

Univerzita Palackého v Olomouci

Přírodovědecká fakulta

**Fenologie a migrace ptáků ve středoevropském regionu**

Habilitační práce

Obor: Zoologie

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### **Prohlášení**

Prohlašuji, že jsem tuto habilitační práci vypracoval samostatně s použitím uvedených literárních zdrojů a bez pomoci AI nástrojů.

V Olomouci, 18. 2. 2026

Mgr. Peter Adamík, Ph.D.



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## Úvod

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”Na Hromnice (2. února) musí skřivánek vrznout, i kdyby měl zmrznout”. Kdo by neznal alespoň tuto základní pranostiku? Celá řada pranostik vycházela z jednoduchého faktu, že naši předci trávili mnoho času prací venku a byli velice dobrými pozorovateli. Opakované jevy tak bylo vhodné formulovat do nějaké lidové moudrosti. Již v průběhu studií se mi k rukám dostala zdařilá kniha o lidových pranostikách z pera Jana Munzara (Munzar 1984). Munzar velice umně kombinoval historické prameny k objasnění celé řady pranostik. Zároveň, se v té době, kdy se mi kniha dostala do rukou, začaly objevovat první fenologické studie o dlouhodobých změnách v časování rytmů a jevů, jako je například doba hnízdění, přiletů na hnízdiště nebo kvetení vegetace a délka vegetační sezóny. Přemýšlel jsem, jaké jsou možnosti dopátrat se k primárním zdrojům dat o fenologii rostlin a živočichů z území Česka a jak propojit staré prameny ve světle probíhající klimatické změny. Paralelně k tomu, jsem se intenzivně začal zabývat kroužkováním ptáků a jako první, co mě napadlo, bylo použít kroužkovací data pro rekonstrukci vybraných fenologických jevů u ptáků. Studium šedé literatury se otevřela samostatná kapitola o fenologii jarních přiletů na naše území. K mému velkému překvapení jsem zjistil, že to co dnes vznešeně nazýváme občanskou vědou (citizen science), tak již v dobách Rakouska-Uherska zde bylo několik dobrovolnických velkoškálových iniciativ na sběr dat o době přiletů a odletů ptáků nebo době kvetení rostlin. Mým cílem se tak stalo, za pomoci studentů, digitalizovat několik historických datových zdrojů a vyhodnotit dlouhodobé změny ve fenologii. Tento aspekt tvoří první ze tří okruhů předložené habilitační práce.

Vyhodnocení dlouhodobých změn ve fenologii ptačích přiletů podnítilo celou řadu otázek. V souvislosti s klimatickou změnou se velice brzo stala diskutovanou otázka rozdílných odpovědí u dálkových migrantů a migrantů na krátké vzdálenosti (např. Jonzén et al. 2006, Usui et al. 2017). Uvědomil jsem si, že vyhodnocením „pouhých“ přiletů nebo odletů z hnízdišť pozorujeme všechno pouze z povrchu. Klíčové bylo pochopení, jaké mají jednotlivé hnízdní populace migrační trasy, kde a jak dlouho se zastavují a zimují. I taková drobnost jako je délka tahové zastávky může významně ovlivnit výsledný vzorec přiletů na hnízdiště (Schmaljohann & Both 2017). Naopak, délka migrační trasy docela dobře predikuje celkovou délku tahu a posléze i přilet na hnízdiště (např. Hötter 2002). Pro ilustraci, představme si nějaký tažný, v Česku hnízdící druh, který má zimoviště jak v oblasti Mediteránu, tak v sub-Saharské Africe. Je zřejmé, že populace, které zimují blíž hnízdištím, budou přilétat dřív než ty, které zimují v Africe. Prakticky by to mohlo znamenat bimodalitu v čase na přiletech do Česka nebo hodně širokou distribuci přiletových dat. Dobrým příkladem je slavík modráček. Na našem území hnízdí populace, které zimují v Asii, Mediteránu či sub-Saharské Africe. Každá z populací se liší dobou přiletů k nám (Cepák et al. 2008, Lislevand et al. 2015, vlastní nepubl. data). Ať jedno nebo druhé, bez podrobnější znalosti migrační ekologie dané populace je mnohem obtížnější vyhodnotit pozorované fenologické trendy. Od klasických zpětných hlášení okroužkovaných ptáků, která propojovala hnízdiště se zimovišti, se bylo nutné posunout k sofistikovanějším

metodám. Právě dostupnost malých geolokátorů a později i tlakových dataloggerů mě navedla na myšlenku studia migrace několika ptačích druhů. Série prací, zejména popisnějšího charakteru, na toto téma tak představuje druhý okruh mé habilitační práce.

Dostupnost podrobných popisných dat o migraci (odlety a přílety z/do hnízdišť a zimovišť, lokace tahových zastávek a délky pobytu na různých místech v průběhu ročního cyklu) pro dostatečně velké datové soubory nebo pro několik populací nám umožnila si klást mnohem složitější otázky v kontextu ptačí fenologie a migrace. V tomto případě se stali lejsci rodu *Ficedula* ideálním modelovým druhem. Třetí část habilitace je tak složená z terénních studií, kde vyhodnocujeme data z geolokátorů v kontextu faktorů, které mají význam na organizaci ročního cyklu ptáků, překonávání velkých bariér, anomálií v počasí, propojení fází ročního cyklu nebo vnitro populačních procesů.

Tuto habilitační práci předkládám, ve smyslu § 72 zákona č. 111/1998 Sb., jako soubor uveřejněných vědeckých prací doplněných komentářem.

## 2. Komentáře k jednotlivým studiím

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### I. Fenologie odvozená z kroužkovacích dat

#### Studie 1

**Adamík, P.** & Pietruszková, J. 2008: Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithologica* 43: 119–128.

#### Studie 2

Hušek, J. & **Adamík, P.** 2008: Long-term trends in timing of breeding and brood size in the red-backed shrike *Lanius collurio* in the Czech Republic, 1964–2004. *Journal of Ornithology* 149: 97–103.

#### Studie 3

Hušek, J., **Adamík, P.**, Cepák, J. & Tryjanowski, P. 2009: The influence of climate and population size on the distribution of breeding dates in the red-backed shrike (*Lanius collurio*). *Annales Zoologici Fennici* 46: 439–450.

#### Studie 4

Najmanová, L. & **Adamík, P.** 2009: Effect of climatic change on the duration of the breeding season in three European thrushes. *Bird Study* 56: 349–356.

Společným jmenovatelem pro první čtyři studie je zdroj dat: kroužkovací data. V roce 2004 jsem se společně se studenty pustil do přepisu kroužkovacích záznamů Kroužkovací stanice Národního muzea v Praze. Z dnešního pohledu, kdy jsou dostupné automatizované postupy pro přepis písemných záznamů, to působí komicky, ale tehdy jsme jednoduše všechny záznamové archy s ročními výkazy od kroužkovatelů ručně přepisovali do programu BirdRing. V té době již kroužkovatelé odevzdávali data elektronicky, ale když jsem se chtěl dostat k starším údajům, nebylo zbylí a museli jsme data přepsat ručně. Organizace práce byla velice jednoduchá, s pracovníky kroužkovací stanice, Jaroslavem Cepákem a Jaroslavem Škopkem, jsem se dohodl, že objemné kroužkovací záznamy budeme přepisovat v Olomouci, a tak jsem v pravidelných intervalech cestoval s velkým batohem mezi Prahou a Olomoucí. Napadlo mě totiž, že desítky let kroužkovacích záznamů jsou velice cenným zdrojem o časování hnízdění pěvců a načasování tahu u bahňáků. Logika byla taková, že pro kroužkování mláďat je poměrně krátké časové okno, kdy mohou kroužkovatele nasadit kroužky, jinak mláďata vyskáčou z hnízda, a že se časová aktivita kroužkování překrývá s dostupností hnízd (Beintema et al. 1985). To stejné jsem předpokládal i pro časování tahu bahňáků. Většina bahňáků přes naše území pouze protahuje, a zejména letní tah, tj. ze severněji položených hnízdišť, je u některých druhů velmi výrazný. Když bahňáci protahují přes naše území, tak jsou i chytáni a kroužkováni. Předpokládal jsem, že intenzita kroužkování je propojená s „nabídkou“ ptáků v terénu, a tudíž fenologické metriky odvozené z data kroužkování budou reflektovat i samotnou fenologii. Jiná data jednoduše nebyla z našeho území dostupná. Na přepisu údajů pracovalo několik studentů

a Tomáš Koutný. Původně jsem uvažoval o časové řadě od roku 1934, kdy započalo kroužkování pod Československou ornitologickou společností, ale způsob archivace dat do roku 1963 byl podle jména kroužkovatele. To by značně navýšilo čas na přepis údajů, a tak jsem se rozhodl pro digitalizaci od roku 1964. Od této doby byly záznamy vedeny dle typu kroužku a roku. To značně zjednodušovalo digitalizaci (Obr. 1). Pro snadnější práci s kroužkovacími daty jsem pro studie o časování hnízdění vybral z pěvců ťuhýka obecného, drozda zpěvného, kosa černého a drozda kvíčalu. U bahňáků jsme přepisovali prakticky všechny druhy a až posléze jsem vybral podmnožinu druhů, u kterých bylo dostatek údajů nejen co do celkového počtu okroužkovaných jedinců, ale i s ohledem na časové rozložení dat mezi lety 1964 až 2005. Původně jsem uvažoval i o vyhodnocení údajů o časování hnízdění čejky chocholaté, ale toto zůstalo v šuplíku a jediné co se z toho publikovalo, byly regionální trendy v poklesu početností (Žídková et al. 2007).

U protahujících bahňáků jsem společně se svou diplomantkou Janou Pietruszkovou, vybral osm druhů, které splňovaly podmínku alespoň 20leté časové řady a s nejméně 10 jedinci pro danou tahovou sezónu v daném roce (**Studie 1**). U jarní migrace jsme zjistili velice konzistentní posun k časnějšímu tahu přes naše území. Nejextrémnější posun byl u časné fáze tahu jespáka bojovného, kdy byl zjištěn posun téměř o jeden den za rok. Naopak v létě, byly trendy variabilní s tím, že u vodouše bahenního, písíka obecného a jespáka obecného byl posun k dřívějšímu průtahu, ale například u jespáka bojovného, bekasiny otavní nebo kulíka říčního došlo naopak k opoždění průtahu.

Kroužkovací stanice  
N. MUZEUM - PRAHA - ČSSR

## Kroužkovací seznam

**DŮLEŽITÉ!**  
Na jednom kroužkovacím seznamu musí být zaznamenány pouze kroužky téhož typu s čísly jdoucími za sebou (téže série)!

Do kroužku vpište písmeno typu kroužků, které jsou zapsány na tomto kroužkovacím seznamu!

Do rámečku nepište!

Jméno kroužkovatele  
Vladislav H á j e k, dipl. tech.,  
Adresa  
Břeclav, Smetanovo nábřeží 32.

	Číslo kroužku	Druh ptáka	Pohlaví stáří (jen lze-li zjistit)	Den měsíc rok kroužkování	Místo okroužkování (u místních názvů uvést jméno nejbližší obce, případně okres)	Poznámka (mládě na hnízdě, létající mladý pták, chycený st. pták atp.)
1	64251	Bekasina otavní	f.g.	28.8.78	Lednice- Pastvisko	chycen
2	2	Jespák bojovný	f l.r.	31.8.	Sedlec, "Nesyt"	
3	3					
4	4	Chřástal vodní	+ l.r.	4.9.		
5	5	Jespák bojovný	m l.r.	10.9.	Lednice-Pastvisko	
6	6	Bekasina otavní	f.g.			
7	7	Chřástal vodní		24.9.	Sedlec, "Nesyt"	

Obr. 1. Vzorový záznamový arch výkazu kroužkování za daný rok pro jednoho kroužkovatele a vybraný velikostní typ kroužku.

V této době byl velký boom ve hledání tzv. univerzální proxy proměnné pro charakteristiku klimatu a index severoatlantické oscilace (NAO index) byl tzv. zlatým standardem (Stenseth & Mysterud 2005). Ten jsme ještě několikrát použili i v následujících studiích. V této práci jsme detrendovaný index korelovali s dobou tahu a u většiny časových řad byl konzistentně negativně asociovaný s dobou tahu. To bylo logické, protože kladné hodnoty NAO indexu jsou spojené s časnějším nástupem jara ve střední a severní Evropě (Menzel et al. 2005). Rukopis jsem zaslal do Acta Ornithologica, kde byl prakticky bez větších obtíží přijat, i když jedna ze stěžejních připomínek byla, do jaké míry jsou kroužkovací data opravdu vypovídající o časování tahu. Zpětně viděno, byla analýza vlivu klimatu na dobu tahu velice jednoduchá. Při dnešních nástrojích, jako je např. R-balík *climwin* (Bailey & van de Pol 2016) a analýza s klouzavou časovou osou (van de Pol et al. 2016), by se určitě dal lépe hledat správný klimatický signál. Na druhou stranu, na rozdíl od pouhých pozorovacích dat publikovaných v jiných studiích, jsem přesvědčený, že kroužkovací data mají velkou výhodu v tom, že umožňují diferenciaci mezi tahem rodičů a juvenilů. Právě u bahňáků je markantní rozdíl mezi časováním tahu, kdy letošní mláďata opouštějí hnízdiště výrazně později než rodiče (Pietruszková & Adamík 2009). Také naše volba ošetřit NAO index od trendu se ukázala jako velice prozíravá, protože re-analýza mnohých časových řad zjistila, že celá řada studií v tomto metodickém aspektu chybovala (Haest et al. 2018).

Práci na kroužkovacích datech mláďat ťuhýka obecného jsem zadal jako diplomku Janu Huškovi. Honza se ujal práce velice aktivně, a záhy jsme měli k dispozici údaje o časování hnízdění z 9 824 ťuhýčích hnízd. Na tento druh se specializovala celá řada kroužkovatelů (Hušek & Adamík 2006), dokonce založili i pracovní skupinu pro výzkum ťuhýkovitých. Byl to tak ideální adept na robustní datový soubor. Ze základního datasetu jsme vyhodnotili změny v časování hnízdění a počtu mláďat na hnízdech. Za léta 1964 až 2004 jsme zdokumentovali posun v hnízdní době o přibližně tři až čtyři dny a nárůst v počtu mláďat na hnízdo o 0,3 mláděte. Rozhodující vliv na hnízdění měly květnové teploty. Neméně zajímavý byl i velice silný vnitro sezónní lineární pokles v počtu mláďat. Rukopis jsme poslali do Journal of Ornithology (**Studie 2**), kde prošel velice hladce a doposud je to asi nejrychlejší recenzní řízení (55 dní mezi submitací a akceptancí), jaké jsem zažil. V té době fenologickému výzkumu těžce dominovaly práce na budkových populacích sýkor a lejsků (Visser et al. 2003, Both et al. 2004). Studií na trendech u otevřeně hnízdících druhů bylo velice málo (např. Møller et al. 2006). Byl to tak jeden z mála příspěvků na jiném než budkovém systému, kde se vyhodnotily dlouhodobé trendy. Až mnohem později se akumulovaly práce na dalších druzích (Halupka et al. 2023).

Toni Laaksonen s kolektivem publikoval v roce 2006 studii na lejsku černohlavém, ve které se zabýval komplexnější analýzou vlivů na dobu hnízdění ale i na samotnou distribuci snůšek (Laaksonen et al. 2006). Tato studie nám byla inspirací, a proto jsme se rozhodli o sofistikovanější analýzu dát na ťuhýkovi. Honza Hušek byl tou dobou na stáži u Piotra Tryjanowskeho v Poznani a nadšeně reportoval, že bychom mohli použít nový index, tzv. Indian Ocean Dipole jako možný prediktor podmínek na zimovišti ťuhýků. Idea byla taková, že bychom vyhodnotili vliv klimatických podmínek z různých částí ročního cyklu ťuhýka na jeho

hnízdění fenologii. Aby toho nebylo málo, zabývali jsme se i samotnou distribucí hnízdění, protože například příhodné podmínky mohou silně synchronizovat hnízdění v dané sezóně. K tomu všemu jsme zohlednili i populační status druhu na celorepublikové úrovni z Jednotného programu sčítání ptáků České společnosti ornitologické. Protože koncept práce byl postavený na poměrně komplexním setu prediktorů, celá práce byla zasazena do informačně teoretického přístupu v modelovací části (**Studie 3**). Zjistili jsme, že lokální klima nejlépe predikuje hnízdění u ťuhýka. Zároveň byl významný také vliv populačního indexu. Jinými slovy, v letech s vyššími hodnotami početnosti (odvozené hodnoty trendu druhu z indexu Jednotného programu sčítání ptáků v Česku) hnízdil ťuhýk dřív. To by mohlo indikovat hustotně-závislé procesy v načasování hnízdění. To, že fenologie může hrát roli v populačních trendech druhu, jsme prokázali o několik let později na datovém souboru s 52 druhy z Česka (Koleček et al. 2020). Možná trochu skromně jsme rukopis zaslali do *Annales Zoologici Fennici*, kde v té době běžně vycházely ekologické studie na ptácích. Dodnes si myslím, že je to trochu pozapomenutá práce a určitě jsme ji mohli prodat lépe.

Kroužkovací data na drozdech rodu *Turdus* měla za úkol zpracovat diplomantka Lenka Najmanová. I zde jsem měl štěstí na dobrého studenta a velice brzo jsme měli digitalizovaná data o 3371 hnízdech kvíčal, 1472 hnízdech kosů a 944 hnízdech drozdů zpěvných z let 1964 až 2006. Přístup byl velice podobný jako u ťuhýků, kde jsme použili klimatické prediktory z různých částí ročního cyklu. Inovací bylo, že jsme v této studii dali důraz na délku hnízdění sezóny, kterou jsme definovali jako roční mezikvartilové rozpětí v datech kroužkování pullat. Do té doby byly fenologické práce o délce hnízdění sezóny poměrně vzácné a syntéza přišla až mnohem později (Halupka & Halupka 2017). Bonusem, s ohledem na urbanizaci kosa a drozda zpěvného, bylo vyhodnocení rozdílů v hnízděních parametrech urbánních a rurálních populací. Z dat jsme zjistili nelineární posun hnízdění fenologie k časnějšímu datu. U délky hnízdění sezóny jsme zjistili, že kos a drozd zpěvný rozšířili svou hnízděcí dobu, kdežto u kvíčalů došlo k jejímu zkrácení. Trochu skromně, i s ohledem na charakter zdroje dat, jsem rukopis zaslal do *Bird Study* (**Studie 4**), kde prakticky hladce prošel recenzním řízením.

## I. Fenologie na budkové populaci

### Studie 5

**Adamík, P. & Král, M. 2008:** Climate and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds. *Journal of Zoology, London* 275: 209–215.

