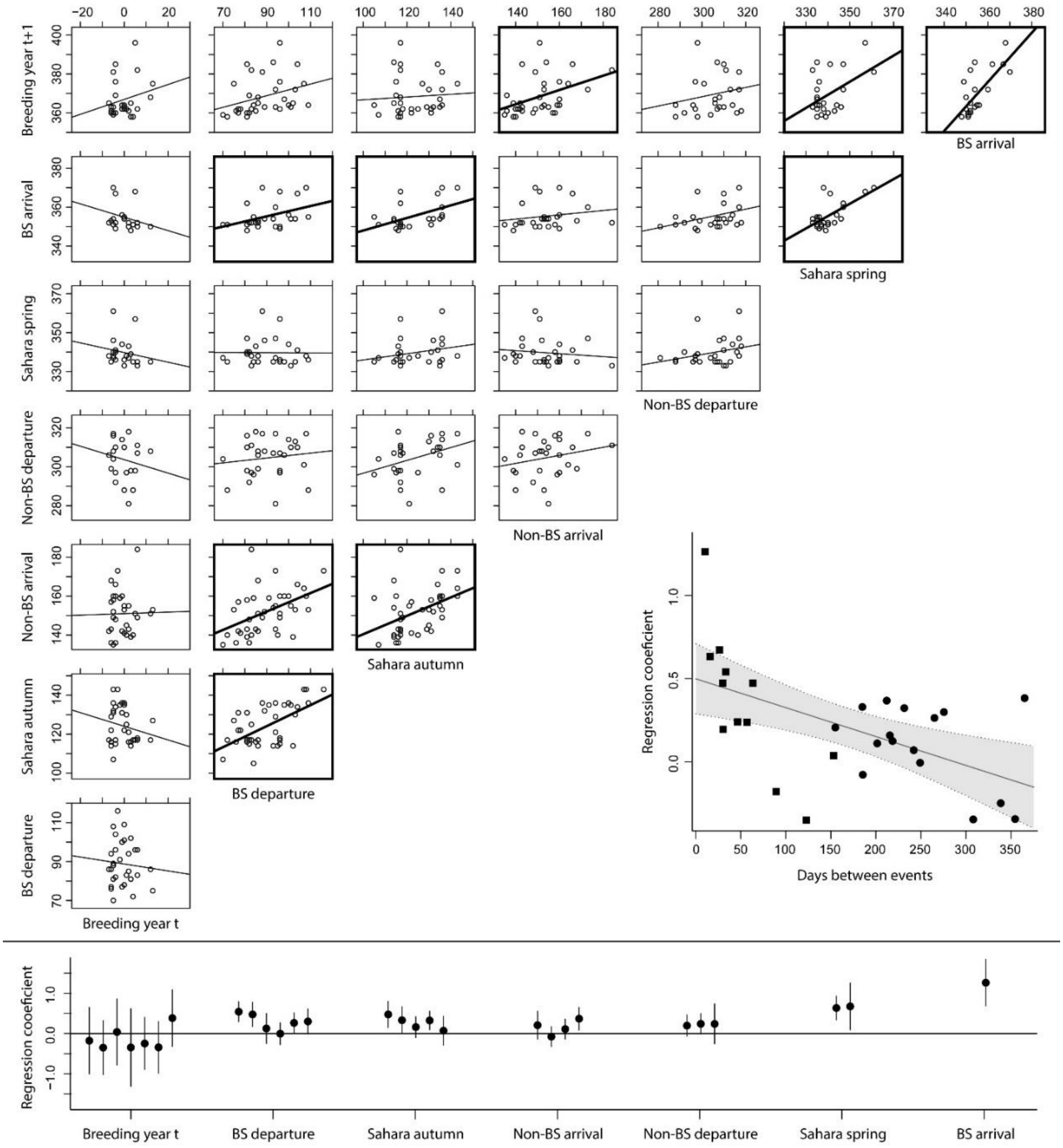

Figure 2. Regression analyses showing the relationship between the timing of different parts of the annual cycle in collared flycatchers, including the onset of egg-laying in the first study year (breeding year t), departure from the breeding site (BS departure), Sahara crossing in autumn (Sahara autumn), arrival at the non-breeding site (Non-BS arrival), departure from the non-breeding site (Non-BS departure), Sahara crossing in spring (Sahara spring), arrival at the breeding site (BS arrival) and the onset of egg-laying in the second study year (Breeding year t+1). Statistically significant ($p < 0.05$) regressions are highlighted in bold. Values represent within-year deviations from mean laying date. *Inset* – the strength of the "domino effect" between consecutive parts of the annual cycle expressed as the relationship between regression coefficients of individual regressions and the timespan between the events ± 95% CI (shaded area). Squares (■) denote regression coefficients of intra-seasonal events and circles (●) denote regression coefficients of inter-seasonal events. *Lower panel* – regression coefficients ± 95% CI for each annual event in relation to all following events. Points left to right within each column correspond to rows bottom to top in the main figure.