V rámci svého doktorského studia jsem se chtěl věnovat interakcím mezi lejskem bělokrkým a černošavlým v jejich hybridní zóně. Dávalo to i logiku s ohledem na množství studií, které proudily z olomouckého pracoviště. Co jsem ovšem netušil je, že jsem do severomoravských hvozduů přišel tak trochu pozdě. Nejlepší roky na hnízdění lejska černošavého byly pryč, a i u lejsků bělokrkých se v posledních letech ukázal nebývalý problém – vysoká míra predace plchem velkým. Na přelomu let 2004 a 2005 jsem započal spolupráci

s Miroslavem Králem na jeho budkových populacích na Sovinecku v Nížkém Jeseníku. Jako mladý a málo zkušený jsem za ním přišel s tím, že budu studovat i zimující sýkory a že bych si přidal ptačí budky k jeho lokalitám. Tehdy jsem nemohl tušit, že si lokalitu zamiluji a že budu pokračovat v monitoringu hnízdní biologie až do dnešních dnů (Adamík & Král 2023). Hned pilotní hnízdní sezóna ukázala, že plši jsou pro ptáky opravdu vážný problém a že smysluplný datový soubor pro nějakou hybridizaci stěží vytvořím. Frustrován z vysoké míry predace jsem uvažoval o smyslu svého snažení. Pak jsem se ale rozhodl lépe porozumět biologii plchů. Psal jsem na všechny strany a velice mi v počátcích pomohli Vladimír Vohralík a Boris Kryštofek. Tak započalo mé studium plchů. Než jsme posléze se studenty nashromáždili nějaká demografická data o plších, uvědomil jsem si, že pečlivé zápisky Mirka Krále obsahují i údaje o výskytu plchů v ptačích budkách. Nastala tak pro nás oba mravenčí práce. Výsledkem bylo, že jsme zpětně zdigitalizovali záznamy plchů až do prvních let studia ptáků na této lokalitě. Z dat bylo patrné, že u plchů je silný trend v časnějším probouzení z hibernace. Ten trend byl mnohem strmější než posun v hnízdní fenologii lejsků, sýkor a brhlíka. Výsledkem bylo, že se mnohem více začala překrývat doba výskytu plchů s dobou hnízdění ptáků. Zároveň jsme v datech viděli výrazné meziroční nárůsty v počtech plchů, kteří se vyskytovali v budkách a také rostla i míra predace. Data tak indikovala poměrně propletené vazby mezi probíhající klimatickou změnou, četností semenných let a reakcí plchů, která se následně pronesla do zvýšených hnízdních ztrát pěvců. Zejména pro lejska byl trend poměrně neradostný, indikující zvýšený predační tlak i do budoucna. Předpokládal jsem, že moje nadšení z objevu budou sdílet i editoři věhlasných časopisů. Rukopis jsem zaslal do Nature.



*Obr. 2. Typický obrázek při jarních kontrolách budek v Nížkém Jeseníku. Plch velký v lejsčím hnízdě.*

Reakce byla rychlá a odmítavá, bez recenzí. Stejný scénář se zopakoval ještě pro několik „elitních časopisů“. Tam, kde se text dostal na recenzi, bylo hlavní výtkou to, že jsme plchy individuálně neznačili, a tudíž není vůbec jisté, co je vlastně námi pozorovaný nárůst obsazených budek. Další výtkou bylo i to, že tím, že jsme ukázali, že za predací stojí hlavně nárůst výskytu plcha, a ne fenologie samotná, není téma dostatečně atraktivní pro klimatem způsobené interakce mezi živočichy. Text jsem postupně se submitacemi vylepšoval, ale nakonec znaven z tlaku redakcí na „novelty“ a z těžké kritiky absence individuálně značených plchů, jsem se rozhodl pro nějaký starý dobrý žurnál, který nepase po „trendy“ tématech (**Studie 5**). Viděno zpětně, dnes bych uměl studii mnohem lépe vystavět. Nyní vím, že zvýšená obsazenost budek na jaře skutečně odráží zvýšené počty jedinců a že dobře koresponduje s celkovým počtem plchů na lokalitě. Co jsem v té době netušil, že počty plchů jsou opravdu tažené cyklem semenných let, hlavně buku a dubu. Častější semenné roky tak vedou k nárůstu početnosti plcha. Z dnešních dat do roku 2025 také vím, že se prudký trend v posunu plší fenologie zastavil kolem roku 2005 a od té doby není patrný. Cyklus semenných let je tedy hlavním tahounem hnízdních ztrát u dutinových hnízdičů v tomto studijním systému. Studií dokumentujících dopady klimatické změny na savce je ve srovnání s jinými taxonomickými skupinami relativně málo. Publikovaná práce se tak opakovaně vyskytuje v metaanalýzách zabývajících se savci (např. Wells et al. 2022).

## I. Fenologie příletů ptáků, fenologie dřevin

### Studie 6

Kolářová, E. & **Adamík, P.** 2015: Bird arrival dates in Central Europe based on one of the earliest phenological networks. *Climate Research* 63: 91–98.

### Studie 7

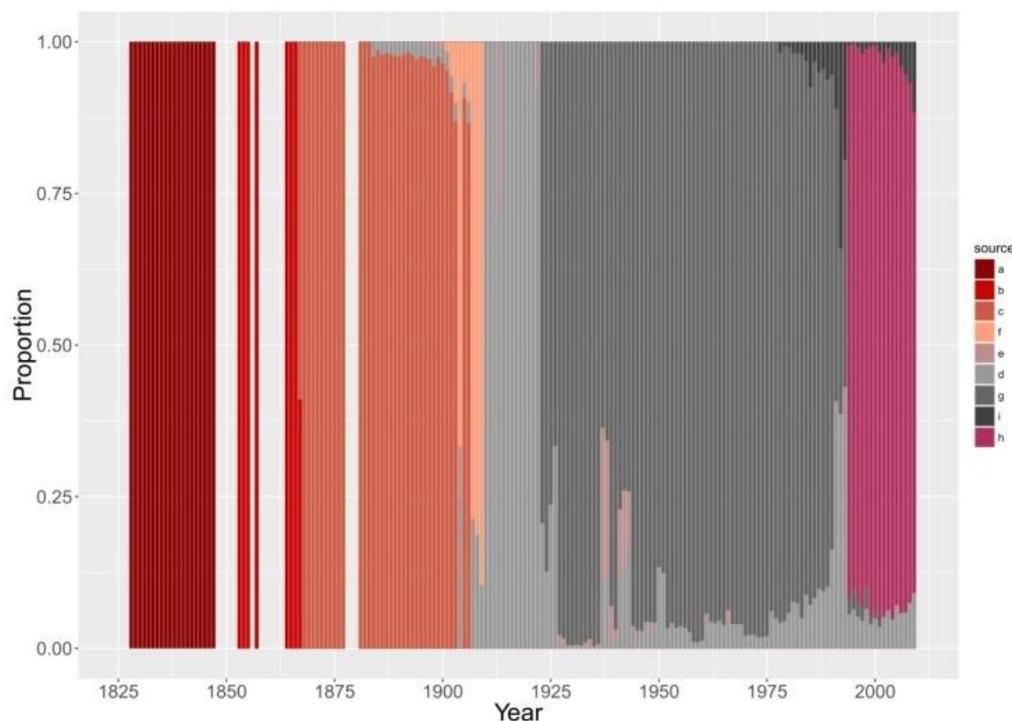
Kolářová, E., Matiu, M., Menzel, A., Nekovář, J., Lumpe, P. & **Adamík, P.** 2017: Changes in spring arrival dates and temperature sensitivity of migratory birds over two centuries. *International Journal of Biometeorology* 61: 1279–1289.

### Studie 8

Kolářová, E., Nekovář, J. & **Adamík, P.** 2014: Long-term temporal changes in central European tree phenology (1946–2010) confirm the recent extension of growing seasons. *International Journal of Biometeorology* 58: 1739–1748.

Vedle fenologických studií stojících na kroužkovacích datech jsem pátral po zdrojích dat pro rekonstrukci jarních příletů. Znamenalo to ponoření se do objemného množství šedé literatury. Nit zdrojů dat jsem rozplétal od těch recentních a postupně jsem rozkrýval vlásečnice dalších a starších pramenů. První kroky vedly k Petru Lumpemu a jeho iniciativě

zaznamenávání jarních příletů, kterou vedl pod patronací České společnosti ornitologické do roku 2010. Další důležitou osobou byl Jiří Nekovář z Českého hydrometeorologického ústavu, který poskytl data o příletech několika druhů ze sítě stanic, která byla dostupná do roku 1990. Mezi členy ČSO jsem rozeslal výzvu o zaslání dlouhodobých pozorování prvních příletů a paralelně probíhal sběr dat z šedé literatury. Prakticky to probíhalo tak, že jsem pátral po zdrojích dat, navštěvoval knihovny, státní archivy, kopíroval záznamy a postupně budoval datovou sadu pro všechny tažené druhy. Stovky hodin při přepisu dat strávilo několik lidí, včetně členů rodiny. Všechny tyto zdroje jsem pak zadal k vyčištění a sumarizaci Evě Kolářové, pro kterou tvořily základ disertační práce. Vznikla tak datová sada s přílety tažených ptáků od roku 1828 až do roku 2010 (Obr. 3).



Obr. 3. Vizualizace zdrojů dat pro rekonstrukci jarních příletů do Česka v letech 1828 až 2010. Pro podrobnosti viz Kolářová et al. (2017).

Počátky systematicky organizovaných fenologických pozorování ptáků jsou na našem území spjaty s Vlastenecko-hospodářskou společností v království Českém (k. k. ökonomisch-patriotische Gesellschaft in Königreich Böhmen). Fenologická pozorování z období 1828–1847 byla publikována v periodících *Neue Schriften* (Obr. 4.) a *Verhandlungen und Mittheilungen*. A právě tato nejranější data jsme se rozhodli vyhodnotit a srovnat s recentním datovým souborem z let 1991 až 2010 (**Studie 6**). Výhodou bylo, že to byla relativně homogenní datová sada pro 35 druhů. Sám jsem byl velice zvědavý, jak dobrá tato stará data jsou. Zjistili jsme, že některé druhy přilétaly dříve, v 1. polovině 19. století, než nyní, a to i přes silný trend k dřívějšímu příletu v posledních dekádách. Zároveň vztahy mezi lokální teplotou a přílety byly velice silné i v historickém datasetu. To poukazuje na spolehlivost příletových dat sesbíraných před dávnou dobou. Co nevíme je, proč některé druhy přilétaly v první půlce 19. století dříve

než dnes, přitom teploty v té době byly na našem území v průměru o přibližně 2 °C nižší. Osobně jsem přesvědčený, že je to efekt density a že v minulosti měly běžné druhy vyšší populační hustoty a díky tomu byl větší tlak na časnější přílety.

Systematické sledování příletů ptáků bylo masověji organizováno od druhé poloviny 19. století v rámci tzv. obecné fenologie, a to zásluhou Karla Fritsche a Gustava von Niessla. Na konci 19. století fenologie silně pronikla i mezi ornitology a sledování příletů ptactva se rozšířilo na celé území Rakouska-Uherska. Z celého císařství byly publikovány velice přehledné ročenky jako příloha časopisu Die Schwalbe s údaji o příletech ptáků. V roce 1923 pak Václav Novák vybudoval celostátní síť fenologických stanic a až do roku 1937 sestavoval detailní fenologické ročenky. Posléze po různých organizačních změnách přebral fenologická pozorování Hydrometeorologický ústav a poslední fenologická ročenka vyšla v roce 1960. Český hydrometeorologický ústav pokračoval ve sledování příletů velice omezeného množství druhů až do roku 1990. Naštěstí obratem na to navázala ČSO svým projektem jarních příletů a díky celé řadě aktérů tak máme k dispozici údaje o jarních příletech za dvě století.

Z databáze jsme vybrali pouze 13 druhů pro rekonstrukci příletů za roky 1828 až 2010. Výčet druhů jsme museli zúžit na ty, pro které jsme měli dostupné co nejkompletnější časové řady. Výsledkem je, že pro Česko je dostupná jedna z nejdelších časových řad příletů na světě (**Studie 7**). Na studii je ještě jeden důležitý aspekt. Ukázali jsme, že síla vztahu mezi přílety a lokální teplotou nemusí být nutně stejná v rámci druhu za různá časová okna.

III. Beobachtung solcher Thiere, welche gegen den Winter in wärmere G.					
	a)	b)			
Der Biehehopf. (Upupa epops.)	Zeit des ersten Erscheinens.	—	—	—	—
	—	Verwindens.	—	—	—
Der Goldamschel. (Oriolus galbula.)	a) —	ersten Erscheinens.	—	1. März	—
	b) —	Verwindens.	—	—	—
Die Feldlerche. (Alauda arvensis.)	a) —	ersten Erscheinens.	26. Febr.	27. Febr.	27. Febr.
	b) —	Verwindens.	—	24. Okt.	—
Die Ringeltaube. (Columba palumbus.)	a) —	ersten Erscheinens.	—	17. März	—
	b) —	Verwindens.	—	30. Sept.	—
Die Holztaube. (Columba oenas.)	a) —	ersten Erscheinens.	—	—	—
	b) —	Verwindens.	—	—	—
Die Tureltaube. (Columba turtur.)	a) —	ersten Erscheinens.	—	27. April	—
	b) —	Verwindens.	—	—	—
Die gemeine Bachstelze. (Motacilla alba.)	a) —	ersten Erscheinens.	—	8. März	12. März
	b) —	Verwindens.	—	6. Okt.	—
Die Nachtigal. (Motacilla luscini.)	a) —	ersten Erscheinens.	—	20. April	20. April
	b) —	Verwindens.	—	—	—
Die Grasmücke. (Motacilla hortensis.)	a) —	ersten Erscheinens.	—	—	—
	b) —	Verwindens.	—	—	—
Das Rothschwänzchen (Haus-) (Motacilla erithacus.)	a) —	ersten Erscheinens.	—	24. März	—
	b) —	Verwindens.	—	—	—
Das Gartenrothschwänzchen. (Motacilla phoenicurus.)	a) —	ersten Erscheinens.	—	30. März	—
	b) —	Verwindens.	—	—	—
Die Hauschwalbe. (Hirundo urtica.)	a) —	ersten Erscheinens.	18. April	25. April	8. April
	b) —	Verwindens.	—	30. Sept.	—

Obr. 4. Ukázka záznamu příletů a odletů tažných ptáků pro rok 1828 z časopisu Neue Schriften.

A do třetice, v literatuře se hodně opakovala teze, že dálkoví migranti mají slabší odpověď na lokální teploty než migranti na krátkou vzdálenost (např. Jonzén et al. 2006). Naše studie ukázala, že toto je dynamický jev a že za poslední desetiletí migranti na krátké vzdálenosti reagují silněji, resp., že síla vztahu akceleruje s teplotou. Proto je důležitá časová škála každé studie. Většina publikovaných studií byla jednoduše příliš krátká pro odhalení dynamiky síly vztahu mezi lokální teplotou a přílety.

Při pracích na časové řadě příletů ptáků jsem se dostal do kontaktu s Jiřím Nekovářem. Zjistil jsem, jak cenná data o fenologii nejen živočichů a rostlin archivuje Český hydrometeorologický ústav. Plodné diskuse s kolegou Nekovářem vedly k tomu, že jsem Evě Kolářové zadal vyhodnocení změn fenologie 18 druhů dřevin v Česku jako diplomovou práci. Fenologie dřevin mě extrémně zajímala z jednoho prostého důvodu. S ohledem na trofické vazby bylo jasné, že fenologie dřevin bude determinovat i fenologii hmyzu, hlavní potravní složky celé řady tažných lesních druhů ptáků. Proto mi přišlo důležité porozumět, co se děje s aspekty jako je jarní olistění, doba kvetení, či délka vegetační sezóny. Celkem jsme vyhodnotili trendy v letech 1946 až 2010 pro osm fenologických charakteristik (**Studie 8**). Překvapila mě rychlá akcelerace fenologie a míra posunu za sledované období. Rukopis jsme zaslali do International Journal of Biometeorology. Posudky byly docela nevyvážené, z mého pohledu až neprofesionálně provedené a editor rukopis zamítl. Rozhodl jsem se tehdy, že to nenecháme jen tak a rukopis jsme v lehce upravené verzi a s kritikou práce recenzentů znovu zaslali do stejného časopisu. S novými recenzenty studie prošla hladce. Zpětně se domnívám, že je škoda, že jsme v tématu nepokračovali. Práce je hodně popisná a líbilo by se mi, kdybychom propojili klimatické proměnné s fenologií a trochu více prostudovali prostorovou variabilitu ve fenologických trendech. Navíc, z citací naší studie se ukazuje, že téma je velice aktuální pro vyhodnocení pylové sezóny ve vztahu k alergikům.

## II. Migrace – popisy zimovišť a migračních tras

### Studie 9

**Adamík, P.** 2008: Čejka chocholatá. In: Cepák, J. et al. (eds) *Atlas migrace ptáků České a Slovenské republiky*. Aventinum, Praha: 184–186.

**Adamík, P.** 2008: Vodouš bahenní. In: Cepák, J. et al. (eds) *Atlas migrace ptáků České a Slovenské republiky*. Aventinum, Praha: 207–209.

**Adamík, P.** 2008: Pisík obecný. In: Cepák, J. et al. (eds) *Atlas migrace ptáků České a Slovenské republiky*. Aventinum, Praha: 210–212.

Mé počátky studia migrace jsou spojené se zpracováním zpětných hlášení okroužkovaných ptáků pro Kroužkovací stanici Národního muzea v Praze. Jaroslavem Cepákem jsem byl v roce 2005 osloven s tím, abych vyhodnotil migraci a zpracoval druhové kapitoly pro několik druhů ptáků. Výsledkem bylo osm druhových kapitol, které jsem na 22 stranách zpracoval pro sýkoru koňadru, sýkoru modřinku, jespáka malého, jespáka obecného, bekasinu otavní, vodouše bahenního, čejku chocholatou a písíka obecného v migračním atlase, který vyšel v roce 2008 (Cepák et al. 2008). Do habilitační práce předkládám, pouze na ukázkou, tři druhové kapitoly (**Studie 9**). Jedná se o tradiční vyhodnocení zpětných hlášení, kdy jsou nálezy rozděleny do různých sezón a z časové distribuce lokací se uvažovalo o výskytu na zimovištích a tahových zastávkách. Ve své době se jednalo o jeden z mála národních migračních atlasů.

## II. Migrace – geolokace

### Studie 10

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: 619–626.

### Studie 11

**Adamík, P.**, Bureš, S., Hahn, S., Oatley, G. & Briedis, M. 2023: Timing of migration and African non-breeding grounds of geolocator-tracked European Pied Flycatchers: a multi-population assessment. *Journal of Ornithology* 164: 875–886.

Na nějakou dobu to tak byla konečná pro můj záměr studia migrace ptáků. Dále jsem se věnoval práci s kroužkovacími daty a jejich využití pro fenologické studie (viz studie výše). V roce 2009 jsem zaregistroval zásadní článek, který použil tzv. geolokátory pro studium migrace drozda lesního a jiříčky modrolesklé (Stutchbury et al. 2009). Jednalo se o archivní datalogery, které zaznamenávaly v předdefinovaném časovém intervalu intenzitu světla. Pták musel v průběhu celého roku nosit „batůžek“ na zádech a po roce ho bylo nutno odchytil a dataloger odebrat. Z intenzity zaznamenaného světla bylo možné zrekonstruovat východ a západ slunce pro každý den a dopočítat čas pravého poledne. Z těchto údajů je možné

odhadnout zeměpisnou délku a šířku výskytu, tedy kromě přibližně dvoutýdenního období jarní a podzimní rovnodennosti. V té době jsem se již intenzivně věnoval výzkumu lejsků v Nížkém Jeseníku a logicky mě napadlo, že světelné datalogery by byly vynikající cesta, jak posunout poznatky o migraci celé řady tažných druhů pěvců ve středoevropském hnízdním prostoru. Do toho roku existovalo v Evropě pouze pět zpětných nálezů okroužkovaných lejsků z oblasti zimovišť. Sondoval jsem možnosti, kde sehnat geolokátory. Kontaktoval jsem i Felixe Liechtiho z Vogelwarte ve švýcarském Sempachu. Švýcarští kolegové se ukázali jako velice vstřícní a započala tak letitá velice produktivní spolupráce, a to zejména se Steffenem Hahnem. Vogelwarte tehdy čerstvě vyvinula své vlastní geolokátory. Přes různé technické potíže jsem v roce 2011 obdržel první sadu geolokátorů pro lejsky. Jak už to bývá, začátky jsou někdy nelehké, a i v případě geolokátorů se ukázalo, že v některých letech byly velice poruchové. To byl osud i mé první sezóny. Těch zklamání pak bylo ještě v průběhu dalších let několik, buď se jednalo o technické problémy, nebo těžkosti se zpětnými odchvy ptáků různých druhů, kterým jsem s kolegy nasazoval zařízení. Od roku 2012 jsem tak ve spolupráci s celou řadou spolupracovníků nasazoval geolokátory na několik ptačích druhů. Motivace bylo pokrýt druhy, o kterých máme relativně kusé informace o migraci. V kontextu mého fenologického výzkumu na příletech, mě také velice zajímalo, jak moc jsou dálkoví migranti flexibilní při časování tahu na a ze zimovišť. Postupně jsem se podílel na výzkumu migrace za pomoci geolokátorů u lindušky úhorní (**Studie 10**), lejska bělokrkého (Briedis et al. 2016a), černošavlého (**Studie 11**), černošavlého (Briedis et al. 2016b), slavíka modráčka (Lislevand et al. 2015), pěnice hnědokřídle (Briedis et al. 2025) a vlašské (Wong et al. 2024). Doposud nepublikované mám data z lejsků malých, pěnice slavíkové ale i slavíků tmavých a obecných. O neúspěších se raději zmiňovat nebudu, ale obecně bylo i několik případů, kdy jsme neměli štěstí na několika druzích nebo populacích. Dnes již vím, že dobrá příprava je naprostá nutnost pro alespoň částečný úspěch.

Z těch několika publikovaných studií se zde, pro ilustraci, zmíním pouze o dvou. První se týká popisu migrace a zimovišť lindušky úhorní (**Studie 10**). Druhá se věnuje lejsku černošavlému. Vašek Beran se začal intenzivně věnovat hnízdní biologii lindušky úhorní v hnědouhelných lomech Mostecké pánve. Při rozpravách o druhu jsme byli někdy zaskočeni chováním lindušek, a to zejména jejich nepravidelnými přílety na hnízdiště a poté tichými vymizeními z lokalit po vyhnízdění. S ohledem na slušnou návratnost již okroužkovaných jedinců, jsem navrhl Vaškovi, ať zkusíme nasadit ptákům geolokátory. V roce 2013 tak byla nasazená první sada datalogerů. Po roce se podařilo odchytit osm jedinců. Dalších osm značených ptáků létalo po lokalitě s datalogery, ale nebylo možné je chytit. Zejména pro Vaška to bylo extrémně frustrující. Z osmi datalogerů bylo funkčních šest, rozhodli jsme se nečekat a zanalyzovat data. Analýzy dat se chopil tehdy můj doktorand Martin Briedis. S ohledem na biotopy, ve kterých se linduška vyskytuje, byla data kvalitní a odhady zimovišť byly velice spolehlivé. Získali jsme tak vůbec první vhled do migrace tohoto druhu. Překvapilo nás, že všichni jedinci zimovali v úzkém pásu západního Sahelu. Dalším zajímavým zjištěním byly tzv. intratropické přesuny, změny zimovišť v průběhu jedné zimy, u pěti ze šesti jedinců.

Do té doby se o tomto jevu u pěvců pouze spekovalo. K lindušce úhorní se v habilitační práci ještě vrátím. O pár let později jsme studii zopakovali s mnohem lepším technickým vybavením.

Druhou studii, kterou zde uvádím, je práce na migraci lejska černohlavého (**Studie 11**). Standa Bureš v letech 2012, 2014 a 2015 nasadil několik desítek geolokátorů na lejsky černohlavé na lokalitách v Jeseníkách a v severních Čechách. Bohužel, kombinace špatných sezón a taktéž predace hnízd vedla k zpětnému získání pouze 9 zařízení. Pro technické potíže jsme měli kompletní data za celý rok pouze u jednoho jedince a u zbylých sedmi byla data alespoň do zimy, a tak jsme mohli odhadnout lokaci jejich zimovišť. Přemýšlel jsem, jak s takhle částečně nekompletními daty naložit. Pro těch našich osm jedinců jsem se rozhodl pro popisná data. Několik let předtím Ouwehand et al. (2016) publikovali data z několika evropských populací. Některé odvážné závěry této studie se mi ale nezdály. Rozhodl jsem se proto sesbírat všechna dostupná data o lejscích černohlavých a re-analyzovat tuto studii s větším datovým souborem. Pro analýzy jsme tak měli údaje o 76 lejscích sledovaných za pomoci geolokátorů. Zjistili jsme, že naši ptáci se na zimovištích značně překrývají s jedinci z jiných západoevropských hnízdních populací. Z dat byl patrný pouze klastr britských a finských jedinců od zbylých populací. Mezi populacemi bylo patrné, jak jsou jednotlivé fáze ročního cyklu spolu silně prokorelované. V kontrastu se studií Ouwehandové, jsme nepotvrdili některé z jejich dřívějších závěrů. Rukopis prošel poměrně hladce recenzním řízením v *Journal of Ornithology*. Za léta recenzních řízení jsem si ale všiml jedné věci. Recenzenti poměrně často řeší návratnost ptáků s geolokátory, současně častokrát ignorují technickou stránku analýzy dat z geolokátorů. Relativně častou kritikou je, že nevíme, jaký dopad mají tato zařízení na chování ptáků.

## II. Migrace – nástup multisenzorových dataloggerů

### Studie 12

Briedis, M., Beran, V., **Adamík, P.** & Hahn, S. 2020: Integrating light-level geolocation with activity tracking reveals unexpected nocturnal migration patterns of the tawny pipit. *Journal of Avian Biology* 51: e02546.

### Studie 13

**Adamík, P.**, Wong, J. B., Hahn, S. & Krištín, A. 2024: Non-breeding sites, loop migration and flight activity patterns over the annual cycle in the Lesser Grey Shrike *Lanius minor* from a north-western edge of its range. *Journal of Ornithology* 165: 247–256.

### Studie 14

Wong, J. B., **Adamík, P.**, Bažant, M. & Hahn, S. 2024: Migration and daily flight activity patterns in the barred warbler *Curruca nisoria* over the annual cycle. *Journal of Vertebrate Biology* 73: 23085-1.

Od roku 2017 se naskytla možnost nasazení nového typu dataloggeru na ptáky. Tento typ zaznamenával kromě klasické intenzity světla i tlak a akceleraci. Nevýhodou byl váha, a to od 1,3 g. Výběr druhů, pro které by byl tento datalogger vhodný, byl tedy omezen na větší pěvce. Rozhodil jsem sítě a znova kontaktoval Vaška Berana s tím, že musíme studii na linduškách úhorních zopakovat, protože s tímto typem loggerů se otevřou doposud nevídané možnosti analýz migračního chování. Také jsme se dohodli s Tonem Krištínem, že vhodným kandidátem pro studium by byl ťuhýk menší. Tona velice zajímaly podrobnosti o migraci tohoto druhu, z důvodu setrvalého poklesu hnízdní populace v oblasti středního Slovenska. Do třetice mě velice lákalo studium migrace pěnice vlašské. Z pěnic je největší, hravě by unesla tento typ zařízení a kumulace zpětných hlášení z Blízkého východu slibovala zajímavá data o východní tahové cestě tohoto druhu. Naštěstí se v té době na lokalitě u Znojma intenzivně věnoval odchytům pěnic Mirek Bažant. Obvykle jsme na každé lokalitě kombinovali klasické světelné geolokátory s multisenzorovými dataloggeri. Velikost vzorku byla pro všechny tři druhy docela skromná, ale to bohatě vyvážily získané poznatky.

Naší první publikovanou studií byla analýza pěti jedinců lindušky úhorní (**Studie 12**). Akcelerometr zaznamenával aktivitu každých 5 minut, barometrické čidlo každých 30 min. Když jsme nastavili hranici aktivity na alespoň 1 hod nepřetržitého letu, zjistili jsme, že lindušky měly v průměru kolem deseti tahových zastávek na jejich cca 5000 km dlouhé cestě na africká zimoviště. Velkým překvapením bylo, že se do té doby lindušky uváděly jako typičtí denní migranti. Naše data ale přinesla důkaz o tom, že kolem dvou třetin doby tahu ptáci letí přes noc. Dalším překvapením bylo, že většina přeletů trvala pouze pár hodin (průměrně 4,5 hod) a maxima byla dosažena při překonávání Sahary (kolem 20 hod non-stop letu). Celá cesta mezi hnízdišti u města Most a africkými zimovišti trvala v průměru 134 hodin čistého letového času. Překvapením bylo i časování odletů v noci. Odehrávalo se převážně po západu slunce, ale rozptyl časování byl extrémní a prakticky se lindušky zvedly kdykoliv v průběhu noci. Tento typ dataloggeru jednoduše přinesl další revoluci v studiu migrace a musím se přiznat, že jsem pokaždé zvědavý jako malý kluk na to, jaké výsledky stažená data přinesou. Toto byl jeden z nejkrásnějších pocitů ve vědě.

Dalším druhem, který přišel na řadu, byl ťuhýk menší. Ťuhýci se ukázali jako jedni z nejhorších druhů pro zpětný odchyt a myslím, že jsme si při tom prošli galejemi. Zpočátku jsme nasadili 10 multisenzorových dataloggerů, ale o dva roky později jsme se rozhodli pro dalších 10 speciálních zařízení, která jako prototypy laskavě poskytl Erich Bächler. Tyto loggery umožňovaly stažení dat přes VHF na dálku. Ale i tak celá studie stojí na analýze dat pouze ze dvou jedinců (**Studie 13**). Osobně si myslím, že víc už asi nikdo nezíská. Oba jedinci zimovali v Botswaně, přičemž podrobné údaje o tahu prezentujeme v práci. Zmíním jenom několik zásadních poznatků. Při podzimním tahu jsme zaznamenali dvouměsíční zastávku v Sahelu/Saharské oáze a až posléze přilet na zimoviště. V průběhu překonávání Sahary docházelo při východu Slunce k náhlému stoupání z letové hladiny kolem 500 až 1000 m n. m až do výšek kolem 3000 m n. m. Obvyklá výška letové hladiny byla kolem 1 až 3 km, maximum 4530 m n. m. Na této práci je ještě jedna důležitá věc. Byla to jedna z prvních studií, ve které

jsme použili nový přístup pro odhad polohy jedince na základě tlaku. Raphaël Nussbaumer přišel s geniální myšlenkou, že veřejně přístupná data o atmosférickém tlaku, dostupná v prostorovém rozlišení 0,25° stupně a časovém rozlišení 1 hod (Hersbach et al. 2023), by se dala propojit s údaji získaných od ptáků. Logika byla taková, že pokud je jedinec na daném místě delší dobu, lze časovou řadu tlaku zaznamenanou na jeho čidle přiřadit s jistou mírou pravděpodobnosti k podobné časové řadě tlaku v globálním datasetu ERA5 (Nussbaumer et al. 2023). Tato metoda vede k mnohem přesnějším odhadům lokace ptáků, přibližně na úroveň 25 x 25 km.



*Obr. 5. Pár tuhýka menšího na hnízdní lokalitě v obci Hriňová, Slovensko. Jedinec vlevo má geolokátor na zádech. Foto: Martins Briedis.*

Třetí studií s novým typem dataloggerů a s určováním lokace na základě tlaku byla práce na pěnici vlašské (**Studie 14**). I zde jsme měli k dispozici mix klasických světelných geolokátorů a multisenzorových dataloggerů. Práce je také se skromným „nkem“ pouze tři jedinců, na druhou stranu o migraci tohoto druhu se doposud vědělo velice málo a každý údaj tak byl cenným příspěvkem. Několik zajímavých poznatků: po překonání Rudého moře se ptáci na delší dobu zastavili v Súdánu (podobnost s tuhýkem menším po překonání velké bariéry). Zimoviště se nacházela v západní Keni a na jihu Etiopie. Je to striktně noční migrant a většina odletů na noční tah se udála obvykle do hodiny od západu slunce. Přesun mezi hnízdištěm u Znojma a východoafrickými zimovišti trval ptákům 140 až 168 hodin čistého letu.

### III. Migrace – od popisů k pochopení mechanismů a klíčových faktorů

#### Studie 15

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

V létě 2013 mě Steffen Hahn pozval do Sempachu na pracovní workshop k jednotné analýze dat z geolokátorů. Při prohlížení syrových data z geolokátorů z našich lejsků nám oběma padla do oka jedna zdánlivá drobnost. Když prohlížíte data za celý rok, tak vidíte, že na základě množství světla, které dopadalo na senzor, je záznam velice variabilní, a i v průběhu jednoho dne se často střídají malé a velké intenzity světla. To je logické, protože obvykle se pták pohybuje ve vegetaci a stínění významně ovlivňuje množství dopadajícího světla. Všimli jsme si ale jedné anomálie. Obvykle pouze na jeden až dva dny v roce bylo v záznamech opravdu hodně světla a tento záznam nebyl téměř přerušován. Jako by každý jedinec byl na jeden nebo dva dny na přímém slunci bez žádného zastínění. Vypadalo to jako chyba přístroje. Prošli jsme ještě několik záznamů jiných jedinců, a i tam se to zopakovalo. Požádal jsem Steffena o možnost podívat se na data z jiných projektů, stejný vzorec se opakoval i u rákosníků. Bylo jasné, že toto není anomálie, ale pravidelně se opakující vzorec, vždy na podzimním a jarním tahu. Shodli jsme se, že jediné možné vysvětlení je, že záznam reflektuje non-stop let přes den. Hned jsem si vzpomněl na kultovní práce Moreaua, který již před desetiletími predikoval, že ptáci musí překonávat Saharu na jeden zátaž, a to dlouhými nepřetržitými lety. Proti tomu ale stály recentní poznatky kolegů ze Sempachu, kteří s radarem sledovali tah pěvců v oblasti západní Sahary. Z intenzity tahu dle sledování tzv. migratory traffic rate na jejich radaru viděli, že nejhustší letový provoz je krátce po západu slunce a že přes den skoro žádní ptáci nad radarovým polem nepřelétali. Z toho usuzovali, že ptáci musí přes den odpočívat na Sahaře (Schmaljohann et al. 2007). Felix Liechti tak krotil mé nadšení. Následovalo velice intenzivní období, ověřovali jsme, kde se ptáci nacházejí před a po zmíněné světelné anomálii. Pracovně jsme si to nazvali „full light mystery“. Ještě ve stejném roce jsem sezval do Olomouce několik kolegů na pracovní workshop, kde jsme podrobně analyzovali všechna dostupná data a intenzivně jsme verifikovali, jestli se opravdu jedná o přelety přes Saharu. Profesně mám z této studie velkou radost, protože znamenala rozsáhlou spolupráci mezi několika kolegy a celé jsem to musel koordinovat. Každé tvrzení muselo být podloženo podrobnými analýzami. Problém ale byl v postoji některých kolegů, kteří byli, s ohledem na jejich dřívější radarové studie, velice skeptičtí. Asi málokdo chce popřít léta svého předchozího výzkumu. Rukopis jsem zaslal do britských Proceedings B, ale posudky byly negativní. Hlavní výtkou byl malý vzorek ptáků a „lack of novelty“, protože právě v tom roce vyšla v Biology Letters první studie, která na severoamerickém pěvci prokázala nonstop přelet Mexického zálivu (DeLuca et al. 2015). Vtipné bylo, že ve stejném časopise vyšla v dubnu 2016 práce pouze na jednom druhu, lejskovi černohlavém, která také potvrzovala nonstop přelety Sahary. Rukopis jsem zaslal do Nature Communications, tam ho ale zamítli bez recenze a doporučili

transfer do Scientific Reports, kde nakonec i vyšel. Viděno zpětně, tato studie změnila pohled na schopnost malých pěvců překonávat velké bariéry dlouhými nepřetržitými lety. V migrační ekologii pěvců je hodně citovaná.

#### Studie 16

Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M. & **Adamík, P.** 2016: Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *Journal of Avian Biology* 47: 743–748.

Po získání společného GAČR projektu s Petrem Procházkou jsme se pustili do nasazení většího množství geolokátorů na lejsky. V prvních letech jsme ale zaznamenali poměrně vysokou poruchovost zařízení, a tak jsem řešil, jak dobře výsledky prodat. Napadlo mě spojit se s kolegy z Uppsaly, kteří tou dobou nasazovali geolokátory na ostrově Gotland v Baltickém moři. Zpracování dat dostal za úkol Martins Briedis. Když jsme seděli nad výsledky a srovnávali data pro moravské a švédské ptáky, všiml jsem si nápadného posunu jednotlivých fází ročního cyklu. Švédští ptáci byli vždy opoždění. Celý cyklus se ale resetoval na zimovištích. Vybavil jsem si stěžejní studii Davida Lacka (1950), který postuloval tezi, že existuje latitudinální gradient v časování hnízdění u evropských pěvců a že ten je formován s postupujícími fenofázemi jara. Celé to sedělo i se studií Conklina et al. (2010) na břehouších, kdy jasně ukázali, jak si latitudinálně separované populace udržují vlastní časování stěžejních fází ročního cyklu. Recenzenti byli z rukopisu nadšeni a šéfredaktor označil článek jako „Editor’s choice“. Velice mě i po letech těší, když v prezentacích kolegů vidím stěžejní obrázek z naší studie.

#### Studie 17

Briedis, M., Hahn, S., Krist, M. & **Adamík, P.** 2018: Finish with a sprint: Evidence for time-selected last leg of migration in a long-distance migratory songbird. *Ecology and Evolution* 8: 6899–6908.

Ve chvíli, kdy byla k dispozici migrační data z několika desítek jedinců lejska bělokrkého, jsme se dostali do komfortní situace. Věděli jsme, že v oblasti migrace ptáků je celá řada hypotéz, která čeká na otestování. Martins Briedis si při přípravě své disertační práce všiml, že poslední kus jarní cesty na hnízdiště nebo ten podzimní na zimoviště trvá kratší dobu. Nápadně to připomínalo hypotézu Thomase Alerstama (2006). Dle tzv. „sprint migration“ hypotézy migranti proměnlivě optimalizují své energetické výdaje a na začátku tahu minimalizují energii. Kdežto v závěrečné části tahu optimalizují dobu přiletů a jsou pod časovým tlakem. Studie tak byla jedním z prvních empirických potvrzení Alerstamova teoretického modelu. Také jsme potvrdili, že vnitro sezónní opozdilci reagují na svou situaci tak, že přidávají tempo a migrují rychleji než jedinci, kteří se vydali na tah dříve.

## Studie 18

Briedis, M., Krist, M., Král, M., Voigt, C. C. & **Adamík, P.** 2018: Linking events throughout the annual cycle in a migratory bird—non-breeding period buffers accumulation of carry-over effects. *Behavioral Ecology and Sociobiology* 72: 93.

Tato studie je pro mě jedna z nejdůležitějších. V terénu jsme pracovali ve dvou týmech, jeden, veden mnou na budkové populaci na Sovinecku v Nížkém Jeseníku a druhý, veden Milošem Kristem na Velkém Kosíři u Prostějova. Na lejsky jsme nasadili 234 geolokátorů a očekávali, že získáme vysněný datový soubor pro komplexní analýzu tzv. přenosových efektů. Vyhodnocení dat ze tří let práce v terénu dostal za úkol, jako nosnou studii pro svou disertační práci, Martins Briedis. V roce 2011 vyšlo zásadní review o tzv. přenosových efektech u živočichů (Harrison et al. 2011). V principu se jedná o to, že zkušenost s dobrými nebo špatnými podmínkami v průběhu nějaké životní fáze se později „vleče“ s daným jedincem i následně v životě. Lejsek bělokrký se jevil jako vhodný modelový druh pro ověření přenosových efektů. Studie byla komplexní, na jedné z ploch byl Milošem Kristem doplněn i manipulační experiment s rodičovským úsilím a pro podmínky na zimovišti jsme se pojistili analýzou izotopů uhlíků, která by indikovala sušší nebo vlhčí zimoviště. Výsledky byly velice komplexní. Zásadní bylo prokázání silného dominového efektu, kdy jednotlivé fáze ročního cyklu byly spolu silně prokorelovány. Zjistili jsme také, že zvýšená rodičovská investice vedla k opoždění podzimní migrace a celkově ke kratší době pobytu na zimovištích. V kontrastu s jinými druhy, jsme nezjistili vliv časování hnízdění na následné fáze ročního cyklu. Také jsme nezjistili žádný vliv podmínek na zimovišti na následné fáze. Svým komplexním přístupem je to dodnes jedna z mála studií na ptácích, která vyhodnotila přenosové efekty.