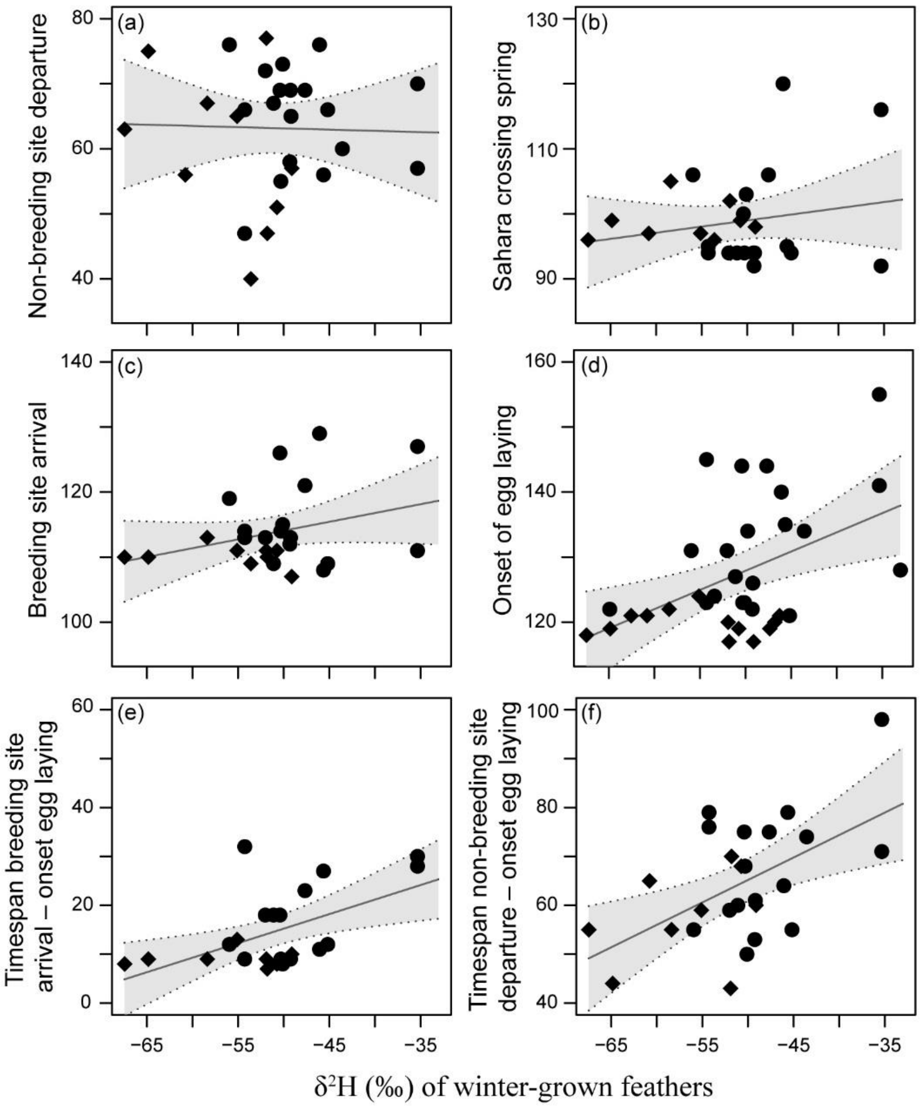

Figure 3. Relationship between δ2H values of collared flycatcher feathers grown at the African non-breeding grounds and the timing of spring events. The timing of events is given as Julian dates from 1 January (a–d), and timespans between events in number of days (e–f). Diamonds (♦) denote data from 2013–2014 and circles (●) denote data from 2014–2015 non-breeding seasons. Linear models are depicted by solid lines with 95% CI (shaded area).

Discussion

In this study we linked summer–winter–summer events in the long-distance migratory collared flycatcher and evaluated carry-over effects of parental investment and non-breeding conditions. Our hypothesis that the experimental increase of brood size would result in delayed autumn migration was not supported as we found no difference between the experimental groups of reduced and enlarged brood sizes. However, when looking at the parental investment (measured as the total number of fledglings), we found that higher parental investment was associated with delayed autumn migration, shorter non-breeding residency and advanced spring migration. The magnitude of carry-over effects from one stage to another faded with increasing timespan between the stages along the annual cycle. We also showed that non-breeding conditions affect the timing of

Table 3. Summary statistics of models showing a relationship between the timing and duration of spring events and non-breeding conditions (δ^2H) and parental investment (above or below the population average) in the previous breeding season. Significant values are given in bold font.

		Estimate	**SE**	**t-value**	**p-value**
(a)	*Departure non-breeding site* (df = 15)				
	Intercept	48.788	17.357	2.811	0.013
	δ^2H	-0.26	0.33	-0.789	0.443
	Parental investment$_{\text{(below)}}$	4.223	5.16	0.818	0.426
(b)	*Sahara crossing spring* (df = 15)				
	Intercept	112.837	11.106	10.16	4.05e-08
	δ^2H	0.304	0.211	1.443	0.169
	Parental investment$_{\text{(below)}}$	8.779	3.302	2.659	**0.018**
(c)	*Arrival breeding site* (df = 15)				
	Intercept	131.331	10.97	11.972	4.46e-09
	δ^2H	0.364	0.208	1.748	0.101
	Parental investment$_{\text{(below)}}$	3.672	3.262	1.126	0.278
(d)	*Onset of egg laying year t+1* (df = 22)				
	Intercept	152.894	11.587	13.195	6.29e-12
	δ^2H	0.548	0.216	2.536	**0.019**
	Parental investment$_{\text{(below)}}$	1.331	3.477	0.383	0.706
(f)	*Timespan arrival breeding site–onset of egg laying* (df = 14)				
	Intercept	121.778	21.431	5.682	5.66e-05
	δ^2H	1.144	0.405	2.826	**0.013**
	Parental investment$_{\text{(below)}}$	-0.592	6.395	-0.093	0.928
(e)	*Timespan departure non-breeding site–onset of egg laying* (df = 14)				
	Intercept	39.818	9.977	3.991	0.001
	δ^2H	0.528	0.189	2.799	**0.014**
	Parental investment$_{\text{(below)}}$	-0.245	2.977	-0.082	0.935

the following breeding period more strongly than the previous parental investment. Individuals originating from wetter non-breeding areas with more depleted δ2H values migrated at a similar time as individuals from more arid habitats, but the former required less time to initiate breeding after the completion of spring migration.

Remarkably, we found similar migration timing for both males and females. This questions whether protandry has been adopted as a migratory strategy in the collared flycatcher. Until now, there has been little evidence for simultaneous spring migration of males and females in songbirds (Rubolini et al. 2004; Tøttrup and Thorup 2008; Saino et al. 2010). Most studies looking into protandry thus far have used migratory passage dates acquired from ringing data at specific locations. Individual-based tracking may open new perspectives by providing insights into full migration schedules of individual birds as they complete different stages of their annual migrations (e.g. Schmaljohann et al. 2016).

Reproduction is an energy- and time-consuming process. Rearing a lower number of chicks should be less energy-demanding, but the total amount of time necessary to complete the breeding cycle should be similar. Previous experimental manipulations of clutch size in the collared flycatcher have shown that an enlarged clutch carries consequences for male secondary sexual traits and results in the reduction of subsequent fecundity (Gustafsson and Sutherland 1988; Gustafsson et al. 1995). However, little is known about the consequences of breeding effort on migration and the non-breeding period, especially in songbirds.