## Studie 19

Briedis, M., Hahn, S. & **Adamík, P.** 2017: Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecology* 17: 11.

Práce na migraci lejsků mě zavedla i k jednomu velice záhadnému druhu. Lejsek černokrký byl donedávna poddruhem lejska bělokrkého, a tak se o jeho migraci prakticky nic nevědělo. Na východě Bulharska jsme měli možnost nasazovat na tento druh po dobu několika let geolokátory, čímž jsme získali velice cenná data, ukazující na zimoviště v oblasti východoafrických jezer (Briedis et al. 2016b). Průběh jara 2015 byl v Bulharsku velice odlišný od předchozích let. V oblasti celého východního Mediteránu bylo tehdy mimořádně chladné jaro. V Bulharsku byla toho roku vegetace opožděná ve vývoji oproti roku 2014 o 29 dní. Pocítili jsme to na vlastní kůži, když jsme na konci března v lesích, v chladu, marně vyhlíželi první přelety lejsků. V roce předtím přiletěli lejsci kolem 2. dubna, v chladném roce až 10. dubna. V tomto studeném roce se nám navrátilo dvakrát méně okroužkovaných kontrolních ptáků než v roce obvyklém. Zpětnou analýzou průběhu migrace a tahových zastávek jsme v těchto dvou rozdílných sezónách ukázali, že ptáci odpověděli na nepřízeň počasí prodloužením délky

tahové zastávky v Mediteránu z obvyklých pěti na 15 dní. Obecně se má za to, že dálkoví migranti jsou vystaveni rizikům kdekoliv na jejich dlouhé cestě mezi hnízdišti a zimovišti (Tøttrup et al. 2012). Tato studie byla a pořád je jednou z mála, které přinesly důkaz o tom, že rizika v podobě nepřízně počasí mohou nastat i v průběhu migrace.

### 3. Závěr

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Předložený habilitační spis tvoří užší výběr z různých směrů, kterým jsem se odborně a často společně se svými studenty věnoval. Záměrně jsem vybral pouze studie spojené s fenologií, migrací a obecně jevy spojenými s organizací ročního cyklu. Některé studie byly čistě konfirmační, jiné rozšiřující rozsah poznatků. Velice rád mám studie, které přinášejí kus dobré „natural history“. Jako dlouholetý muzejník jsem za léta studia pramenů vyzoroval jeden robustní vzorec. Dobré „natural history“ studie nestárnou a bývají zdrojem dat i desetiletí po jejich publikování.

Zejména studie o migraci přinesly naprosto zásadní informace o ekologii jednotlivých tažných druhů a prolomily tak bariéru domněnek nebo indicií. To je samo o sobě velice přínosné, protože nám to pomáhá lépe chápat organizaci ročního cyklu dálkových migrantů. Ve světle rychle probíhajících změn v krajině a klimatu je dobré mít základní referenční data o těchto druzích. Dalším důležitým aspektem je, že dílčí poznatky od jednotlivých druhů jsou průběžně propojovány do syntetických studií, které se dívají komplexněji na některé ekologické aspekty. I díky tomu některé z mých prací přispěly do komplexních studií o protandrii (Briedis et al. 2019), vzorcích přiletů do Evropy (Briedis et al. 2020), adaptivních odpovědích na klimatickou změnu (Radchuk et al. 2019) nebo vlivu samotných geolokátorů na ptáky (Brlík et al. 2020).

### 4. Poděkování

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Děkuji všem svým studentům za obohacení, které mi přinesla práce s nimi. Největší radost jsem vždy měl a mám z těch, kteří mě přerostli. Tak by to mělo být. Děkuji i těm, kteří dělali školu jenom pro titul, a spolu jsme se trápili. Bylo podnětné poznávat vlastní limity. Práce vysokoškolského pedagoga dokáže být nesmírně tvořivá a já se vždy těším na konzultace se zvědavými studenty, kdy se ponoříme do hlubin poznání.

Děkuji všem svým spolupracovníkům za společné projekty a tvrdou práci vydřená data v terénu. Jsem rád, že mám kolem sebe mnoho inspirativních lidí a děkuji jim za všechny plodné diskuse, rady a pomoc. Také děkuji všem těm, kteří mě nasměrovali do Olomouce. Vřelé díky patří i těm, kteří mě podporovali a vytvořili zázemí pro výsledky této habilitační práce.

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### III. Migrace – od popisů k pochopení mechanismů a klíčových faktorů

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

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Briedis, M., Hahn, S. & **Adamík, P.** 2017: Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecology* 17: 11. DOI: 10.1186/s12898-017-0121-4.

## 7. Publikace tvořící habilitační spis

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## Studie 1

Adamík, P. & Pietruszková, J. 2008: Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithologica* 43: 119–128.

## Advances in spring but variable autumnal trends in timing of inland wader migration

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Adamík P., Pietruszková J. 2008. Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithol.* 43: 119–128. DOI 10.3161/000164508X395225

**Abstract.** Advancement of spring migration in response to recent global climate change is well documented for a variety of bird species, but the pattern for autumn migration is rather equivocal. During a 42-year period (1964–2005) the changes in timing of spring and autumn migration of eight wader species were studied at multiple inland sites in Central Europe (Czech Republic and Slovakia) using ringing data. While a clear pattern was found for the advancement of the spring passage, there were variable trends in the timing of the autumn passage. Three species significantly advanced (Wood Sandpiper, Common Sandpiper and Dunlin), three species delayed (Ruff, Snipe and Little Ringed Plover), and two species did not change the timing of the autumn passage (Little Stint and Green Sandpiper). Earlier studies had predicted that long-distance migrants wintering south of the Sahara would advance the timing of autumn migration, while short-distance migrants would postpone it. However, our findings do not fully conform to these predictions. Across species, the timing of both the spring and autumn passages was negatively associated with the winter North Atlantic Oscillation (NAO) index, suggesting that even in long-distance migrants the timing of migration might be under direct environmental control. In conclusion, phenological responses of birds to recent changes in climate are quite coherent for the early phenological phases; however, the responses to later phases are not so straightforward, and the present study contributes to this diverse pattern.

**Key words:** *Tringa*, *Calidris*, *Actitis hypoleucos*, *Gallinago gallinago*, *Philomachus pugnax*, autumn migration, bird ringing, climate change, limnic habitat, passage

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### INTRODUCTION

Humans are increasing their pressure on the world's ecosystems in multiple ways. This pressure is mirrored in recent changes in climate, land use, biogeochemical cycles and mobility of organisms (Chapin et al. 2000, Parmesan 2006). As a consequence, those animals whose life cycles take place over large spatial scales or at multiple sites might be under increased threat. This is because human-induced alterations are likely to affect some part of the animal's life cycle. Waders, one of the world's longest-distance-travelling groups of animals, are among the most likely candidates to be negatively affected by human activities. Indeed, their populations have been declining at an accelerated rate (Stroud et al. 2004). The vulnerability of waders stems from their life histories. Many of them breed at high latitudes where

adverse weather conditions can easily lead to failed breeding attempts and higher mortality (Ganter & Boyd 2000). During migration they rely on stopover sites, which occur as discrete patches in mostly unsuitable landscape, for refuelling and moult, and similarly their wintering sites are often limited to a dozen or so places. Both the stopover and wintering sites are frequently located in coastal areas, estuaries, limnic habitats, ponds or sewage farms; all of which are either close to human settlements, or human activities are high in these sites. Successful refuelling, a necessary prerequisite for their further migration (Zwarts 1990), might not only be affected by direct human disturbance (Baker et al. 2004), but also indirectly, through the interplay of weather and availability of food. Since most waders rely on an arthropod diet, and arthropod activity is linked to weather, their migration must be fine-tuned to available

food and prevailing weather conditions (Piersma et al. 1994, Lindström & Agrell 1999, Baker et al. 2004, Green et al. 2004, Piersma & Lindström 2004).

Recent changes in climate are also expected to affect waders in several of their life-history stages (Boyd & Madsen 1997, Lindström & Agrell 1999, Rehfisch & Crick 2003, Piersma & Lindström 2004). Climate has been identified as an important factor influencing their distribution in wintering quarters (Cepák 2001, Austin & Rehfisch 2005), timing of breeding (Both et al. 2005, Pearce-Higgins et al. 2005), breeding productivity (Beale et al. 2006), and timing of migration (Hildén 1979, Anthes 2004). However, comprehensive data on long-term changes of their passage are rather rare (e.g. Anthes 2004), and the majority of phenological studies, focusing mostly on songbirds, considered only a few wader species (reviewed in Lehikoinen et al. 2004). In addition, studies from the spring passage heavily outnumber those on autumn migration.

In this study we present phenological data on changes in timing of spring and autumn passage for eight wader species from the Czech Republic and Slovakia covering a time span of 42 years, 1964–2005. We used bird ringing records to document changes in migration phenology. The use of ringing records has two main advantages. Nearly all birds can be aged and no repeated counts of staging individuals are included in calculations of phenology statistics (observations of passing birds might be biased due to repeated counts of staging individuals). Since age-related differences in timing of migration are well recognized in waders (van de Kam et al. 2004), failing to discriminate between age groups (i.e. pooling data from all age groups) may lead to erroneous conclusions (Anthes 2004).

## METHODS

Data on the timing of wader migration were compiled from the ringing records archived in the Bird Ringing Centre of the National Museum in Prague, Czech Republic. These records comprise data on birds ringed during spring and autumn passage at multiple sites (mostly fishponds, water reservoirs and wetlands) in the Czech Republic (74% of records) and Slovakia (26% of records). The majority of waders pass through these sites, however, four of the eight studied species (Snipe *Gallinago gallinago*, Little Ringed Plover *Charadrius dubius*, Common Sandpiper *Actitis hypoleucos* and

Green Sandpiper *Tringa ochropus*) breed in small numbers in both countries (Danko et al. 2002, Štátný et al. 2006). Therefore, it is likely that a small fraction of the ringed birds were local breeders. Based on ringing data we could not separate local breeders from birds on passage for the Lapwing *Vanellus vanellus*, therefore we omitted this species from our analyses (Žídková et al. 2007). We also included only those species that had been continuously ringed for > 20 years with a minimum of 10 individuals per passage period. In this study data from all ringing sites were pooled together. This is because, given the very small span in latitude of the former Czechoslovakia, there are likely to be negligible between-site differences in timing of migration. Between-site differences are visible at much larger spatial scales, e.g. southern and northern European stopover sites (OAG Münster 1994).

To separate spring and autumn passage, for each species, we used the local minimum of the number of ringed birds between these two migration events over the whole year. For this study we only considered data covering the years 1964–2005. Prior to 1964 there was a different data archiving system and the extraction of ringing records prior to this date would be extremely time-demanding. For each ringed bird we recorded its date of ringing, age, sex and ringing location. For autumn birds we split waders into two age groups: 1<sup>st</sup> year birds and adults. As 1<sup>st</sup> year birds (juveniles) we considered those individuals that were hatched in the year of ringing, i.e. they were on their first passage to wintering quarters. The numbers of ringed birds during spring passage were too small to be divided into the two age categories.

Data on the timing of migration are presented in two ways. First, for each year and species we calculated from all ringing dates the onset, median and end (5<sup>th</sup>, 50<sup>th</sup> and 95<sup>th</sup> sample percentiles) of each migration period with birds of all age groups pooled together (i.e. including also those birds which could not be reliably aged). To date, this is the most common way of presenting either spring or autumn passage (Lehikoinen et al. 2004). However, it is well known for waders and many other migratory birds that adults leave the breeding sites well ahead of the juveniles (e.g. van de Kam et al. 2004). This time lag could lead to bimodality in data but also it could obscure age-related trends in timing of migration. Therefore, annually separate phenology statistics were calculated for juvenile and adult birds.

To detect trends in timing of passage, we assessed the relationship between year and phenology variables. Trends in timing of migration were assessed by least square regression and by quantile regression (QR). In QR each ringed bird is included in calculating the 5<sup>th</sup>, 50<sup>th</sup> and 95<sup>th</sup> sample percentile. The QR has several advantageous properties (e.g. it does not assume homogeneity of variances, data can be autocorrelated) over the least square regression (Cade & Noon 2003). On the other hand, years with different numbers of caught birds do not contribute equally to calculations. Therefore, following Tøttrup et al. (2006), we prefer presenting the least square regression results and the QR estimates are presented in Appendices I and II. The QR estimates were calculated in SAS version 9.1 (quantreg procedure).

As a second step, we assessed whether the timing of migration is linked to the North Atlantic Oscillation (NAO) index (Hurrell 1995). We used the mean winter NAO index (calculated for the months December–March, i.e. for the period preceding the spring and autumn passage) available at <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>. The Czech and Slovak ringing recoveries suggest that the northern breeding locations of the eight studied species spread from Scandinavia to the Russian Far East (Cepák et al. 2008); therefore, we did not attempt to include local climate variables from the breeding grounds to explain the phenology. Similarly, birds on passage were ringed at several sites across the two countries. Thus, it would be rather difficult to use local weather variables at these stopover sites. While we feel that the inclusion of local weather would help to better

understand the link between climate and avian phenology, our multiple-site collected data are unsuitable for this purpose. Here we rather use a large-scale composite variable which might be better suited for this type of data (Stenseth & Mysterud 2005). During 1964–2005 there was a significantly positive trend in the mean winter NAO index (slope =  $0.06 \pm 0.02$  SE,  $p = 0.026$ ). Therefore, we used the residuals (dNAO) from the linear regression of the NAO index on year as an explanatory variable.

## RESULTS

### Spring passage

Four (Wood Sandpiper *Tringa glareola*, Common Sandpiper, Ruff *Philomachus pugnax* and Little Ringed Plover) of eight wader species were ringed in sufficient numbers to calculate trends in their spring passage. All four species advanced their timing of passage (Table 1). Of the 12 series, 11 showed trends towards earlier passage, of which six were significant. The advancement was most prominent for the Wood Sandpiper (Fig. 1), Common Sandpiper and the early migratory phase of Ruff. The Little Ringed Plover passage showed a very weak shift. Results from the QR produced very similar results (Appendix I).

### Autumn passage

There was no coherent trend in autumn migration. Three species (Wood Sandpiper, Common Sandpiper and Dunlin *Calidris alpina*) significantly advanced their phenology in at least one phenological phase. Similarly, three species (Ruff, Snipe

Table 1. Regressions of timing of spring passage on year and the detrended mean winter NAO index, 1964–2005. Years — number of years with available data. Median date — median passage dates.

Spring passage	Years	Phase	Median date	Passage on year			Passage on dNAO		
				B	SE	p	B	SE	p
<i>Tringa glareola</i>	36	5%		-0.20	0.09	0.025	-1.44	0.51	0.008
		50%	5.5.	-0.26	0.07	< 0.001	-0.66	0.45	0.149
		95%		-0.28	0.09	0.003	-1.17	0.55	0.041
<i>Actitis hypoleucos</i>	26	5%		-0.34	0.10	0.003	-0.76	0.45	0.102
		50%	3.5.	-0.23	0.09	0.015	-0.42	0.36	0.258
		95%		-0.03	0.25	0.901	-0.32	0.93	0.738
<i>Philomachus pugnax</i>	24	5%		-0.97	0.32	0.006	-2.92	1.27	0.031
		50%	25.4.	-0.35	0.27	0.199	-1.73	0.96	0.085
		95%		0.03	0.21	0.860	0.46	0.77	0.561
<i>Charadrius dubius</i>	37	5%		-0.15	0.16	0.371	-1.45	0.85	0.096
		50%	7.5.	-0.16	0.11	0.131	-0.71	0.57	0.022
		95%		-0.14	0.09	0.171	0.41	0.54	0.450

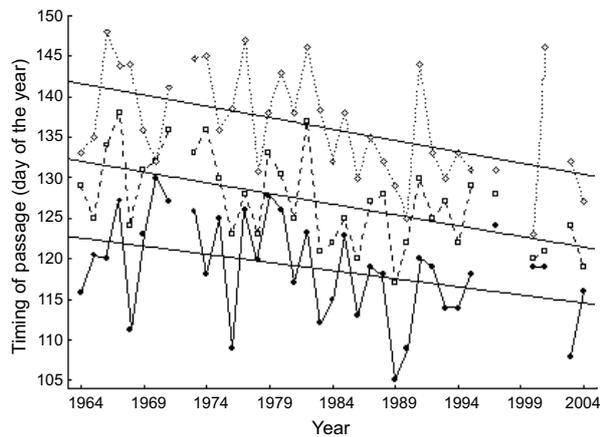


Fig. 1. Changes in timing of spring passage of the Wood Sandpiper in the Czech Republic and Slovakia, 1964–2005. Separate linear regression lines are shown for the onset, median and end of the passage (i.e. 5<sup>th</sup>, 50<sup>th</sup> and 95<sup>th</sup> sample percentiles of ringing dates). Only years with > 10 ringed individuals are included ( $n = 36$ ).

and Little Ringed Plover) significantly delayed their phenology in at least one phenological phase (i.e. the onset, median and the end of passage). No consistent trends were found for the Little Stint

*Calidris minuta* and Green Sandpiper (Table 2 and 3). Overall, within species, the phenological patterns were very similar between 1<sup>st</sup> year and adult birds. Division of the dataset on 1<sup>st</sup> year and adult birds did not lead to significantly different trend estimates (paired t-tests on slopes between the full dataset from Table 2 and dataset with 1<sup>st</sup> year birds only from Table 3,  $n = 8$ ,  $p = 0.08$ – $0.74$ ). The QR produced similar pattern in trends as the least square regressions, though more trend estimates from QR were significant at  $p = 0.05$  (Appendix II).

### Phenology and NAO

The winter NAO index was mostly negatively associated with all stages of both spring and autumn passage. In spring, 10 out of 12 series, of which three were significant, showed a negative relationship with NAO. In autumn, 20 out of 24 series, of which seven were significant, showed a negative relationship. Similarly, when 1<sup>st</sup> year and adult birds were evaluated separately, all 12 series for adults were negative, while 20 out of 24 series for juveniles showed a negative relationship with NAO. Division of the dataset on 1<sup>st</sup> year and adult birds did not improve the fit in any

Table 2. Regressions of timing of autumn passage on year and the detrended mean winter NAO index, 1964–2005. Regressions were fitted to pooled data for all age classes. WQ — principal wintering quarters (A — Africa, M — the Mediterranean region). Median date — median passage dates.

Autumn passage	WQ	Years	Phase	Median date	Passage on year			Passage on dNAO		
					B	SE	p	B	SE	p
<i>Tringa glareola</i>	A	40	5%		-0.06	0.14	0.688	-1.97	0.56	0.001
			50%	10.8.	-0.16	0.07	0.028	-0.76	0.32	0.022
			95%		-0.10	0.07	0.168	0.09	0.32	0.779
<i>Actitis hypoleucos</i>	A	41	5%		-0.06	0.07	0.386	-0.59	0.32	0.070
			50%	7.8.	-0.17	0.06	0.006	-0.46	0.28	0.104
			95%		-0.16	0.09	0.106	-0.67	0.43	0.133
<i>Philomachus pugnax</i>	A	39	5%		0.55	0.20	0.011	-1.16	0.99	0.251
			50%	27.8.	0.51	0.18	0.008	-0.55	0.90	0.545
			95%		0.04	0.15	0.793	-0.34	0.66	0.606
<i>Charadrius dubius</i>	A	39	5%		0.08	0.11	0.487	-0.81	0.63	0.202
			50%	6.8.	-0.19	0.11	0.111	0.16	0.68	0.816
			95%		-0.17	0.14	0.224	0.36	0.78	0.648
<i>Calidris minuta</i>	A	33	5%		-0.19	0.27	0.413	-1.74	1.09	0.124
			50%	9.9.	-0.07	0.13	0.593	-1.53	0.59	0.016
			95%		-0.06	0.13	0.629	-0.84	0.62	0.189
<i>Calidris alpina</i>	M	31	5%		-0.24	0.34	0.486	-1.25	1.43	0.389
			50%	18.9.	-0.40	0.25	0.114	-2.43	0.99	0.019
			95%		-0.29	0.20	0.169	-2.22	0.78	0.008
<i>Gallinago gallinago</i>	M	41	5%		0.30	0.12	0.017	-0.64	0.64	0.318
			50%	24.8.	-0.06	0.16	0.695	-1.83	0.72	0.015
			95%		0.28	0.18	0.136	-1.46	0.91	0.117
<i>Tringa ochropus</i>	M	38	5%		-0.10	0.19	0.597	-2.51	0.76	0.002
			50%	7.8.	-0.10	0.11	0.364	-0.25	0.51	0.615
			95%		-0.22	0.16	0.181	0.16	0.72	0.826

phase of migration (paired t-tests on slopes between the full dataset from Table 2 and dataset with 1<sup>st</sup> year birds only from Table 3,  $n = 8$ ,  $p = 0.17-0.85$ ).