A study of Cory’s shearwaters showed that experimentally-induced breeding failure resulted in the early onset of autumn migration (Catry et al. 2013). Experimentally-manipulated birds were freed from energetic and time-dependent costs of reproduction alike and theoretically could engage in southbound migration before their conspecifics had completed their respective breeding cycles. These results contradict our findings since we did not observe differences in autumn migration schedules between our two experimental groups. This raises the question of whether changing brood size by one chick in a multi-egg laying species carries consequences for the annual schedules of migrants. It could be that the total number of chicks fledged may better reflect the costs of breeding if they carry over to subsequent annual cycle phases. Another reason for the lack of unambiguous differences between the two experimental groups may be the limited sample size in our study. Furthermore, we looked only at male annual schedules in relation to our experimental manipulation and parental investment by provisioning of young may differ between the sexes.

When looking at parental investment as the total number of fledglings, we found a negative effect of the absolute number of chicks fledged on autumn migration schedules. Higher parental investment has been reported to delay autumn migration in numerous water birds, e.g. Cory’s shearwater (Catry et al. 2013), brent goose *Branta bernicla* (Inger et al. 2010), and black-legged kittiwake *Rissa tridactyla* (Bogdanova et al. 2011), but there is little evidence of this effect in passerines (but see Mitchell et al. 2012). Theoretical models indicate that the onset of migration highly depends on an individual’s body condition (McNamara et al. 1998). It is important to note that collared flycatchers undergo a complete body moult before commencing autumn migration (Stresemann and Stresemann 1966). Feather moult is a highly energetically-demanding process and there must be trade-offs between shortening the duration of moult and increasing the quality of newly-grown feathers (Vágási et al. 2012). It is likely that the energy expenditure of parental care has consequences which influence moult, further affecting the onset of autumn migration. Such interactions could explain why the individuals fledging more young departed later from the breeding sites.

Interestingly, we found no relationship between the timing of breeding and other parts of the annual cycle. Mitchell et al. (2012) and Saino et al. (2017) reported a positive correlation between the completion of breeding and autumn migration departure in savannah sparrows *Passerculus sandwichensis* and barn swallows *Hirundo rustica*, respectively. Similarly, an elongated breeding period was associated with delayed autumn departure in Manx shearwaters *Puffinus puffinus* (Fayet et al. 2016), highlighting the time-dependent costs of reproduction. Late-nesting wood thrushes *Hylocichla mustelina* initiated their post-breeding moult later than early-breeding conspecifics, possibly resulting in delayed departure for autumn migration, but no effect was found on the timing of arrival at their non-breeding site (Stutchbury et al. 2011). In wood thrushes, late breeding was also associated with higher reproductive success. The positive relationship between high breeding effort and delayed autumn departure coincides with our findings. Thus, energetic and time-dependent carry-over effects of parental investment could be more important determinants for the onset of autumn departure than the timing of the onset of breeding.

A pivotal finding in our study was that higher parental investment not only delayed autumn migration schedules, but was also associated with a shorter non-breeding residency. Fayet et al. (2016) have shown that experimentally increasing the duration of provisioning for young delayed autumn migration departure and resulted in a shorter non-breeding residency period in Manx shearwaters. Although these findings come from a long-lived seabird, they are in line with our findings concerning the non-breeding ecology of a short-lived passerine bird.

Individuals with higher previous breeding effort resided at the non-breeding sites for a shorter period and caught up time-wise with individuals of lower breeding effort. This may at least partially be explained by non-breeding conditions, as birds with higher parental investment on average resided in wetter areas with more depleted δ2H values (Table 2). Thus, seasonal matching of habitat quality seems to play an important role in the annual cycle ecology of migratory birds (Gunnarsson et al. 2005). Dominant individuals are known to eliminate subordinates from optimal non-breeding habitats in American redstarts *Setophaga ruticilla* (Norris et al. 2004). This pattern further translates into better body condition, advanced spring migration and higher breeding performance of dominant individuals. Despite later arrival at the non-breeding areas, collared flycatchers with higher previous breeding effort occupied wetter, seemingly better-quality habitats during the non-breeding period resulting in shorter total non-breeding residency duration, advanced spring migration and earlier breeding the following spring.

We also observed a pronounced “domino effect” (Piersma 1987) between consecutive parts of the annual cycle. Such a pattern is expected to arise under the time-minimization migration strategy (Hedenström 2008). When adopting this strategy, individual birds should travel as fast as possible given their body condition and environmental conditions, therefore making it difficult to overcome the costs of being late at a particular stage of migration. However, we also observed that the relationship was stronger between annual cycle stages directly following each other and gradually faded along the annual cycle with increasing timespan between the stages (Fig. 2 inset). The strong links found within (rather than across) migration seasons suggest that the “domino effect” can be overcome during the non-breeding season. Collared flycatchers that had higher breeding effort migrated later in autumn, but earlier in spring, supporting this hypothesis.

Carry-over effects from non-breeding areas are known to influence the spring migration schedule and following breeding period in several species (Marra et al. 1998; Saino et al. 2004; Norris et al. 2004; Studds and Marra 2005; Tonra et al. 2011; Rockwell et al. 2012; Paxton and Moore 2015), coinciding with our findings. Even though the non-breeding conditions only had a minor influence on the timing of early stages of spring migration, flycatchers originating from more arid non-breeding habitats took longer to initiate breeding after their arrival at the breeding sites (Fig. 3). This suggests that flycatchers may have followed a time-minimization migration strategy (Hedenström 2008), but those individuals of poorer body condition (due to sub-optimal non-breeding sites) suffered penalties of slightly slower migration speed, followed by an elongated period to regain the body condition necessary for breeding. On the contrary, Pedersen et al. (2016) found no carry-over effects of non-breeding habitat quality on late stages of spring migration and the following breeding period in red-backed shrikes *Lanius collurio*. Similarly, no carry-over effects of non-breeding habitat quality were found in yellow warblers *Setophaga petechial* (Drake et al. 2014), magnolia warblers *Setophaga magnolia* (Boone et al. 2010), and Hudsonian godwits *Limosa haemastica* (Senner et al. 2014). Such contradicting results across species suggest that carry-over effects of non-breeding conditions may not be limiting for all species and populations, or may vary in their detectability.

Spring migration and the following breeding season might be affected by a combination of factors, like previous breeding effort and conditions experienced during the non-breeding residency. In the present study, we showed that previous breeding effort had a marginal influence on the timing of the following breeding period, while residing in wetter non-breeding areas translated into early breeding. Long-lasting carry-over effects of previous breeding effort have been shown to influence following breeding attempts in migratory birds (Inger et al. 2010; Catry et al. 2013). On the other hand, Bogdanova et al. (2011) reported no differences in spring migration schedules caused by previous breeding experience. Similar to our study, Ouwehand and Both (2017) demonstrated that the rank order of birds from autumn migration was disrupted during the non-breeding period and the timing of spring migration was not related to the timing of autumn migration in the closely-related pied flycatchers *Ficedula hypoleuca*. Carry-over effects from various parts of the annual cycle may play different roles in population dynamics of species with different life history strategies. Therefore, it is important to consider full annual cycles to gain a better understanding of carry-over effects operating in animal populations.

It is likely that the recent decline of long-distance migrants (Vickery et al. 2014) has been caused by the complex interaction of events and processes taking place at temperate breeding grounds, tropical non-breeding areas and during migration between them. Our results indicate that both energetic and time-dependent costs of reproduction and conditions at the non-breeding grounds play key roles in altering annual schedules and defining individual variation via carry-over effects. Linking summer–winter–summer events around the entire year can give us an in-depth insight into underlying processes driving animal population dynamics. This may open new perspectives in our understanding of the ecology of migratory animals and further be of service to conservation efforts. We hope that our study will stimulate more comprehensive animal ecology studies with respect to full annual cycles.

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Author contribution statement

MB, MKri, PA conceived and designed the study, MB, MKri, MKra, PA carried out the field work, CCV performed stable isotope analyses, MB analysed the data and led writing of the manuscript, all authors commented on and approved the final version of the manuscript.

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Appendix 5

Supplementary information for Chapter 7

Table S1. Summary statistics of general linear models of year, age and sex effect on schedules of the annual events of collared flycatchers.

		Estimate	SE	t–value	p–value
(a)	*First egg year t* (df = 38)				
	Intercept	4.329	1.613	2.684	0.011
	Year	−1.373	2.023	−0.679	0.502
	Age	5.346	1.664	3.212	0.003
	Sex	−2.704	2.276	−1.188	0.243
(b)	*Departure breeding site* (df = 39)				
	Intercept	85.967	3.510	24.491	2e−16
	Year	13.300	4.188	3.176	0.003
	Age	−3.883	3.193	−1.216	0.232
	Sex	0.748	4.880	0.153	0.879
(c)	*Sahara crossing autumn* (df = 40)				
	Intercept	129.379	3.674	35.217	2e−16
	Year	7.251	4.703	15.42	0.132
	Age	−4.514	3.572	−1.264	0.214
	Sex	−5.236	5.292	−0.989	0.329
(d)	*Arrival non-breeding site* (df = 40)				
	Intercept	150.635	3.750	40.167	2e−16
	Year	10.742	4.801	2.237	0.031
	Age	−3.041	3.647	−0.834	0.410
	Sex	−0.778	5.403	−0.144	0.886
(e)	*Departure non-breeding site* (df = 28)				
	Intercept	308.986	5.317	58.113	2e−16
	Year	6.336	5.076	1.248	0.224
	Age	−1.972	4.097	−0.481	0.634
	Sex	−4.653	6.657	−0.699	0.491
(f)	*Sahara crossing spring* (df = 27)				
	Intercept	346.886	3.849	90.122	2e−16
	Year	0.692	3.664	0.189	0.852
	Age	−2.273	3.019	−0.753	0.459
	Sex	−3.553	4.814	−0.738	0.468
(g)	*Arrival breeding site* (df = 25)				
	Intercept	358.331	3.201	111.953	2e−16
	Year	6.592	3.278	2.001	0.057
	Age	−4.163	2.564	−1.624	0.119
	Sex	−2.131	4.138	−0.515	0.612
(h)	*First egg year t+1* (df = 36)				
	Intercept	366.632	2.952	124.189	2e−16
	Year	11.482	3.969	2.893	0.007
	Age	−3.352	2.868	−1.169	0.251
	Sex	−0.465	4.355	−0.107	0.915