## DISCUSSION

The timing of spring passage shifted in all four studied species toward earlier dates. This finding is consistent with other studies conducted on birds all over Europe (Lehikoinen et al. 2004, Gordo 2007). The earlier onset of spring migration was confirmed for waders across various sites (e.g. Gilyazov & Sparks 2002, Anthes 2004, Hubálek 2004, Croxton et al. 2006, Sparks et al. 2007).

However, for autumn passage we found variable trends among species. Three species advanced, three delayed and two species did not show any clear pattern in timing of passage. These variable shifts in timing of autumn migration are in line with other studies, which were mostly done on songbirds (Gatter 1992, Sokolov et al. 1999, Gilyazov & Sparks 2002, Jenni & Kéry 2003, Hüppop & Hüppop 2005, Tøttrup et al. 2006). Hence, the apparent dichotomy in trends found for a variety of songbirds holds also for waders. Jenni & Kéry (2003) predicted that long-distance migrants wintering south of Sahara would advance timing of autumn migration, while short-distance migrants would postpone it. Our findings do not fully conform to these predictions.

Table 3. Regressions of timing of autumn passage on year and the detrended mean winter NAO index, 1964–2005. Separate regressions were fitted to 1<sup>st</sup> year and adult birds. Median date — median passage dates.

Autumn passage	Years	Phase	Median date	Passage on year			Passage on dNAO		
				B	SE	p	B	SE	p
<i>Tringa glareola</i> ad	31	5%		-0.12	0.17	0.498	-1.66	0.49	0.002
		50%	25.7.	-0.64	0.23	0.001	-0.53	0.85	0.543
		95%		-0.51	0.24	0.038	-0.99	0.83	0.240
<i>Tringa glareola</i> juv	41	5%		-0.11	0.08	0.152	-1.00	0.31	0.003
		50%	13.8.	-0.18	0.07	0.016	-0.83	0.31	0.010
		95%		-0.06	0.08	0.480	0.25	0.35	0.487
<i>Actitis hypoleucos</i> ad	41	5%		-0.04	0.07	0.627	-1.00	0.28	< 0.001
		50%	28.7.	-0.44	0.08	< 0.001	-0.98	0.43	0.028
		95%		-0.51	0.14	< 0.001	-0.67	0.67	0.321
<i>Actitis hypoleucos</i> juv	41	5%		-0.15	0.07	0.034	-0.37	0.40	0.365
		50%	11.8.	-0.22	0.07	0.002	-0.78	0.31	0.015
		95%		-0.21	0.09	0.026	-0.24	0.50	0.639
<i>Philomachus pugnax</i> juv	30	5%		0.57	0.17	0.002	0.62	0.76	0.427
		50%	31.8.	0.34	0.17	0.053	-0.02	0.70	0.973
		95%		-0.11	0.23	0.603	-0.27	0.85	0.752
<i>Charadrius dubius</i> juv	40	5%		1.14	0.27	< 0.001	-1.03	1.91	0.591
		50%	8.8.	0.35	0.16	0.037	-0.05	0.99	0.962
		95%		0.05	0.18	0.787	1.03	1.03	0.324
<i>Calidris minuta</i> juv	31	5%		0.21	0.29	0.479	-1.62	1.40	0.257
		50%	9.9.	0.04	0.13	0.778	-0.96	0.63	0.137
		95%		-0.01	0.13	0.924	-0.62	0.63	0.082
<i>Calidris alpina</i> juv	28	5%		0.10	0.26	0.692	-1.79	0.89	0.054
		50%	19.9.	-0.59	0.26	0.029	-2.06	0.96	0.042
		95%		-0.54	0.22	0.022	-2.41	0.79	0.005
<i>Gallinago gallinago</i> ad	38	5%		0.27	0.16	0.102	-1.05	0.81	0.202
		50%	23.8.	0.34	0.21	0.109	-1.96	1.00	0.059
		95%		0.33	0.21	0.119	-0.71	1.05	0.504
<i>Gallinago gallinago</i> juv	42	5%		0.45	0.14	0.067	-1.07	0.72	0.145
		50%	24.8.	-0.09	0.19	0.610	-2.51	0.84	0.005
		95%		0.45	0.21	0.040	-1.83	1.06	0.093
<i>Tringa ochropus</i> juv	26	5%		0.21	0.22	0.343	-0.65	0.85	0.450
		50%	8.8.	-0.07	0.14	0.565	-0.20	0.52	0.697
		95%		0.22	0.22	0.330	0.76	0.85	0.382

For example, two long-distance migrants, the Ruff and Little Ringed Plover delayed their passage, while the Dunlin, a short-distance migrant wintering in the Mediterranean, advanced its passage. In northern Germany, Anthes (2004) found delays in timing of autumn migration in three species of *Tringa* sandpipers. In contrast to that study, we found an advancement of autumn passage for the Wood Sandpiper. As suggested by Wichmann et al. (2004), Wood Sandpipers passing through northern Germany use the East Atlantic Flyway (c.f. Anthes et al. 2002), while central European sites serve as refuelling sites for birds using the Mediterranean Flyway. In addition, in this species there are considerable differences in stopover ecology (e.g. body mass, stopover length) at various sites (Scebba & Moschetti 1996, Meissner 1997, Wichmann et al. 2004, Włodarczyk et al. 2007). Any long-term changes in site suitability (e.g. food supply, fluctuations in water levels) could on its own be responsible for changes in migration phenology. For example, increased food supply might lead to higher fattening rates of birds. Birds with sufficient fuel loads could leave the stopover site earlier and this could, in turn, affect the phenology statistics (i.e. seemingly advancing the timing of passage). However, the observed pattern of delays and advances could be a result of different trends in climate dynamics at breeding grounds. Despite the overall warming pattern in northern Europe, there are sites further east that show the opposite. Ahas et al. (2002) found that while plant phenology shifted toward earlier dates in western and central Europe, an opposite phenological shift was observed further east. Hence, if some of the wader populations breed in those sites that cooled, then this could explain the delays in their passage. Detailed knowledge of breeding sites for birds passing through inland Europe would be of great help. However, there is generally a lack of sufficient numbers of ringing recoveries from birds ringed at breeding grounds. Possibly, an analysis of stable isotopes from birds on both breeding and stopover sites could help (Procházka 2006).

The timing of both spring and autumn passage was negatively associated with the winter NAO index. This is a finding consistent with other studies (e.g. Hüppop & Hüppop 2003, Hubálek 2004, Stervander et al. 2005, Rainio et al. 2006). Hence, in years with high NAO index the timing of migration shifted toward earlier dates. The positive NAO index is associated with earlier onset of spring in much of northern and central Europe

(Aasa et al. 2004, Menzel et al. 2005). This could create favourable conditions for migratory birds on their spring passage (Vähätalo et al. 2004). Interestingly, the negative association between phenology and the NAO persisted even for the autumn passage. This could indicate that in years with a positive NAO phase there was a rapid progress of snowmelt at breeding grounds enabling earlier onset of breeding for waders. For example, it was shown that the timing of ice break-up in Scandinavian lakes is negatively associated with the winter NAO index (Blenckner et al. 2004). The earlier onset of breeding could then lead to earlier departure from these sites. In waders there is a well-known link between snowmelt, timing of arrival and breeding (Holmes 1966, Niehaus & Ydenberg 2006, Meltofte et al. 2007). However, whether this also mirrors an earlier onset of southward migration, except for years with low breeding success (e.g. Meissner 2005), is poorly known (c.f. Niehaus & Ydenberg 2006). Another possibility is that there are no environmentally forced changes in departure dates from both breeding and wintering sites (e.g. Piersma et al. 1990), but the shifts in passage phenology are mediated through changes at stopover sites. If climate changes the temporal dynamic of prey availability at stopover sites, then this could affect the length of stay and moulting pattern for these species. Given that the eight studied species use a variety of migration strategies, which often differ even within species' age classes (Gromadzka 1987, Gill et al. 1995, Meissner 1996, Balmori 2003, Remisiewicz & Wennerberg 2006, Włodarczyk et al. 2007), a mixed pattern in trends of passage phenology is likely to occur.

In conclusion, phenological responses of birds to recent changes in climate are quite coherent for the early phenological phases (i.e. spring migration, onset of breeding), however the responses to later phases (i.e. autumn migration, arrival at wintering quarters) are not so straightforward and the present study contributes to this diverse pattern. The above described example with different shifts for the two populations of the Wood Sandpiper emphasizes the need for more in-depth data on stopover ecology and from other sites across Europe.

## METHODOLOGICAL CONSIDERATIONS

The main advantage of using ringing records is that they enable separate estimates of phenological trends for different age classes and avoid

repeated counts of staging individuals. However, the main drawback is that the data may not be collected in a standardized way, leading possibly to biased estimates that could be a result of different activity of ringers (e.g. high activity during summer ringing camps) or different trapping methods. This could be a serious problem with single-site data. Our approach, when we calculated phenological characteristics across multiple sites where dozens of bird ringers were involved, is likely to minimize this problem. Comparisons between phenological characteristics derived from ringing records with local Czech studies (i.e. those based on counts of observed birds) show a good match for the majority of wader species (Pietruszková & Adamík, in prep.). The second major drawback of studies conducted at inland sites, in contrast to island or coastal bird observatories, is that the estimates of phenological characteristics are contaminated with local breeders. In particular in spring it is practically impossible to separate local breeders from birds on passage. In our case only the Little Ringed Plover and Common Sandpiper breed locally in sufficient numbers to possibly confound the phenological estimates. Despite these drawbacks, we have shown that the signal of changing phenology is clear even in data containing a considerable amount of noise.

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## STRESZCZENIE

### [Zmiany w terminach wędrówki jesiennej i wiosennej u siewkowców na śródłądziu]

Przyspieszenie terminów wiosennych wędrówek u ptaków w związku z globalnymi zmianami klimatycznymi jest dobrze udokumentowane dla wielu gatunków, natomiast taka sama prawidłowość w odniesieniu do migracji jesiennych jest raczej dyskusyjna. Podczas 42 lat badań (1964–2005) prowadzonych na obszarze dawnej Czechosłowacji obserwowano zmiany w terminach wędrówek wiosennych i jesiennych 8 gatunków siewkowców w oparciu o archiwalne dane z obrączkowań. Dla każdego roku i każdego gatunku określano początek, medianę i koniec okresu wędrówkowego. Ponieważ jednak u siewkowców terminy wędrówek dorosłych ptaków i osobników młodocianych mogą być różne, osobno potraktowane te grupy wiekowe (dorosłe i ptaki w 1 roku kalendarzowym). By uchwycić różnice w czasie wędrówki, użyto regresji kwadratowej oraz regresji QR. Ponieważ jednak w tym

drugim przypadku liczba schwytanych ptaków może znacząco wpływać na uzyskany obraz, wyniki przedstawiono w Appendix I i II. Kolejnym krokiem było sprawdzenie, czy czas wędrówki jest związany ze wskaźnikiem Oscylacji Północnego Atlantyku (NAO index). W pracy wykorzystano średnie zimowe wartości NAO dla grudnia–marca. Dla łączaka, piskliwca, bataliona i sieweczki rzecznej zebrano wystarczającą liczbę danych by oszacować kierunki zmian terminów wędrówki wiosennej. U wszystkich stwierdzono przyspieszenie (Tab. 1), przy czym najwyraźniej zmiany zaznaczone były u łączaka (Fig. 1). W przypadku migracji jesiennej zgromadzone dane nie dały jednoznacznego obrazu kierunku zmian. U łączaka, piskliwca i biegusa zmiennego zaobserwowano wyraźne przyspieszenie terminów wędrówki, natomiast u bataliona, kszczyka i sieweczki rzecznej wędrówka jesienna wyraźnie opóźniła się w badanym okresie. Dwa gatunki — biegus malutki i samotnik nie wykazały żadnych istotnych zmian (Tab. 2 i 3). Osobne analizy dla młodych i dorosłych osobników nie wpłynęły na uzyskane wyniki. Wartości NAO były w większości negatywnie skorelowane ze wszystkimi fazami wędrówki zarówno jesiennej jak i wiosennej.

Appendix I. Quantile regression estimates of changes in timing of inland spring migration, 1964–2005. N — the numbers of ringed birds.

Spring passage	N	Phase	All birds	
			B	p
<i>Tringa glareola</i>	2 108	5%	-0.27	< 0.001
		50%	-0.33	< 0.001
		95%	-0.39	< 0.001
<i>Actitis hypoleucos</i>	1 047	5%	-0.33	< 0.001
		50%	-0.30	< 0.001
		95%	0.05	0.768
<i>Philomachus pugnax</i>	2 658	5%	-2.00	< 0.001
		50%	-0.25	< 0.001
		95%	-0.15	< 0.001
<i>Charadrius dubius</i>	2 178	5%	-0.19	0.264
		50%	-0.17	< 0.001
		95%	-0.23	< 0.001

Appendix II. Quantile regression estimates of changes in timing of inland autumn migration, 1964–2005. Sample sizes, i.e. the numbers of ringed birds, for all and separate age categories are indicated below species names.

Autumn passage	Phase	All birds		1 <sup>st</sup> year birds		Adults	
		B	p	B	p	B	p
<i>Tringa glareola</i> 11 097, 7 179, 1 888	5%	0.10	0.070	-0.09	0.011	-0.07	0.451
	50%	-0.16	< 0.001	-0.18	< 0.001	-0.41	< 0.001
	95%	-0.11	0.003	-0.06	0.309	-0.83	< 0.001
<i>Actitis hypoleucos</i> 13 750, 7 428, 4 679	5%	-0.06	0.008	0.08	0.072	-0.06	0.167
	50%	-0.17	< 0.001	-0.11	< 0.001	-0.43	< 0.001
	95%	-0.29	< 0.001	-0.17	< 0.001	-0.65	< 0.001
<i>Philomachus pugnax</i> 2 572, 1 351, -	5%	0.75	< 0.001	0.10	0.643	-	
	50%	0.45	< 0.001	0.31	< 0.001	-	
	95%	-0.07	0.277	-0.17	0.182	-	
<i>Charadrius dubius</i> 3 160, 2 673, -	5%	0.04	0.521	0.20	0.009	-	
	50%	0.07	0.086	0.18	0.011	-	
	95%	-0.11	0.106	-0.12	0.105	-	
<i>Calidris minuta</i> 2 739, 1 996, -	5%	0.08	0.578	0.05	0.397	-	
	50%	0.00	0.999	0.00	0.999	-	
	95%	-0.31	< 0.001	-0.31	< 0.001	-	
<i>Calidris alpina</i> 2 960, 2 162, -	5%	-1.00	< 0.001	-0.11	0.343	-	
	50%	-0.22	< 0.001	-0.36	< 0.001	-	
	95%	-0.50	< 0.001	-0.75	< 0.001	-	
<i>Gallinago gallinago</i> 7 032, 2 931, 1 866	5%	0.19	< 0.001	0.25	< 0.001	0.17	0.002
	50%	0.00	0.999	-0.08	0.095	0.39	< 0.001
	95%	0.24	< 0.001	0.26	0.023	0.27	< 0.001
<i>Tringa ochropus</i> 1 378, 602, -	5%	-0.17	0.210	0.17	0.137	-	
	50%	-0.18	0.011	0.00	0.999	-	
	95%	0.12	0.499	0.50	0.031	-	

## Studie 2

Hušek, J. & Adamík, P. 2008: Long-term trends in timing of breeding and brood size in the red-backed shrike *Lanius collurio* in the Czech Republic, 1964–2004. *Journal of Ornithology* 149: 97–103.

# Long-term trends in the timing of breeding and brood size in the Red-Backed Shrike *Lanius collurio* in the Czech Republic, 1964–2004

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**Abstract** Climate change has affected breeding dates and clutch sizes in many bird species. To date, most of the studies aimed at assessing the effects of climate change on these phenological events in birds have been on hole-nesting species and the changes linked either to local climate variation or to some large-scale composite variables, such as the North Atlantic Oscillation (NAO). Relatively less is known about the climate responses of open-nesting birds and on the relative roles of climate variables at different scales. Using bird ringing records covering a time span of 41 years, we documented shifts in the timing of breeding and brood size in a long-distance migrant, the Red-Backed Shrike (*Lanius collurio*) from a central European population. We found a 3- to 4-day shift towards earlier breeding and an increase in brood size by approximately 0.3 nestlings since 1964. The Red-Backed Shrikes start to breed in May and rear the first nestlings in June. During the period 1964–2004, temperatures in May significantly increased, while the increase in June temperatures was not significant. Simultaneous tests on the influence of local climate

variables and the NAO index revealed a better performance of local climate. The increasing temperature in May was positively associated with the advancement of breeding. Similarly, at a local scale, higher May temperatures were followed by larger brood sizes, while a high amount of rainfall had a strong negative effect.

**Keywords** Breeding biology · Climate change · *Lanius collurio* · Long-term study · Red-backed shrike · Ringing data

## Introduction

Climate change has been shown to affect various aspects of bird phenology (Przybylo et al. 2000; Rodríguez and Bustamante 2003; Dunn 2004). Such studies have mainly focused on spring migration (Forchhammer et al. 2002; Tryjanowski et al. 2002; Cotton 2003; Hüppop and Hüppop 2003; Hubálek 2004; Vähätalo et al. 2004), egg-laying dates (Winkel and Hudde 1997; Przybylo et al. 2000; Both and Visser 2001; Sanz 2002; Cresswell and McCleery 2003), clutch size (Winkel and Hudde 1997; Przybylo et al. 2000; Sanz 2002; Winkler et al. 2002; Cresswell and McCleery 2003), fledging success (Przybylo et al. 2000; Rodríguez and Bustamante 2003) and/or egg size (Järvinen 1994; Tryjanowski et al. 2004).

Most of these studies have directly linked the observed phenological shifts to either changes in the local climate or to one or more large-scale composite variable(s), such as the North Atlantic Oscillation (NAO) index. This has resulted in the question of whether to use local climatic variables or large-scale composite indices, which has been the subject of widespread discussion (Stenseth et al. 2003; Hallett et al. 2004; Stenseth and Mysterud 2005). Local

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climate changes have been shown to advance breeding dates (e.g. Crick et al. 1997; Brown et al. 1999; Dunn and Winkler 1999; Both et al. 2004; Pearce-Higgins et al. 2005); in particular, a number of productivity variables have been found to be affected by local spring temperatures and rain (Cresswell and McCleery 2003; Rodríguez and Bustamante 2003; Both and Visser 2005). Other studies, however, focused solely on the use of the NAO index (e.g. Przybylo et al. 2000; Møller 2002; Sanz 2002; Stenseth et al. 2002; 2003), while only a few studies have examined the effect of local climate variables and the NAO index simultaneously (Ahola et al. 2004; Møller et al. 2006; Weidinger and Král 2007). In some areas, local weather is a much better predictor of bird phenology, while in other areas, the NAO index outperforms local weather variables. Consequently, a simultaneous analysis of both of these climatic datasets is necessary for a better understanding of their spatial role.