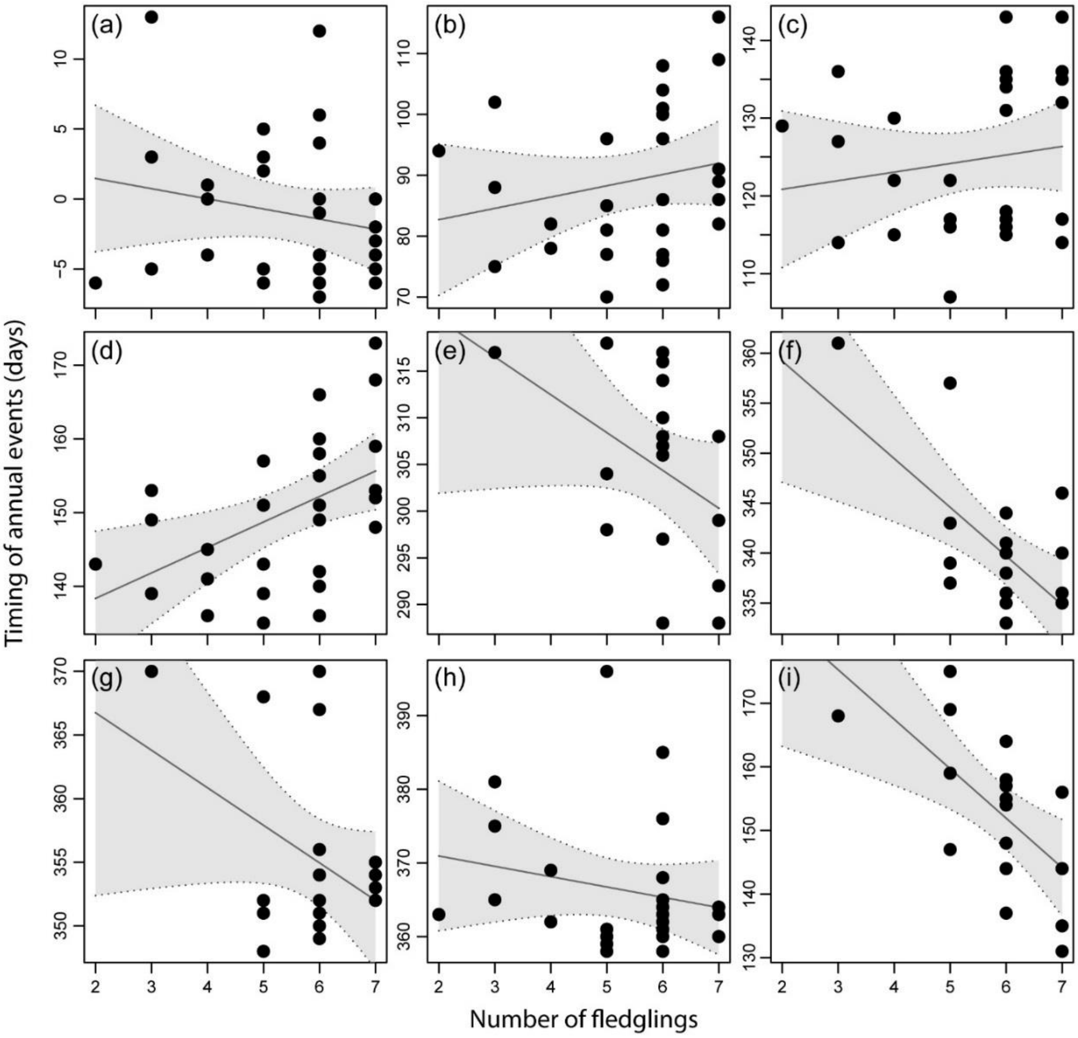

Figure S1. Relationship between fledgling numbers and timing of annual events (days since median onset of egg laying = 7 May) in collared flycatchers, including (a) onset of egg laying, (b) departure from the breeding grounds, (c) Sahara crossing in autumn, (d) arrival at the non-breeding grounds, (e) departure from the non-breeding grounds, (f) Sahara crossing in spring, (g) arrival at the breeding grounds, (h) onset of egg laying, and (i) non-breeding residency duration. Values represent within-year deviations from mean laying date. Linear models are depicted by solid lines with 95% CI (shaded area).

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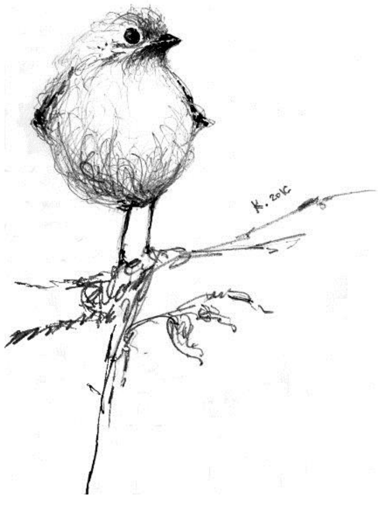

I expect that most people who skim through these pages will likely skip the main chapters and end up here instead. This is the only part of the thesis where birds are not the main focus. It’s about people! People who helped me along the way and made this work possible. That being said, there are several layers of gratitude that I would like to unpack here.

Bird-nerds

First, I would like to thank my superb supervisor Peter for giving me a chance and accepting my application. Working in the lab and field with you has been a real pleasure. Your support, passion for birds, and open-minded attitude made these four years exciting and inspiring. And thanks for helping me with so many other matters – whether it was serving as my personal translator on so many occasions or figuring out that the ‘garbage people’ are after me.

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Oskars might be the person to blame for getting me in all this mess. You were the one who reached out to me and made that phone call to my grandmother’s house back in 2005. I think even you did not anticipate that it will have such huge consequences and lead to me moving out of the country in order to peruse birds. Thanks for all your help through these years.

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Petr has to take some responsibility for why I applied for this PhD position in the first place. Seeing your name on the position announcement was very much assuring that I should at least give it a try as I still remembered your exciting talk from the SEEN meeting in Poland.

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Family – Ģimene (in Latvian)

My family deserves a big credit for getting me this far, therefore, I will address them in my mother tongue in the following lines.

Mamma, liels Tev paldies par nerimstošo atbalstu gan skolas laikā, gan vēlāk studiju gados. Tu nekad neiebildi un nemēģināji mani atrunāt no plāniem studēt bioloģiju, lai arī cik dīvaina (vismaz es noteikti bērnībā šī iemesla dēļ jutos nedaudz kā dīvainis pārējo vidū) vārētu likties kāda vēlme pētīt putnus. Bez Tavas piedalīšanās un atbalsta šis darbs noteikti nebūtu tapis.

Visnotaļ nozīmīgi daļu savas bērnības es pavadīju laukos pie vecmammas Ligitas. Tur arī dzima mana agrīnā interese par putniem. Paldies vecmammai, par uzticību, atļaujot man mazam puišelim, ‘spēlēties’ ar vectēva dārgo binokli, lai vērotu ķīvītes, dzērves, meža zosis un citus putnu sētmalē un netālajās pļavās.

Paldies arī opapam Leonam, kurš reiz dzimšanas dienā man pasniedza grāmatu “Latvijas ūdeņu putni”. Tā bija mana pirmā nopietnā putnu grāmata un palīdzēja spert plašu soli pretī putnu pasaules izzināšanai. Turklāt tās iekšpusē atradās anketa, ko arī 2004. gadā liktu lietā, lai kļūtu par Latvijas Ornitoloģijas biedrības biedru.

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Kārlis deserves a huge thanks for the wonderful flycatcher illustration that starts out this thesis (take a look if you somehow managed to miss it).

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Thanks – Paldies,
Mārtiņš

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Linking events through the annual cycle in migratory songbirds:

causes and consequences of different spatiotemporal strategies

Propojení fází ročního cyklu u tažných ptáků: příčiny a důsledky
rozdílných časoprostorových strategií

Summary of the Ph.D. Thesis / Autoreferát disertační práce

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Abstract

Each year animals move across and between continents to track seasonal changes in resource availability and abundance to improve their survival and reproductive opportunities. Birds represent one of the largest animal group that engage in these global-scale migration events. Afro-Palearctic bird migration system is estimated to facilitate more than 2 billion individual birds that link ecological communities of the two continents.

Recent advances in tracking technology, like light-level geolocators, have enabled us to follow even the smallest of individual migrants as they complete their annual cross-continental journeys. This has opened a new era in bird migration research allowing us to gain unique insights into spatiotemporal organization of full annual cycles of individual songbirds. Furthermore, these technological advances allow for estimation of migratory connectivity between breeding and non-breeding populations as well as linking spatially and temporarily distinct phases of the annual cycles of migratory birds.

In my dissertation I couple geolocator tracking with stable isotope signatures, breeding data, and environmental variables to unravel spatiotemporal migration strategies and identify the importance of carry-over effects operating in wild populations of long-distance migrants. I reveal how annual events are interlinked with one another and the environment on the level of individual birds, populations, and species. I use three Afro-Palearctic migratory birds – Tawny Pipit *Anthus campestris*, Collared Flycatcher *Ficedula albicollis*, and Semi-collared Flycatcher *F. semitorquata* – as model species.

Besides answering trivial questions of where and when each of the model species migrate, I found that there is a great deal of variation in the migration strategies among individuals and populations. Breeding site phenology is the main driver of migratory schedules on a population level, while individual variation in timing of migratory episodes are mediated via carry-over effects of previous breeding effort and conditions experienced at the non-breeding sites. Crossing of the Sahara Desert, which majority of the successful migrants accomplish in a single endurance flight, serves as a gateway between Europe and Africa for long-distance migratory birds. Only after the cross-desert flight, environmental and phenological cues can be picked up and used for accurate timing of spring migration and timely arrival for breeding.

Studies from the perspective of full annual cycles are still underrepresented in animal ecology research. The chapters comprising this dissertation adds only a drop in the vast pool of knowledge in animal migration ecology. However, such information is of topmost priority for understanding the drivers of population dynamics as many migratory species are currently declining.

Abstrakt

Každoročně živočichové podnikají dlouhé přesuny mezi kontinenty. Přizpůsobují se tak sezónním změnám v dostupnosti zdrojů a jejich početnosti, a to vše v zájmu přežití a snahy o reprodukci. Ptáci představují jednu z nejpočetnějších skupin, které podstupují takové globální migrační přesuny. Mezi Evropou a Afrikou se každoročně přesouvají více jak dvě miliardy ptáků.

Recentní pokroky ve vývoji sledovací techniky, jako například geolokátorů, nám umožnily sledovat pohyby mezi kontinenty i u těch nejmenších ptáků. Tento technický pokrok nám tak otevírá nové možnosti pro výzkum ptačí migrace a to na úrovni jedinců a organizace jejich celoročních cyklů. Dále tak můžeme lépe porozumět konektivitě mezi populacemi, tj. jak jsou různé populace propojeny na zimovištích a hnízdištích.

Za účelem odhalení časoprostorových migračních strategií u ptáků kombinuji, ve své disertační práci, hnízdní data a environmentální proměnné s daty získanými pomocí geolokátorů a analýzy stabilních izotopů z peří. Zároveň zhodnocuji význam tzv. carry-over efektů v průběhu ročního cyklu u dálkových migrantů. Na úrovni jedinců, populací a druhů odhaluji, jak jsou jednotlivé fáze ročního cyklu vzájemně propojené a také ovlivněné prostředím. Jako modelové druhy jsem použil tři dálkové migranty: lindušku úhorní Anthus campestris, lejska bělokrkého Ficedula albicollis a lejska černokrkého Ficedula semitorquata.

Vedle odpovědí na základní otázky typu kam a kdy každý z modelových druhů táhne, jsem zjistil, že je značná variabilita v migračních strategiích mezi jedinci i mezi populacemi. Například fenologie na hnízdišti byla hlavním faktorem určujícím načasování migrace napopulační úrovni, kdežto individuální rozdíly v časování jednotlivých migračních událostí byly poháněny carry-over efekty na základě předchozího hnízdního úsilí a také podmínkami, kterým byli jedinci vystaveni v průběhu tahu nebo na zimovišti. Dalším poznatkem je, že většina drobných pěvců překonává Saharu v jednom non-stop letu. Zdá se, že teprve po překonání této bariéry ptáci využívají environmentální a fenologické indikátory k doladění příletu na hnízdiště.

Studií, které sledují celoroční cyklus života živočichů, je stále poměrně poskrovnu. Poznatky, které představuji v jednotlivých kapitolách své dizertace, jsou pouze kapkou v moři vědomostí o migraci živočichů. Přesto jsou ale tyto informace klíčem k porozumění populační dynamiky celé řady tažných druhů a to zejména v souvislosti s recentním poklesem početností u mnohých dálkových migrantů.

Introduction

Every year billions of animals engage into a phenomenon we call migration. Among those, birds are especially praised for their remarkable migratory ability and diversity. An estimated 2.1 billion passerine and near-passerine birds migrate from Europe to sub-Saharan Africa each autumn (Hahn et al. 2009). This makes Afro-Palearctic migratory system the world's largest bird migration network (Moreau 1972; Newton 2008). Migratory birds link ecological communities of the two continents altering diversity and stability of the local communities (Bauer and Hoye 2014). They transform various trophic levels by foraging themselves as well as becoming prey for the resident animals.

Birds' annual cycles are optimized to the seasonal patterns of changing environmental conditions. Long-distance migratory birds travel thousands of kilometres between their temperate breeding grounds and tropical – sub-tropical non-breeding regions. By doing so they are able to track seasonal changes in resource availability and affect their survival (Thorup et al. 2017). They exploit the relatively short but productive summers of high latitudes to rise their young and (in some species) moult their feathers, and escape the unfavourable winter conditions by traveling to more hospitable regions which are typically found in lower latitudes.

Along their way migrants have to optimize their migration routes and schedules according to the environmental factors, like prevailing winds, temperatures, and food availability. Additionally, they have to cross inhospitable areas like deserts and seas where food, shelter and other vital resources are scarce or lack completely (Moreau 1961). Mortality during migration is typically higher compared to the stationary breeding and non-breeding periods (Sillett and Holmes 2002; Lok et al. 2015). Furthermore, young, inexperienced first-time migrants typically show higher mortality rates than experienced adult individuals (Newton 2008). Thus, local knowledge of suitable stopover sites capable of providing enough resources to fuel to the next flight bout is crucial.