In this study, we demonstrate how data from ringing records of the Red-Backed Shrike *Lanius collurio* nestlings are usable for the long-term monitoring of phenological changes. Apart from the few standardized bird-monitoring schemes across Europe, large-scale, long-term datasets on breeding phenology are seriously lacking. However, recorded bird ringing has been carried out over a century, and these records, which are stored in national ringing centers, contain an immense amount of valuable data. They are not only a source of ringing recoveries (Baillie 1995), but they also provide valuable information on population monitoring (Rintala et al. 2003), productivity estimations (Blomqvist et al. 2002) and/or climate-mediated changes in wintering areas (Fiedler et al. 2004) and changes in breeding phenology (Beintema et al. 1985; Møller et al. 2006). For example, Møller et al. (2006) analyzed long-term changes in breeding dates of young Arctic Terns *Sterna paradisaea* based on their ringing dates in Denmark. Using data covering a time-span of 70 years, these researchers showed an advance in breeding dates that were accurately explained by both local weather and the NAO index.

In keeping in line with such research on the effects of climate on birds, the main aims of our study were to (1) use ringing records from the Czech Republic for documenting shifts in phenology and brood size of an open-nesting passerine, the Red-Backed Shrike, over the last 41 years and (2) simultaneously test the influence of both local weather variables and a large-scale weather pattern (the NAO index) on shrike phenology and brood size.

## Methods

Annual ringing records of Red-Backed Shrike nestlings for the Czech Republic were obtained from the Prague Bird

Ringling Center. Although bird ringing in the Czech Republic started in 1910, for the purposes of our study we only considered data for the period 1964–2004 because prior to 1964 there was a different data archiving system; consequently, the extraction of data prior to 1964 would be extremely time-consuming. We digitalized information on the ringing of 46,872 nestlings from 9,824 nests. These records contained information on ring type, ring number, the date of ringing, location and a note (e.g. the number of nestlings in one nest) for an individual bird. We only used ringing data on nestlings that had been unequivocally marked as being from one nest. The Red-Backed Shrike is single-brooded, but when first breeding attempts fail, a second or even third replacement clutches are initiated. The ringing records therefore contain data that include both first and replacement broods. As the inclusion of replacement broods is likely to influence phenology statistics (i.e. many replacement broods in a given year would delay the mean ringing day), we defined first clutches as those nestlings ringed before July 1, based on the assumption that first clutches are initiated before June 5 (for a similar approach, see Kuźniak 1991; Tryjanowski 2002), adding 5 days of egg-laying (Cramp and Perrins 1993), 14 days of incubation (Cramp and Perrins 1993) and 7 days posthatch when the majority of nestlings is ringed (Hušek and Adamík 2006). We used only nests with birds ringed prior to July 1 for subsequent analyses. Thus, the analyzed dataset consists of 29,986 nestlings ringed in 6,720 nests. For our analysis, we used the ringing date of a nest as the “phenology” variable (phenology thereafter) and the number of nestlings in one nest at the time of ringing as the “brood size” variable (brood size thereafter). In earlier study we demonstrated that breeding data obtained from ringing records very closely match data from local studies and that the brood size closely matches the number of nestlings per successful nest (Hušek and Adamík 2006).

Annual tenth percentile and mean ringing dates of nests were used as phenology variables. Similarly, the mean annual number of nestlings in nests at the time of ringing were used as the brood size variable. Analyses were carried out for the whole Czech Republic (6,720 nests during the period 1964–2004) and, at a finer scale, for the Trutnov-Jičín area (1,448 nests during the period 1969–2004). The Trutnov-Jičín area, with a surface area of 2034 km<sup>2</sup>, is located in north-eastern Bohemia and extends from 225 to 1600 m a.s.l. We purposefully selected this area to find out whether ringing data collected on a smaller scale are able to provide reliable parameter estimates. Only a very small number of ringers actively ring shrikes in the Trutnov-Jičín area each year. We did not analyze the first 5 years (1964–1968) in this area because the sample sizes were too small.

To investigate the effect of climatic factors on the timing of breeding and brood size, we used local climate data

and the NAO index for the months of April, May and June ( $NAO_{AMJ}$ ). For the Czech Republic, the local climate variables were total precipitation for the months of May and June, and mean temperature in May. These represent average figures for the entire Czech Republic from more than 20 main meteorological stations. For the Trutnov-Jičín area, we used mean monthly temperature and number of days with more than 10 mm of precipitation per day (“rainy days”) in May and June. These data were obtained from three meteorological stations in Jičín (1969), Trutnov (1970–1971, 2004) and Slatiny (period 1972–2003). These stations are located right in the center of the focal area. All climate data were provided by the Czech Hydrometeorological Institute in Prague and Hradec Králové. The seasonal station-based  $NAO_{AMJ}$  index (Hurrell 1995) was obtained from <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naostatseas>.

Nestlings from between 40 and 638 nests (mean  $\pm$  SD =  $239 \pm 181$ ) are ringed annually in the Czech Republic. Because of this large variation in the numbers of ringed birds, we used weighted linear regressions to test for trends in phenology and brood size. The number of nests per year was used as weighting variable. Ordinary linear regressions were used for testing within-seasonal trend in brood size and between-seasonal trend in variance of ringing dates. We used multiple regressions to assess the relationships between the selected variables and timing of breeding and brood size. Variables explaining the timing of breeding were NAO index for the period from April to June ( $NAO_{AMJ}$ ), mean temperature in May (May temperature), total precipitation in May (May precipitation) and year. Variables explaining brood size were mean temperature in May (May temperature), total precipitation in June (June precipitation),  $NAO_{AMJ}$  and year. For the local Trutnov-Jičín area, we entered the number of days with rainfall  $>10$  mm (June rainy days) into the model. All predictors were selected a priori based on their potential biological importance. Therefore, the multiple regression models contain all selected predictors instead of the routinely used step-wise approach. All statistical analyses were carried out using JMP software of SAS Institute, Cary, NC (USA).

## Results

In the Czech Republic during the study period (1964–2004), the May temperature significantly increased (linear regressions:  $F_{1,39} = 7.582$ ,  $R^2 = 0.163$ ,  $P = 0.009$ ; slope  $\pm$  SE =  $0.051 \pm 0.019$ ), but there were no significant changes in either the June temperature ( $F_{1,39} = 0.967$ ,  $R^2 = 0.024$ ,  $P = 0.332$ , slope =  $0.018 \pm 0.018$ ), May rain ( $F_{1,39} = 2.783$ ,  $R^2 = 0.067$ ,  $P = 0.103$ ; slope =  $-0.525 \pm 0.315$ ) or June

rain ( $F_{1,39} = 1.864$ ,  $R^2 = 0.046$ ,  $P = 0.180$ ; slope =  $-0.441 \pm 0.323$ ). In the Trutnov-Jičín area during the 1969–2004 study period, the same trend was observed, with the May temperature increasing significantly ( $F_{1,34} = 7.265$ ,  $R^2 = 0.172$ ,  $P = 0.011$ , slope =  $0.057 \pm 0.021$ ) and the June temperature ( $F_{1,34} = 1.883$ ,  $R^2 = 0.051$ ,  $P = 0.179$ , slope =  $0.029 \pm 0.021$ ), May rain ( $F_{1,34} = 2.971$ ,  $R^2 = 0.078$ ,  $P = 0.094$ , slope =  $-0.835 \pm 0.484$ ) and June rain ( $F_{1,34} = 2.476$ ,  $R^2 = 0.066$ ,  $P = 0.125$ , slope =  $-0.731 \pm 0.465$ ) showing no significant changes. The  $NAO_{AMJ}$  index did not show any trend ( $F_{1,37} = 1.493$ ,  $R^2 = 0.039$ ,  $P = 0.230$ , slope =  $-0.0285 \pm 0.0233$ ) over the study period.

The ringing dates of Red-Backed Shrikes advanced significantly and the brood size increased significantly in the Czech Republic (Table 1), but neither the date of ringing nor brood size advanced significantly at a local scale in the Trutnov-Jičín area (Table 1). Within year, brood size significantly declined ( $F_{1,59} = 830.082$ ,  $R^2 = 0.935$ ,  $P < 0.001$ , slope =  $-0.027 \pm 0.001$ ); between years, the variance in ringing dates did not change significantly either in the Czech Republic ( $F_{1,39} = 2.379$ ,  $R^2 = 0.058$ ,  $P = 0.131$ ) or in the Trutnov-Jičín area ( $F_{1,35} = 1.459$ ,  $R^2 = 0.042$ ,  $P = 0.235$ ).

In multiple regression models, the only significant predictor of both the tenth percentile and the mean ringing dates was May temperature. These results were consistent at both the national (Czech Republic) and regional (Trutnov-Jičín area) scale (Table 2). With respect to brood size, we did not find any of the selected variables to be significant predictors at the national level. However, on a local scale (Trutnov-Jičín area), heavy rainfall (rainy days) with its negative influence on brood size was the main significant predictor (Table 2).

## Discussion

There is currently a large body of evidence confirming that temperatures in northern latitudes have increased during the last 100 years (Easterling et al. 1997; IPCC 2001). In our study, we found a significant increase in the temperature in May for both the entire Czech Republic and at a regional scale, while we were unable to detect this trend in the June temperature. In line with this increasing May temperature, the ringing dates of Red-Backed Shrike nestlings have advanced by approximately 3–4 days since 1964. The pattern of earlier breeding is consistent with the results of similar studies on other long-distance migrating songbirds (e.g. Dunn 2004). Most of the data on trends toward earlier breeding come from the United Kingdom (Crick and Sparks 1999; Dunn 2004). In continental Europe, the most frequently studied birds have been the

**Table 1** Trends in the tenth percentile ringing dates, mean ringing dates and brood sizes of Red-Backed Shrike nestlings for the Czech Republic ( $n = 41$ ) and the Trutnov-Jičín study area ( $n = 36$ ), 1964–2004

Variable	Czech Republic				Trutnov-Jičín area			
	Slope (SE)	$t$	$P$	$R^2$	Slope (SE)	$t$	$P$	$R^2$
Tenth percentile	-0.106 (0.050)	-2.12	0.040	0.104	-0.046 (0.055)	-0.84	0.406	0.020
Mean date	-0.073 (0.035)	-2.10	0.043	0.101	-0.048 (0.035)	-1.39	0.175	0.054
Brood size	0.008 (0.004)	2.30	0.027	0.119	0.006 (0.006)	1.00	0.326	0.028

$P$  values < 0.05 indicate significant changes during the study period

**Table 2** Multiple regression models of Red-Backed Shrike phenology and brood size on climatic predictors and year for the Czech Republic ( $n = 41$ ) and a selected local Trutnov-Jičín area ( $n = 36$ ) during 1964–2004

	Czech Republic			Trutnov-Jičín area		
	Slope (SE)	$t$	$P$	Slope (SE)	$t$	$P$
Tenth percentile date						
Year	-0.032 (0.053)	-0.59	0.556	-0.015 (0.062)	-0.25	0.806
NAO <sub>AMJ</sub> <sup>a</sup>	0.270 (0.255)	1.06	0.298	0.688 (0.354)	1.94	0.061
May temperature	-1.081 (0.383)	-2.82	0.008	-1.484 (0.405)	-3.66	0.001
May precipitation	-0.010 (0.019)	-0.54	0.595	0.013 (0.018)	0.75	0.462
Mean date						
Year	-0.028 (0.037)	-0.76	0.454	0.004 (0.044)	0.08	0.934
NAO <sub>AMJ</sub>	0.196 (0.178)	1.10	0.279	0.279 (0.229)	1.22	0.233
May temperature	-0.671 (0.268)	-2.51	0.017	-0.889 (0.263)	-3.38	0.002
May precipitation	-0.011 (0.014)	-0.80	0.428	-0.009 (0.013)	-0.74	0.463
Brood size						
Year	0.008 (0.004)	1.89	0.068	-0.001 (0.007)	-0.02	0.985
NAO <sub>AMJ</sub>	-0.001 (0.020)	-0.07	0.944	0.021 (0.040)	0.52	0.607
May temperature	-0.011 (0.029)	-0.37	0.710	0.024 (0.046)	0.51	0.613
June precipitation	0.000 (0.001)	-0.29	0.777	–	–	–
June rainy days	–	–	–	-0.161 (0.056)	-2.93	0.007

$P$  values < 0.05 indicate significant changes during the study period

<sup>a</sup> NAO<sub>AMJ</sub>, North Atlantic Oscillation index for the period April to June

hole-nesting birds, such as the flycatchers *Ficedula* and tits (e.g. Both and Visser 2001; Sanz 2002, 2003; Visser and Both 2005); extensive datasets on non-hole nesting species or from more continental sites are still lacking (but see Zalakevicius et al. 2006; Weidinger and Král 2007). It is important to document the temporal changes in the food supply of these hole-nesting species. In years with an early food peak (caused by temperature increase), the Pied Flycatcher *Ficedula hypoleuca* was found to lay its eggs late relative to this food peak and, consequently, experienced a mismatch with the food supply (Visser and Both 2005). If temperature changes at different rates, the synchrony between birds and food supply may become distorted (Visser and Both 2005). The diet of the Red-Backed Shrike consists of insects, mainly Coleoptera, Hymenoptera and Orthoptera, and to a lesser extent of vertebrates (Cramp

and Perrins 1993; Tryjanowski et al. 2003). We suspect that any possible mismatch with its food supplies would be less relevant for the Red-Backed Shrike due to this variable diet.

We also found that the mean brood size of first clutches increased in the Czech Republic. It has been established that those females that lay later within a given breeding season lay smaller clutches (Lack 1968). As the Red-Backed Shrikes are breeding earlier nowadays, the brood size of first clutches may have increased as a result. However, we did not detect similar trends in phenology and brood size at the local scale in the Trutnov-Jičín area. This difference should be taken as a caution that ringing records on scales that is too small may suffer from sampling biases, such as the irregular activity of individual ringers between and within years (Bibby et al. 2000).

Our simultaneous testing of the influence of several climatic variables revealed a significant effect of the May temperature on phenology in the Czech Republic and in the Trutnov-Jičín area. May is the month that Red-Backed Shrikes arrive in the Czech Republic and when most birds make their first breeding attempts. Therefore, it is a logical assumption that May temperature would be the most important climatic factor affecting the onset of clutch initiation and, consequently, ringing dates. Despite the fact that many studies have shown that the NAO index is frequently the most significant factor affecting various aspects of a bird's breeding season, we were unable to detect any significance of this factor in any of our models. Our finding of a tighter relationship between local climates rather than with the NAO index is in line with results from other recent studies (Ahola et al. 2004; Weidinger and Král 2007). The weak effect of the NAO index might be a consequence of the geographical location of the Czech Republic. While the interpretation of the NAO index is quite straightforward in coastal or north-western Europe (Ottersen et al. 2001), it becomes less clear in inland Europe or areas further to the east (Sanz 2002, 2003; Menzel et al. 2005; Zalakevicius et al. 2006).

When brood size at the national level was considered in the multiple regression models, we did not find that any of the selected variables reasonably explained the observed variation. Similar findings for the weak impact of temperature or rainfall variables on the breeding success in the Red-Backed Shrike have been recently reported by Müller et al. (2005). However, at the regional scale, we found that brood size was negatively affected by the number of days with >10 mm of precipitation per day. Due to the fine-scale temporal and spatial variability in the occurrence of high rainfall, we could not add this variable into the models for the whole Czech Republic. Shrikes, as open-nesting passerines, are likely to be vulnerable to inclement weather during the breeding period, especially rainy spring conditions. High rainfall causes partial brood losses, either directly by damaging nests and chilling nestlings, or indirectly by reducing the availability of food (Mann and Brandl 1986; Holáň 1997; Fornasari and Massa 2000; Takagi 2001; Goławski 2006). Thus, periods of inclement weather can result in partial losses in the brood and decreased brood size.

In conclusion, we have demonstrated that shrikes have shifted their breeding phenology toward earlier dates. This shift has been accompanied by an increase in brood size. Given that early broods are usually larger (Lack 1968; this study) and that they have a higher nest success (Müller et al. 2005), this may have a positive effect on future population increases as the temperature continues to rise. However, nest predation is likely to be the most important factor in determining the shrike's breeding performance (Fornasari and Massa 2000; Lovász et al. 2000; Jakober and Stauber

2002; Müller et al. 2005). If the brood losses caused by predators do not increase, we may expect a positive impact of the recent climate changes on this species.

## Zusammenfassung

Langfristige Veränderungen in Legedatum und Brutgröße beim Neuntöter *Lanius collurio* in Tschechien, 1964–2004

Bei vielen Vogelarten hat die Klimaveränderung das Legedatum und die Brutgröße beeinflusst. Diese Veränderungen sind meist an Höhlenbrütern untersucht und entweder zum lokalen Klima oder zu großskaligen Mischvariablen (z.B. Nordatlantische Oszillation) in Bezug gesetzt worden. Über die Reaktion von frei brütenden Vogelarten auf die Klimaveränderung und die relative Rolle einzelner klimarelevanter Variablen in unterschiedlichen Maßstabsbereichen wissen wir ziemlich wenig. Unter Verwendung von Beringungsdaten aus einem Zeitraum von 41 Jahren haben wir die Verschiebung in Legedatum und Gelegegröße an einer mitteleuropäischen Population des Neuntöters, einem Langstreckenzieher, belegt. Im Vergleich zu 1964 fanden wir eine Verschiebung des Legedatums in Richtung früheren Brutbeginns um 3–4 Tage und einen Anstieg der Brutgröße um annähernd 0,3 Nestlinge. Der Neuntöter beginnt im Mai mit der Brut und zieht die ersten Nestlinge im Juni auf. Im Zeitraum von 1964–2004 stiegen die Temperaturen im Mai signifikant an, während der Anstieg der Junitemperaturen nicht signifikant ausfiel. Gleichzeitiges Testen des Einflusses lokaler Klimavariablen und des Index für die Nordatlantische Oszillation erbrachte eine bessere Passung zum lokalen Klima. Der Temperaturanstieg im Mai war positiv mit einer Verfrühung des Brutbeginns korreliert. Analog folgte auf lokalem Niveau auf höhere Maitemperaturen eine größere Brutgröße, wohingegen hohe Niederschläge einen stark negativen Einfluss hatten.

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### Studie 3

Hušek, J., Adamík, P., Cepák, J. & Tryjanowski, P. 2009: The influence of climate and population size on the distribution of breeding dates in the red-backed shrike (*Lanius collurio*). *Annales Zoologici Fennici* 46: 439–450.

# The influence of climate and population size on the distribution of breeding dates in the red-backed shrike (*Lanius collurio*)

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There are now a growing number of studies linking environmental conditions operating at different life stages of birds to their arrival on breeding grounds. Here we focus on one of the major fitness determinants; timing of breeding. We examined the influence of climate relevant to different parts of the birds' annual life cycle, and the impact of population size on distribution traits in a central European population of the red-backed shrike *Lanius collurio*. Timing of breeding was affected by breeding ground climate as well as by population size. In years with higher population densities shrikes started to breed earlier. In contrast to previous studies we did not find that our climatic variables adequately explained the variability of timing of breeding. We argue that density-dependent processes are also important for the reproduction of shrikes and that in phenological studies; attention should also be paid to other factors operating at breeding grounds.

## Introduction

Climatic conditions have a wide range of impacts across the annual life cycle of birds. In the majority of studies, they were shown to influence arrival dates, timing of breeding, and population sizes in birds (Sæther *et al.* 2004, Gordo 2007, Newton 2007). The impact of climate on birds may be direct, e.g. ambient temperature or wind

speed and direction affecting body reserves of migrating birds (Newton 2007), or indirect, via changes to food resources (Jones *et al.* 2003, Gordo 2007, Pulido 2007). Events occurring at one life stage might have a prolonged effect on the individual's performance later in its life (Marra *et al.* 1998, Drent *et al.* 2006). It has been shown that conditions experienced in the wintering quarters (e.g. food availability) have

a direct effect on body condition and survival (Strong & Sherry 2000), causing birds in poorer condition to delay their departure (Marra *et al.* 1998, Norris *et al.* 2004). In addition, ecological conditions encountered en route may postpone migration, because leaner individuals would delay departure in order to obtain the fuel reserves necessary for self-maintenance during migration (Newton 2007). Condition-dependent arrival dates in migrants, i.e. when individuals in better condition arrive earlier than those in a poorer condition, have been documented in a range of avian taxa (e.g. Møller 1994a, Lozano *et al.* 1996, Marra *et al.* 1998, Kokko 1999, Drent 2006, Newton 2007). For example, Saino *et al.* (2004a) demonstrated that the arrival dates of barn swallows *Hirundo rustica* in Italy were earlier after winters with favourable ecological conditions in their African wintering quarters, and Møller (1994b) found in Danish barn swallows that the pattern of arrival to their breeding grounds was more variable in years with adverse ecological conditions in their wintering grounds, when many individuals in poor condition had presumably died.