The optimal migrations theory suggests that birds should minimize the energy expenditure and maximize the total migration speed i.e., minimize the total migration duration, when moving between different sites of residency (Alerstam 2011). Thus, in both seasons birds should follow the time minimization migration strategy and complete their migration swiftly (Hedenström 2008). Under a theoretically ideal scenario, an individual would complete its entire migratory journey in a single long-distance flight. This would allow to reduce the likelihood of morality and to outcompete conspecifics for early arrival. Typically, long-distance migrants cannot complete the entire length of the journey in a single flight and need to stop over, sometimes multiple times, for refuelling (Hedenström and Alerstam 1997) and/or due to unfavourable weather conditions (Tøttrup et al. 2012).

Our knowledge about the non-breeding populations is still relatively scarce. The concept of migratory connectivity (Webster et al. 2002) has really come about during the last few decades. Recent advances in individual-based tracking systems, have enabled us to follow migratory animals as they complete their annual journeys (Stutchbury et al. 2009, Lisovski and Hahn 2012). This has boosted research in animal migration ecology, particularly in small bodied songbirds, allowing us to link breeding populations to non-breeding populations.

After the non-breeding residency period in the tropics, successful, surviving individuals return to their natal or previous breeding sites – a phenomenon called philopatry (Greenwood 1980). How exactly they are able to find their natal origins is still unknown. Nevertheless, this allows to follow individual birds throughout their reproductive lifetime as the likelihood of encountering the same individuals each year is relatively high.

Individual based tracking technologies and remote sensing techniques enable us to look into not only broad scale migration patterns, but also individual level experiences across the annual cycle. Methods like stable isotope analyses can provide us with the information about the environmental conditions at the wintering sites to further study seasonal interactions and link different events across the animal's annual cycle (Marra et al. 1998). It is well documented that individual experiences in one season can carry consequences on individual's performance in the following seasons via carry-over effects (Harrison et al. 2011). Thus, the annual cycles of animals should be considered as unified sequences of mutually interlinked events, rather than separate happenings, even if the events are spatially and temporarily segregated.

These seasonal large-scale movements of birds have long fascinated humans. Now with the help of technology we are able to follow bird migration and look into the details more closely than ever before. We can gain an in-depth understanding of when birds migrate, where they go, how they get there. Thus, we can also monitor how human induced activities like habitat modification and climate change influence migratory animals and if they are able to adapt to the changing environment. We can get a glimpse in their lives on the move and away from the breeding sites before they once again return the following spring.

Thesis focus

Thus far, over 70% of the published studies on birds have been focused solely on the breeding period and only 6–7% of the studies take a multi-season year-round approach. Furthermore, only slightly more than 5% of the studies examine seasonal interactions (Marra et al. 2015). In respect to migratory birds, this means that we still know relatively little about the migration and non-breeding periods, which comprise up to 9–10 months of the year for some long-distance migrants.

The technological development in the last decade has opened new horizons in bird migration research. For some species just one year of tracking has provided more data on their migration and non-breeding periods than 100 years of scientific bird ringing. Tracking data also allow us to get a clearer picture of the annual cycles of individual migrants. Furthermore, if we want to know not only where and when birds go but also how they get there, we need to look into their movement patterns in connection with the environment, migrants' own physical state, and past experiences leading up to the migration.

The key aims of my thesis are (1) to provide a comprehensive knowledge of migration patterns and organization of the annual cycles of the three study species – Tawny Pipit, Semi-collared Flycatcher, and Collared Flycatcher, (2) to gain deeper understanding of the interactions between the long-distance migrants and the environment, and (3) to examine year-round seasonal interactions of individual migrants.

Thesis outline

As stated earlier, the Afro-Palearctic bird migration system consists of three major flyways – the western, the central and the eastern flyway. In **Chapter 2**, I start out on the western flyway by looking at the annual cycle and migration strategies of the Tawny Pipit. In 2013 we equipped 35 adult breeders with geolocators at our Central European study site. A year later in 2014, we obtained tracking data of six individuals revealing that the birds migrated and spent the northern hemisphere winter in the Sahel zone in Western Africa. During the both migration seasons the majority of the birds followed a migration route through the Iberian Peninsula utilizing stopover sites in Northern Africa. In autumn, three of the six tracked birds crossed the Sahara Desert inland, and the other three followed the Atlantic coastline, while all individuals flew along the coastline in spring. During the wintering period we observed high site itinerancy with five individuals moving westward in mid-winter and thus, utilizing two main wintering sites. On average the tracked individuals spent only ¼ of the year at the European breeding sites. Another ¼ was spent on annual migrations, while ½ of the year was spent at the wintering sites in the Western Sahel. We discuss the choice of migration routes and wintering areas in respect to the breeding longitude. We also provide rainfall data from the Western Sahel to gain deeper understanding of the observed non-breeding site itinerancy.

In **Chapter 3**, I move from the western to the eastern flyway, and look into the annual cycle of the Semi-collared Flycatcher. We again used light-level geolocators to track the flycatcher migration between a breeding site in Eastern Bulgaria and wintering locations in Central Africa. By tracking the birds over two consecutive seasons, we confirm the location of wintering sites in Eastern-Central Africa and reveal a clock-wise loop migration system where autumn migration routes lay east from the spring migration routes. The tracked individuals on average spent about seven months in the sub-Saharan Africa, while only 5 months were spent north of the Sahara Desert (including 3 months at the breeding sites). During the migration periods all birds congregated at certain stopover regions indicating high migratory connectivity *en route*. Such migratory strategy may increase the vulnerability of this already declining species as habitat degradation at these stopover hotspots may affect birds of different origins from across the breeding range.

In **Chapter 4**, I shift back to the west and my third study species, the Collared Flycatcher, representing the central Afro-Palearctic flyway. We investigate the importance of breeding site latitude on the organization of the annual cycle by comparing the migration tracks of Swedish and Czech breeding populations. We expose how phenology at the breeding sites dictates the timing of events across the entire annual cycle. The southern study population always completed the annual events i.e., breeding, start and finish of the migrations earlier compared to their counterparts breeding at higher latitude. Even though, the temporal schedules of the two populations were different, spatial organization of the annual cycle was fairly similar with both populations using similar migration routes and wintering regions. Such spatiotemporal pattern of the annual cycle suggests that annual schedules of long-distance migrants are predominantly under endogenous control and are mainly driven by spring phenology at breeding sites. Furthermore, we found that wintering sites of both populations laid west from the previously known wintering distribution which calls for re-evaluation of the species' non-breeding range.

After answering the trivial questions of where and when each of my study species migrate, I take a broader look at how they get there. More specifically, in **Chapter 5** we look into barrier crossing strategies of four small-bodied passerine species as they are crossing the Sahara Desert and the Mediterranean Sea. The chosen range of study species (Collared Flycatcher, Pied Flycatcher, Reed Warbler, and Aquatic Warbler) represents all three Afro-Palearctic flyways. We found that these otherwise typical nocturnal migrants often prolong their migration into the day or even fly non-stop for up to 70–80 hours while crossing an ecological barrier. The prolonged daytime flights were more frequent in spring suggesting tighter migration schedules, possibly associated with higher pressure for early arrival at the breeding sites. As we observed the prolonged diurnal flight in the vast majority of the tracked individuals, we discuss the possibility that this might be the prevailing barrier crossing strategy yielding the lowest mortality. Nevertheless, the light pattern data recorded by the geolocators also revealed a high degree of variability among the individuals, thus birds may act opportunistically and make a daytime stopover in Sahara if encountering a suitable resting site.

Further in **Chapter 6**, I look at how migratory birds cope with weather extremes faced during their migrations. We used Semi-collared Flycatcher as our model species and compared tracking data of two consecutive spring seasons. The spring of 2014, when the first group of tagged birds returned back to Europe, was exceptionally warm in the Mediterranean Basin and at the breeding site of the flycatchers. In contrast, the spring of 2015 when the second group of tagged birds returned, was exceptionally cold, delaying plant phenology for several weeks. Such extreme and contrasting conditions present an ideal opportunity to study phenotypic plasticity in a natural setting. We found that in both years flycatchers started their spring migration from the wintering sites in Eastern-Central Africa and crossed the Sahara Desert at approximately the same time. However, when reaching the Mediterranean Basin where the first cues for weather and environmental conditions of the temperate regions can be assessed, the flycatchers adopted different strategies. In the warm spring of 2014, birds quickly continued their migration and returned to their breeding sites, while in the cold spring of 2015 birds spent a prolonged period in the Mediterranean Basin waiting for improved weather conditions before returning to their breeding sites. Additionally, we observed a lower apparent individual survival in the cold spring, suggesting that some individuals lacked an appropriate response strategy or may have chosen an inappropriate response to the cold weather. Males and older individuals that typically migrate earlier paid a higher cost and suffered a higher degree of mortality compared to females and younger birds.

As climate change is predicted to bring an increasing number of extreme weather events, animals’ ability to flexibly adjust their behaviour seems to be an essential necessity for survival. Long-distance migratory birds are especially challenged in their responses to weather extremes as they have limited or no ability to predict the weather at their distant breeding areas while residing in the tropics. The onset of spring migration in long-distance migrants is determined by photoperiod and endogenously controlled circannual rhythms. While on migration, combining the internal clock with external cues from the environment seems to be vital to withstand the changing climate.

In **Chapter 7**, I take a closer look at the annual cycles of the tracked Collared Flycatchers from the Central European breeding population and examine how carry-over effects from the breeding and non-breeding seasons modify individual timing of migration. We used the number of fledglings as a gauge for the parental investment with higher number of fledglings corresponding to a higher parental investment. To infer the non-breeding habitat quality and to assess the carry-over effects from the non-breeding season, we used stabile isotope (δ2H) signatures of the winter-grown feathers. We found that individuals with higher absolute parental investment delayed their autumn migration, had shorter non-breeding residency period and advanced spring migration compared to the individuals with lower breeding effort. Timing of spring events, particularly the onset of breeding, were more dependent on the conditions at the non-breeding areas, rather than the previous parental investment. We also observed a strong "domino effect" (i.e., high dependency of the timing of consecutive events) for intra-seasonal events, but it was weaker for inter-seasonal events. Thus, it seems that the costs of previous breeding could be overcome during the wintering period.

We also conducted a brood manipulation experiment to disentangle the true carry-over effects from individuals' intrinsic quality. Brood size of the geolocator-tagged males were experimentally increased or reduced by one chick prior to the tracking of migration. We did not find unambiguous differences in the annual schedules between the individuals of reduced and increased broods; however, the latter were earlier with Sahara crossing in spring and arrival at the breeding grounds.

These results demonstrate that annual schedules of individual migratory birds depend on both, their previous parental investment and the environmental conditions at the non-breeding residency areas. Our findings highlight the tight links between spatially- and temporally-distinct phases of the annual cycles of migrants.

Conclusions

The studies comprising this thesis looks into spatiotemporal migration strategies of selected long-distance migrants spanning across all major flyways linking Europe to Africa. We revealed different approaches of how these migrants cope with their annual movements and the encountered environmental challenges. Among those, Tawny Pipits adopted non-breeding site itinerancy while in sub-Saharan Africa, Semi-Collared Flycatchers migrate in a clock-wise loop fashion using different migration pathways and stopover sites in autumn and spring, and different populations of Collared Flycatchers have different migration scheduled that are linked to their breeding site phenology. Carry-over effects from the breeding and non-breeding seasons can have severe consequences on the annual schedules of individual migrants, thus seasonal interactions play an important role in individuals' annual cycles. An effective barrier crossing strategy and phenotypic plasticity *en route* can be the key issues that decide between successful breeding and mortality.

Knowing where and when certain populations reside is crucial for developing appropriate conservation measures. Such knowledge, even on species that are currently 'doing well', is important for future references and detecting changes in long-term. Common species can also serve as so called 'model species' for investigating more complex issues of bird migration, like seasonal interactions and carry-over effects. Thus, building a comprehensive knowledge can go a long way in protecting migratory species as well as predicting consequences of future climate change.

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1. **Briedis M.**, Beran V., Hahn S., Adamík P. 2016. Annual cycle and migration strategies of a habitat specialist, the Tawny Pipit *Anthus campestris*, revealed by geolocators. Journal of Ornithology 157(2): 619–626.

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