These examples emphasize the potential links between conditions experienced by migratory birds in different phases and places of their annual activities. When considering changes in life-history traits that result from climate change, it is also essential to consider changes in environmental conditions affecting the whole annual life cycle, because there are interactions among different stages of the cycle (Coppack & Both 2003). However, studies linking all aspects are still quite rare (Gordo 2007, 2008, Newton 2007). Moreover, the majority of published papers have focused on early arrivals or on average arrival values (mean, median) which may not be representative of the whole population (Sparks *et al.* 2005, Knudsen *et al.* 2007). More detailed information is available from the shape of the frequency distribution of life-history traits, which implicates causes and consequences in the fitness of individuals. The shape reflects the distribution of condition-dependent arrival (Kokko 1999) and breeding dates, with resulting consequences in population demography. This is because, for example, female breeding strategies and the frequency of extra-pair paternities might be affected

by the form of the distribution of arrival dates. The frequency of extra-pair paternities depends also on breeding synchrony, which affects the intensity of sexual selection among individuals (Møller & Ninni 1998, Saino *et al.* 1999, Spottiswoode & Møller 2004), and the spread and symmetry of the distribution will affect the potential buffering of the reproductive output of the population. Overall, and most importantly, the shape of the distribution (skewness) and its changes could indicate selective pressures on life-history traits. Until recently, only a few studies have considered the possible role of climate change in influencing the shape of the frequency distribution of arrivals at breeding grounds (Ptaszyk *et al.* 2003, Sparks *et al.* 2005, Møller 2008a), breeding dates and clutch sizes (Winkler *et al.* 2002, Laaksonen *et al.* 2006). Laaksonen *et al.* (2006) found no clear trend in the skewness of laying dates during 1943–2003 in a Finnish population of the pied flycatcher *Ficedula hypoleuca*, a hole nesting species, but among-year variation in the skewness of laying dates increased and this appeared to be explained by variable temperature trends along the migration route. Skewness in clutch size appeared to change from more negative values to a more symmetrical distribution and variation in clutch size increased when wintering conditions were favourable. The distribution was then skewed with a tail of small clutches indicating that when ecological conditions during winter were good, low quality individuals were also able to breed (Laaksonen *et al.* 2006).

In this study, we analyzed the impact of climate from different parts of the annual life cycle and the impact of population size on breeding dates distribution in a Czech population of a long-distance migrant, the red-backed shrike *Lanius collurio*. Besides considering the effects of breeding ground climate on timing of breeding (Hušek & Adamík 2008), we also considered wintering ground climate and climate during migration. For migratory birds, climatic conditions encountered both on wintering grounds and during migration are important as they determine their physical condition (e.g. Marra *et al.* 1998, Bearhop *et al.* 2004, Saino *et al.* 2004b, Studds & Marra 2007), which results in variable arrival dates and condition on breeding grounds (Stolt & Fransson 1995, Sandberg & Moore 1996, Marra

*et al.* 1998). Arrival dates and physical condition of birds on breeding grounds then affect habitat occupancy as well as timing of breeding (e.g. Møller 2008b). We also considered the effects of intraspecific competition, as expressed by an index of population size, on timing of breeding. In summary, we assumed that the timing of breeding is influenced by condition and arrival dates mediated effects of wintering and migration ground climate, and by direct effects of breeding ground climate and effects of intraspecific competition.

## Material and methods

### Breeding data

For this study we used ringing data on red-backed shrike nestlings that were ringed during 1983–2006. In an earlier study we demonstrated that data obtained from ringing records are quite reliable and could be successfully used in phenological studies (Hušek & Adamík 2006). Hušek and Adamík (2006) showed that the mean number of ringed nestlings in nests at the time of ringing matched well with the mean number of nestlings from successful nests and that mean first laying dates strongly correlated with mean ringing dates. Annual ringing records of red-backed shrike nestlings for the Czech Republic were obtained from the Prague Bird Ringing Centre. We computerized information on the ringing of 36 076 nestlings from 8368 nests ringed during 1983–2006. We used the 10th percentile, median, skewness and variance of ringing dates as descriptors of timing of breeding for all clutches. The red-backed shrike is single-brooded, but when a first breeding attempt fails, replacement clutches are initiated. Thus, our dataset clearly contains unknown proportion of replacement clutches. Initiation of replacement clutches depends both on the rate and timing of first clutch failure (Antczak *et al.* 2009). Consequently, the proportion of replacement clutches mirrors various reasons of nest failure (predation, inclement weather) which are highly variable in both time and space. The values of nest failure of first clutches span from 11.3% (Horvath *et al.* 2000) through 23.6% (Pasinelli

*et al.* 2007) to 47.9% (Jakober & Stauber 2002) for shrikes during different time periods and at different study sites. In an attempt to avoid inclusion of replacement clutches we also performed the analyses with a truncated dataset. Considering roughly 25% of ringed nests at the end of the distribution to be replacement clutches each year, we defined first clutches as the 75th percentile of ringed nests annually for truncated dataset. We were cautious in inference from this dataset, as some varying proportion of replacement clutches might still have been included. Hence, the truncated dataset of first clutches consisted of 28 046 nestlings ringed in 6284 nests during the period 1983–2006. Similarly, the 10th percentile<sub>first</sub>, median<sub>first</sub>, skewness<sub>first</sub> and variance<sub>first</sub> of ringing dates were used as the “timing of breeding of first clutches” descriptors. Our ringing dataset dates back to 1964 but due to restriction in the availability of climatic variables (*see below*) we performed the analyses with 24 years only (*see Appendix*).

### Climatic data

#### Wintering ground climate

As we were unable to precisely define particular wintering quarters of the Czech population (due to insufficient numbers of Czech ringing recoveries from Africa) and match them with finer-scaled climatic variables, we considered the shrikes' whole wintering range in eastern and southeastern Africa (Lefranc & Worfolk 1997).

Quite recently it was shown that the climate variability in East Africa is linked to the inter-annual sum of Indian Ocean sea surface temperature (SST) variations, termed the Indian Ocean Dipole (IOD; Marchant *et al.* 2007). The IOD represents the zonal dipole structure of the various coupled ocean–atmosphere parameters such as SST, surface pressure, outgoing long wave radiation and sea surface height anomalies (Yamagata *et al.* 2003). This unique independent ocean atmosphere coupled phenomenon in the Indian Ocean is characterized by anomalously warming of SST over the western Indian Ocean and anomalously cooling of SST in the eastern Indian Ocean which is associated with

rainfall and moisture supply into eastern and southern Africa (Saji *et al.* 1999). Intensity of the IOD is thus represented by anomalous SST gradient between the western equatorial Indian Ocean and the south eastern equatorial Indian Ocean. This gradient is named as Dipole Mode Index (DMI; Saji *et al.* 1999). When the DMI is positive, the phenomena referred as the positive IOD, an increased rainfall and moisture supply cause vegetation development over the tropical eastern Africa (Saji *et al.* 1999, Marchant *et al.* 2007). As insect abundance depends on plant productivity, positive values of DMI are in fact likely to influence physical condition and departure dates of shrikes via prey availability (*see* Studds & Marra 2007).

Shrikes arrive at wintering grounds in eastern and southeastern Africa in November and start to depart in the second half of March (Lefranc & Worfolk 1997). For the analysis of the influence of wintering ground climate on breeding parameters we thus used the mean of the Dipole Mode Index (DMI) for the months from November to March. The mean of the DMI from November to March covers the period of the shrikes' stay on the wintering grounds. The DMI data were obtained from Frontier Research Center for Global Change, Japan (available at <http://www.jamstec.go.jp/frsgc/research/d1/iod/>).

### Migration route climate

Czech ringing recoveries provide some evidence that red-backed shrikes regularly pass through the Middle East during their northward migration (Cepák *et al.* 2008). We used mean temperature anomalies for April and May for Israel (hereafter  $T_{\text{passage}}$ ), spanning the whole spring passage period. Northward spring migration of red-backed shrikes via Israel has two peaks, usually at the end of April and in the second half of May (Cramp & Perrins 1993). The area under consideration was defined by a grid 33°N, 30°N, 34°E and 36°E which covers most of Israel. The temperature data were obtained from National Climatic Data Center, Asheville, NC (available at: <http://www.ncdc.noaa.gov/gcag/gcag.html>). The correlation between  $T_{\text{passage}}$  and DMI ( $r = 0.17$ ,  $n = 24$ ,  $p = 0.426$ ) was not significant.

### Breeding ground climate

We used mean May temperature ( $T_{\text{May}}$  hereafter) and mean May precipitation ( $P_{\text{May}}$  hereafter) to study the effect of breeding grounds climatic factors. These consist of average values for the entire Czech Republic derived annually from more than 20 main meteorological stations. Data were provided by the Czech Hydrometeorological Institute in Prague. There was neither significant correlation between  $T_{\text{May}}$  and DMI ( $r = 0.18$ ,  $n = 24$ ,  $p = 0.397$ ), between  $T_{\text{May}}$  and  $T_{\text{passage}}$  ( $r = 0.29$ ,  $n = 24$ ,  $p = 0.169$ ), between  $T_{\text{May}}$  and  $P_{\text{May}}$  ( $r = -0.26$ ,  $n = 24$ ,  $p = 0.221$ ), between  $P_{\text{May}}$  and DMI ( $r = -0.26$ ,  $n = 24$ ,  $p = 0.214$ ) nor between  $P_{\text{May}}$  and  $T_{\text{passage}}$  ( $r = -0.09$ ,  $n = 24$ ,  $p = 0.671$ ).

### Population size data

Data on population numbers of the red-backed shrike in the Czech Republic were provided by the Czech Society for Ornithology. The population numbers are converted into an index of abundance (hereafter IA) and these data are based on a standardized national breeding bird monitoring program (Reif *et al.* 2006). There was no significant correlation between IA and number of ringed nests ( $r = -0.13$ ,  $n = 24$ ,  $p = 0.546$ ).

### Candidate models

Factors and the sets of candidate models were selected *a priori* based on their potential biological importance. Candidate models for measurement of central tendencies of timing of breeding (median, median<sub>first</sub>, 10th percentile and 10th percentile<sub>first</sub>) were built as follows: First, only breeding ground climatic conditions were supposed to influence the timing of breeding yielding model with factor  $T_{\text{May}}$  and model with  $T_{\text{May}}$  and year. Second, density-dependent processes were supposed to influence the timing of breeding alongside breeding-ground climate. We thus defined model with factors  $T_{\text{May}}$  and IA and model including  $T_{\text{May}}$ , IA and year. Third, we hypothesized the timing of breeding to be influenced by climatic conditions during the whole annual life cycle yielding model with

climatic factors from the breeding ground as well as from the wintering ground ( $T_{\text{May}}$ , DMI), model including also migration route climate ( $T_{\text{May}}$ , DMI and  $T_{\text{passage}}$ ) and same models with the year effect were also included. Fourth, combination of the whole annual life cycle climate conditions and density-dependent processes on breeding grounds were considered in model with  $T_{\text{May}}$ , IA, DMI; model with  $T_{\text{May}}$ , IA, DMI,  $T_{\text{passage}}$ ; model with  $T_{\text{May}}$ , IA, DMI, year and global model with  $T_{\text{May}}$ , IA, DMI,  $T_{\text{passage}}$ , year. May temperature was included as covariate in all candidate models because of its known effect on the timing of breeding of first clutches (Hušek & Adamík 2008).

Variability of breeding dates of both all clutches (variance) and first clutches (variance<sub>first</sub>) was supposed to be influenced by unfavorable breeding ground climate (model with  $P_{\text{May}}$  and model with  $P_{\text{May}}$ , year).  $P_{\text{May}}$  was chosen as a climatic descriptor here, because of known effect of rainy weather on nest failure in shrikes (e.g. Holáň 1994, Takagi 2001). Alternatively, density-dependent processes (model with IA; model with IA, year) were hypothesized to affect the distribution of the timing of breeding. Then, combination of breeding ground climate effects and density-dependent processes (model with  $P_{\text{May}}$ , IA; model with  $P_{\text{May}}$ , IA, year); whole annual life cycle climate (model with  $P_{\text{May}}$ , DMI; model with  $P_{\text{May}}$ , DMI, year; model with  $P_{\text{May}}$ , DMI,  $T_{\text{passage}}$  and model with  $P_{\text{May}}$ , DMI,  $T_{\text{passage}}$ , year) and combination of whole annual life cycle climate and density-dependent processes (model with  $P_{\text{May}}$ , IA, DMI; model with  $P_{\text{May}}$ , IA, DMI,  $T_{\text{passage}}$ ; model with  $P_{\text{May}}$ , IA, DMI, year and global model with  $P_{\text{May}}$ , IA, DMI,  $T_{\text{passage}}$ , year) were supposed. Finally we hypothesized the variance and variance<sub>first</sub> to be affected by climatic conditions on wintering ground only (model with DMI; model with DMI, year), and by climatic conditions on wintering ground and density-dependent processes (model with DMI, IA and model with DMI, IA, year).

Candidate models for skewness and skewness<sub>first</sub> were built, following the same hypothesis framework as for variance and variance<sub>first</sub>, but  $T_{\text{May}}$  was used instead of  $P_{\text{May}}$ . The number of ringed nests was included as a covariate in candidate models because of its correlation

with variance<sub>first</sub>, skewness, skewness<sub>first</sub> and also variance (Table 1). Year was included as a continuous covariate in some candidate models to account for inter-annual variation and possible effects of temporal trends in the data.

## Statistical analyses

Because breeding data are a time series, we examined the residuals (regressions on years) of all variables for the presence of autocorrelation. We used the Durbin-Watson test with the AUTOREG procedure of SAS 9.1 (SAS Institute 2004). None of the response variables were autocorrelated (all  $D > 1.7$ ,  $p > 0.18$ ). Therefore, we used each year's values as statistically independent observations.

We fitted general linear models with GENMOD procedure assuming identity link and normal distribution (SAS Institute 2004). An information-theoretic approach was used to examine which variables and models of an *a priori* defined set of candidate models best described the data (Burnham & Anderson 2002). Model selection was based on Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ; Burnham & Anderson 2002). Akaike model weights, based on  $AIC_c$  were then calculated. Akaike weights are considered a measure of probability that a specific model best explains the data, given the set of all candidate models and they sum to one by definition. Model averaging was used for parameter estimation if no single model had Akaike weight  $> 0.9$ . Akaike weights were calculated for individual variables as the sum of Akaike weights of all models in which the variable in question appeared. Model fit was checked with a residual analysis (McCullagh & Nelder 1989).

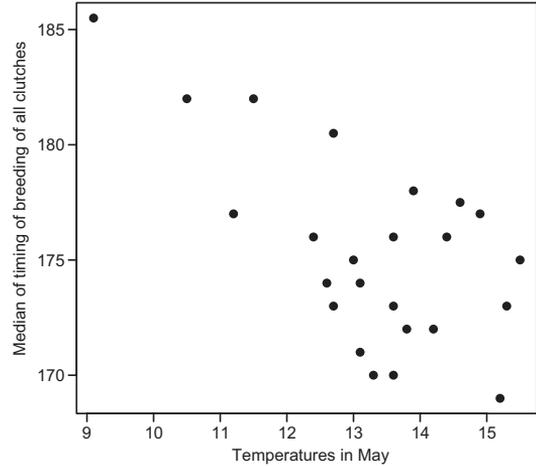
## Results

### General findings and correlations between distribution descriptors

During 1983–2006, the mean 10th percentile of timing of breeding of all clutches and first clutches was  $165.73 \pm 0.77$  ( $\pm$  SE) and  $164.70$

**Table 1.** Pearson correlations between the distribution descriptors of the timing of breeding and ringing activity in the Czech population of red-backed shrike during the period 1983–2006 ( $r$  and  $p$  values in parentheses,  $n = 24$  years). Variables denoted with subscript refer to a truncated dataset (for details see Material and methods). Significant correlations ( $\alpha = 0.05$ ) are set in boldface.

	Median	Median <sub>first</sub>	10th percentile	10th percentile <sub>first</sub>	Variance	Variance <sub>first</sub>	Skewness	Skewness <sub>first</sub>
No. of ringed nests	-0.21 (0.323)	-0.08 (0.712)	0.04 (0.836)	0.04 (0.853)	-0.34 (0.107)	-0.40 (0.053)	0.39 (0.057)	<b>-0.41 (0.047)</b>
Median		<b>0.94 (&lt; 0.001)</b>	<b>0.76 (&lt; 0.001)</b>	<b>0.74 (&lt; 0.001)</b>	-0.05 (0.817)	<b>0.45 (0.029)</b>	<b>-0.57 (&lt; 0.040)</b>	-0.07 (0.753)
Median <sub>first</sub>			<b>0.88 (&lt; 0.001)</b>	<b>0.85 (&lt; 0.001)</b>	-0.24 (0.259)	0.18 (0.415)	-0.36 (0.081)	-0.24 (0.263)
10th percentile				<b>0.98 (&lt; 0.001)</b>	-0.39 (0.062)	-0.19 (0.364)	0.01 (0.957)	-0.14 (0.527)
10th percentile <sub>first</sub>					<b>-0.41 (0.048)</b>	-0.19 (0.378)	0.02 (0.916)	-0.15 (0.487)
Variance						<b>0.56 (0.002)</b>	<b>-0.44 (0.030)</b>	<b>0.42 (0.042)</b>
Variance <sub>first</sub>							<b>-0.88 (&lt; 0.001)</b>	0.22 (0.293)
Skewness								-0.08 (0.710)



**Fig. 1.** Relationship between the median of timing of breeding of all ringed clutches (day 1 = 1 January) and mean May temperature in a Czech population of the red-backed shrike *Lanius collurio*.

$\pm 0.73$ , respectively (day 1 = 1 January). Mean median of all clutches and first clutches was  $175.35 \pm 0.87$  and  $171.98 \pm 0.80$ , respectively and mean variance of all clutches and first clutches was  $135.31 \pm 5.38$  and  $39.32 \pm 3.16$ , respectively. Distribution of the timing of breeding was usually positively skewed (i.e. having a concentrated range of values with a right hand tail) for all clutches (mean  $\pm$  SE =  $0.95 \pm 0.07$ ), but was negatively skewed for only first clutches ( $-0.26 \pm 0.10$ ). Correlations between distribution descriptors from the whole and truncated dataset showed that all 10th percentile, 10th percentile<sub>first</sub>, median and median<sub>first</sub> were robust against truncating (Table 1). Obviously, these measures were not much hampered by including replacement clutches into the analyses. Skewness was significantly negatively correlated with the number of ringed nests, but correlation between variance and number of ringed nests was marginally not significant (Table 1).

### Relationships of climatic factors and population size with timing of breeding

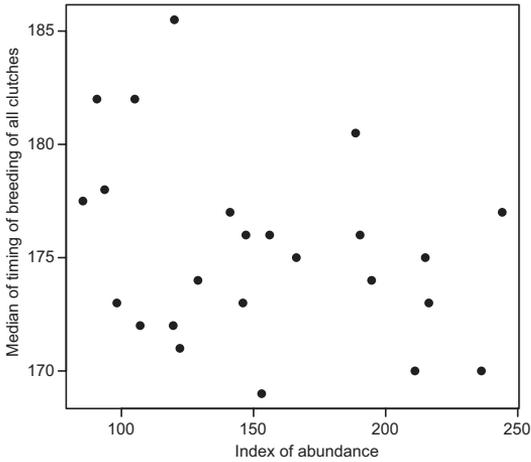
For the median,  $T_{\text{May}}$ , IA and year had Akaike weights  $> 0.85$  (Tables 2 and 3). Median of all clutches was earlier with higher  $T_{\text{May}}$  ( $b \pm$  SE =  $-2.05 \pm 0.36$ , Fig. 1) and with higher IA ( $b =$

**Table 2.** Results of the model selection on factors influencing the timing of breeding in the red-backed shrike. All models contain an intercept term. Abbreviations:  $\log L$  = maximum likelihood estimates,  $K$  = number of parameters,  $AIC_c$  = AIC value corrected for small sample size,  $\Delta AIC_c$  = difference in  $AIC_c$  to the best model. Akaike weight ( $w_i$ ) indicates measure of support of a model relative to all other models considered. Models are ranked according to Akaike weights and only models with  $\Delta AIC_c \leq 3$  are presented.

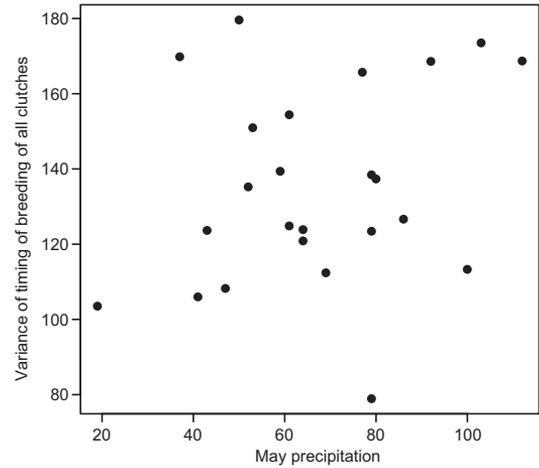
Response variable	Model	$\log L$	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
Median	$T_{May}^?$ IA, year	-54.6	4	119.3	0.0	0.74
Median <sub>first</sub>	$T_{May}^?$ IA, year	-53.2	4	116.6	0.0	0.70
10th percentile	$T_{May}^?$ IA	-57.1	3	121.4	0	0.30
	$T_{May}^?$ IA, DMI	-56.0	4	122.0	0.7	0.22
	$T_{May}^?$ IA, year	-56.2	4	122.6	1.2	0.17
	$T_{May}^?$ IA, DMI, year	-55.2	5	123.8	2.4	0.09
	$T_{May}^?$ IA, DMI, $T_{passage}$	-55.5	5	124.3	2.9	0.07
10th percentile <sub>first</sub>	$T_{May}^?$ IA	-55.6	3	116.3	0.0	0.57
	$T_{May}^?$ IA, DMI	-54.2	4	118.6	2.3	0.18
	$T_{May}^?$ IA, year	-54.6	4	119.2	2.9	0.13
Variance	No. of nests, $P_{May}^?$ year	-106.0	4	222.1	0.0	0.24
	No. of nests, $P_{May}^?$ DMI, year	-104.6	5	222.4	0.3	0.21
	No. of nests, DMI, year	-106.8	4	223.7	1.5	0.11
Variance <sub>first</sub>	No. of nests, IA, year	-107.5	4	225.1	3.0	0.05
	No. of nests, DMI	-96.1	3	199.5	0.0	0.20
	No. of nests, $P_{May}^?$ DMI	-94.8	4	199.8	0.3	0.17
	No. of nests, $P_{May}$	-96.5	3	200.3	0.8	0.13
	Intercept	-99.3	1	200.7	1.3	0.10
	No. of nests, IA	-97.2	3	201.6	2.1	0.07
	No. of nests, IA, DMI	-96.0	4	202.2	2.7	0.05
Skewness	No. of nests, DMI, year	-96.1	4	202.4	2.9	0.05
	No. of nests, $T_{May}$	-5.8	3	18.7	0.0	0.17
	Intercept	-8.4	1	18.9	0.2	0.15
	No. of nests, IA	-6.0	3	19.1	0.4	0.14
	No. of nests, DMI	-6.0	3	19.2	0.5	0.13
	No. of nests, $T_{May}^?$ DMI	-5.2	4	20.6	1.8	0.07
	No. of nests, $T_{May}^?$ IA	-5.3	4	20.8	2.0	0.06
	No. of nests, IA, DMI	-5.3	4	20.8	2.1	0.06
	No. of nests, $T_{May}^?$ year	-5.8	4	21.6	2.9	0.04
	Skewness <sub>first</sub>	No. of nests, IA	-10.8	3	28.8	0.0
No. of nests, IA, year		-10.3	4	30.7	2.0	0.14
No. of nests, $T_{May}^?$ IA		-10.5	4	31.2	2.4	0.11
No. of nests, IA, DMI		-10.8	4	31.7	2.9	0.09

**Table 3.** The Akaike weights of individual explanatory variables over all models in which the variable in question was included. Covariate values are in parentheses.

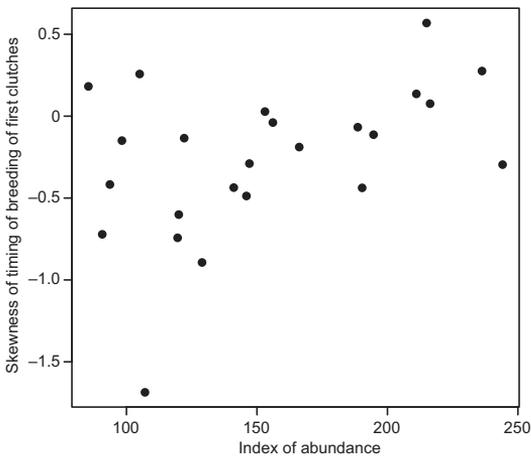
Response variable	Explanatory variables						
	$T_{May}$	$P_{May}$	DMI	IA	$T_{passage}$	Year	No. of ringed nests
Median	(1.00)	–	0.20	0.98	0.05	0.93	–
Median <sub>first</sub>	(1.00)	–	0.21	0.99	0.05	0.88	–
10th percentile	(0.99)	–	0.49	0.88	0.13	0.32	–
10th percentile <sub>first</sub>	(0.99)	–	0.29	0.95	0.07	0.17	–
Variance	–	0.69	0.56	0.22	0.08	0.80	(0.97)
Variance <sub>first</sub>	–	0.50	0.60	0.24	0.05	0.17	(0.90)
Skewness	0.44	–	0.39	0.32	0.03	0.14	(0.84)
Skewness <sub>first</sub>	0.27	–	0.23	0.83	0.01	0.27	(0.95)



**Fig. 2.** Relationship between the median of timing of breeding of all ringed clutches (day 1 = 1 January) and index of abundance in a Czech population of the red-backed shrike *Lanius collurio*.



**Fig. 3.** Relationship between the variance of timing of breeding of all ringed clutches and May precipitation in a Czech population of the red-backed shrike *Lanius collurio*.



**Fig. 4.** Relationship between the skewness of timing of breeding of first clutches and index of abundance in a Czech population of the red-backed shrike *Lanius collurio*.

$-0.06 \pm 0.02$ , Fig. 2) but slightly delayed over the study period ( $b = 0.29 \pm 0.13$ ). Principally the same results were found for the median<sub>first</sub> ( $T_{\text{May}}$ :  $b \pm \text{SE} = -1.87 \pm 0.34$ ; IA:  $b = -0.06 \pm 0.02$ ; year:  $b = 0.24 \pm 0.12$ ). Similarly, the 10th percentiles for the whole and truncated dataset yielded similar parameter estimates (10th percentile;  $T_{\text{May}}$ :  $b \pm \text{SE} = -1.33 \pm 0.38$ ; IA:  $b = -0.03 \pm 0.02$  and 10th percentile<sub>first</sub>;  $T_{\text{May}}$ :  $b \pm \text{SE} = -1.28 \pm 0.34$ ; IA:  $b = -0.03 \pm 0.01$ ; Table 2). However, there was no evidence for

effect of year on either 10th percentile or 10th percentile<sub>first</sub> over the study period (Tables 2 and 3).

A weak effect of climatic variables and population size was found for variance, where only  $P_{\text{May}}$  ( $w_i = 0.69$ ) and year ( $w_i = 0.80$ ) had some weights in explaining it (Tables 2 and 3). Variance tended to increase over the study period ( $b = 1.60 \pm 1.06$ ) and tended to be higher with higher  $P_{\text{May}}$  ( $b = 0.26 \pm 0.32$ , Fig. 3). Only DMI had some weight ( $w_i = 0.60$ ) in explaining variance<sub>first</sub> (Table 3).

No variable affected the skewness of all clutches (Tables 2 and 3). For skewness<sub>first</sub> only the IA had Akaike weight  $> 0.80$  besides the number of ringed nestlings (Table 3). The negatively skewed timing of breeding of first clutches tended to become positively skewed with an increase of IA ( $b = 0.003 \pm 0.002$ , Fig. 4).

## Discussion

In this study, we found that the timing of breeding of a central European population of the red-backed shrike was influenced both by spring temperatures and population size. We highlight the effects of population size on timing of breeding and suggest considering also other relevant factors in studies of climatic effects on avian phenology.

During 1983–2006 the distributions of the timing of breeding of the red-backed shrike were mostly positively skewed for all ringed nests. This is because right-hand tail (positive skewness) of all clutches contains also replacement clutches. On the other hand, when only first clutches (i.e. truncated dataset) were considered, the distributions of the timing of breeding were mostly negatively skewed. Left hand tail of distribution of first clutches mirrors the onset of breeding, when a few exceptionally early breeders start to breed early. These could represent birds in better condition which are able to start breeding soon after their arrival (Newton 2004) and earlier than the bulk of the population. Earlier nesting individuals then have better reproductive performance (e.g. van Noordwijk & de Jong 1986, Sheldon *et al.* 2003), which was also shown for early nesting red-backed shrike pairs (Kuźniak 1991, Müller *et al.* 2005, Hušek & Adamík 2008). However, it must be noted that pronounced negative skewness in breeding dates with left hand tail of breeders tends to be overestimated in our study, because most probably among the first breeders there is also a tail of individuals in inferior condition, which were cut away among the 25% when analysing the truncated dataset.

The timing of breeding was affected by both breeding ground climatic conditions and by intensity of intraspecific competition processes as approximated by population size. The timing of breeding measured as medians and 10th percentiles was earlier when May temperature was higher for both all clutches and first clutches. Additionally, medians of timing of breeding in both datasets slightly delayed over the study period. No such effect was found for the 10th percentiles. Variance of timing of breeding of all clutches also slightly increased during 1983–2006. Spring temperature during the onset of breeding plays an essential role in shrike's breeding phenology. Shrike has advanced both its timing of arrival, as well as the timing of breeding in central Europe since the 1960s/1970s (Tryjanowski & Sparks 2001, Hušek & Adamík 2008, Z. Hubálek unpubl. data), latter due to an increase in the mean May temperature. Here the pattern of slightly delaying medians and growing variance in timing of breeding might be caused

by increasing proportion of replacement clutches in recent years, but this hypothesis should be tested in future studies.

We found that beside the breeding ground climate, population densities also affected the timing of breeding. With a higher population size, medians and 10th percentiles were earlier for all clutches as well as first clutches. This finding is also supported by the influence of population size on skewness of timing of breeding of first clutches, which makes it even more robust. Skewness of timing of breeding of first clutches turned from being negatively skewed to being positively skewed with higher population size. This means that larger proportion of individuals starts to breed earlier when population size is higher. Higher population densities are likely to lead to more intense intraspecific competition; as a consequence, birds may be forced to start breeding earlier (for general discussion of the subject *see also*: Møller 2008a).

Both (2000) hypothesized that the pattern of density-dependent breeding dates is more common in resident than in migratory species, and he found no density dependence in either breeding date or clutch size in a long-distance migrant, the pied flycatcher. However, we argue that density-dependent processes also affect the timing of breeding and that they are important for reproduction in the open nesting red-backed shrike (*see also* Müller *et al.* 2005). Overall, we found that the timing of breeding is not only influenced by climatic conditions encountered within the birds annual life cycle (Laaksonen *et al.* 2006), but also by density-dependent processes.

In contrast to previous studies (Winkler *et al.* 2002, Laaksonen *et al.* 2006), we did not find evidence that our climatic variables adequately explained the variance of timing of breeding of first clutches. Only the precipitation in May and year had some power in explaining variance of timing of breeding of all clutches. Variance of all clutches increased with more precipitation in May indicating that inclement weather causes some first nesting attempts to fail. This is in agreement with previous findings on sensitivity of nesting shrikes to inclement weather (Holáň 1994, Takagi 2001, Goławski 2006, Hušek & Adamík 2008, but *see* Goławski 2008). The

effect of individual bird condition (e.g. Sæther *et al.* 2004, Stokke *et al.* 2005, Robinson *et al.* 2007) on variability of timing of breeding of first clutches, as indicated by some weight of DMI in explaining it, should be further tested in shrikes.

In conclusion we demonstrated that ringing data could successfully be used in bird phenological studies on a large scale (*see also* Hušek & Adamík 2008). However, using ringing data for more detailed studies in bird populations is likely to be problematic and is possible only for local populations of abundant species if these are ringed in sufficient numbers and when sufficient information is recorded about ringed nestlings.

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**Appendix.** Distribution descriptors of timing of breeding in red-backed shrike used in the analyses (day 1 = 1 January).

Year	Median	Median <sub>first</sub>	10th percentile	10th percentile <sub>first</sub>	Variance	Variance <sub>first</sub>	Skewness	Skewness <sub>first</sub>	No. of nests
1983	171	169	165	164	78.94330	15.67765	1.513403	-0.134182995	266
1984	182	178	172	171	123.44595	48.13900	0.66678	0.25768871	329
1985	172	169	163	162	138.42143	36.82396	0.803776	-0.743165111	322
1986	177.5	171	163	163	168.67865	78.40801	0.435844	0.181330793	352
1987	182	178	171	169.2	113.32208	43.35672	0.50621	-0.721672931	410
1988	172	170	164	164	105.99063	30.15133	1.207336	-1.685905088	606
1989	174	171	165	164	108.24919	28.42940	0.989095	-0.112759247	672
1990	173	170	165	164	123.63688	30.67766	1.028991	-0.148980681	502
1991	185.5	183	174	172	123.86160	40.85216	0.717597	-0.600978414	251
1992	178	175	170	169	103.52768	27.39473	1.227695	-0.417035044	454
1993	173	172	166	163	135.22858	25.25677	1.250338	-0.487773524	576
1994	174	173	167	167	112.40147	23.63873	1.107453	-0.893401769	517
1995	176	173	168	167	126.65863	27.41329	1.495698	-0.437444572	542
1996	173	169	165	164	173.51784	35.57413	1.221015	0.075751459	562
1997	170	166	162	161	120.87322	29.00237	1.465975	0.275430613	402
1998	170	166	159	158	169.82196	47.72002	0.771947	0.135964422	334
1999	176	173	167	165	179.61133	43.52002	0.83594	-0.038583618	281
2000	177	175	169	168	124.84227	34.15261	1.187967	-0.436465884	303
2001	176	171	163	161.7	154.39451	57.53593	0.581077	-0.289997217	250
2002	175	172	162.6	161.5	150.95610	55.28023	0.580776	-0.188660415	358
2003	169	166	161	161	165.70125	25.78246	1.252214	0.027828556	180
2004	177	172	161	160	139.37148	62.90132	0.490196	-0.295633822	184
2005	175	171.5	168.9	168	137.34058	30.71725	1.062065	0.568908536	156
2006	180.5	174	166	165.3	168.57940	65.32202	0.406176	-0.067483165	221

## Studie 4

Najmanová, L. & Adamík, P. 2009: Effect of climatic change on the duration of the breeding season in three European thrushes. *Bird Study* 56: 349–356.

# Effect of climatic change on the duration of the breeding season in three European thrushes

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**Capsule** Evidence for extension of breeding seasons in Song Thrushes and Blackbirds (multiple-brooded species) and shortening in Fieldfares (a single-brooded species).

**Aims** To analyse breeding data from central Europe during 1964–2006 in relation to climatic conditions operating at breeding and wintering grounds, and to compare breeding phenology in urban and rural habitats.

**Methods** Using chick ringing data we evaluated long-term changes in breeding phenology of Fieldfares *Turdus pilaris*, Song Thrushes *T. philomelos* and Common Blackbirds *T. merula*. Changes in phenology were analysed for the 5th percentile, median, 95th percentile, inter-quantile range (IQR) and brood size.

**Results** All thrushes showed consistent trends towards earlier onset of breeding. However, there was a contrasting pattern in the later phenological characteristics (median, 95th percentile and IQR) that were associated with single- versus multiple-brooded species. The single-brooded Fieldfares revealed an advancing trend in all phenological phases, which caused shortening of its breeding period. In contrast, the multiple-brooded Song Thrushes and Blackbirds delayed both medians and the 95th percentiles of breeding dates leading to extension of their breeding seasons. Temperatures at both wintering and breeding grounds were generally negatively associated with the onset of breeding. Urban birds bred significantly earlier than their rural conspecifics, but brood sizes did not differ.

**Conclusion** Multiple-brooded species may respond differently to increasing spring temperatures than single-brooded species.

## INTRODUCTION

It seems unarguable that recent increases in temperatures all over the globe are having a substantial impact on most plant and animal species (McCarty 2001, Walther *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 2003, Watkinson *et al.* 2004, Parmesan 2006, IPCC 2007). Among the studies on vertebrates, birds play the main role in our understanding of animals' responses to climate change. During the last three decades birds have shown significant changes in their phenologies, such as earlier spring migration (Lehikoinen *et al.* 2004, Gordo 2007) and earlier onset of breeding (Crick & Sparks 1999, Both *et al.* 2004). However, not all phenological variables (e.g. departure dates, migration

distances) shift in a similar manner (Lehikoinen *et al.* 2004, Rivalan *et al.* 2006, Fiedler *et al.* 2004, Adamík & Pietruszková 2008). One very little studied aspect of birds' response to climate change is how multi- and single-brooded species adjust their timing of breeding in relation to rising spring-time temperatures. Theoretically, earlier onset of spring could provide birds with more re-nesting opportunities and multiple-brooded species could raise more broods per season. However, if the breeding cycle is fine-tuned with available food for the nestlings, then the within-seasonal pattern of prey abundance might primarily influence the number of breeding attempts. This might reduce the number of subsequent breeding events, as has been shown for Blue Cyanistes caeruleus and Great Tits *Parus major* (Visser *et al.* 2003).

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In our study, using ringing records of nestlings, we documented changes in breeding phenology of three species of thrushes (the single-brooded Fieldfare *Turdus pilaris*, and multiple-brooded Song Thrush *Turdus philomelos* and Common Blackbird *Turdus merula*) from their central European breeding grounds during 1964–2006. We hypothesized that the globally observed trend in rising spring-time temperatures would lead to changes in breeding phenology. All three thrushes are migratory, though urban populations of Blackbirds are considered as sedentary (Luniak & Muslow 1986, Luniak *et al.* 1990). In addition, ringing records have been collected across a variety of habitat types and birds living in urban habitats breed ahead of the rural populations (Havlín 1963, Pikula 1973, Luniak & Muslow 1986, Luniak *et al.* 1990, Partecke *et al.* 2005). We therefore evaluated whether ringing records would adequately mirror these differences in the breeding phenology between urban and rural populations of Blackbirds and Song Thrushes.

## MATERIALS AND METHODS

### Ringing records

We used data on birds ringed as nestlings to document changes in phenology. Data on ringed nestlings of Song Thrushes, Fieldfares and Blackbirds were obtained from the Bird Ringing Centre in Prague. The computerized dataset contains records collected in the Czech Republic during 1964–2006 and in Slovakia during 1964–2002. Ringing activity in Slovakia was quite low, localized mainly in the western part of the country, and we pooled the records with those from the Czech Republic. The ringing records prior to 1964 were archived differently and their extraction would be extremely time-demanding. For each nest we recorded the number of ringed nestlings, date of ringing, locality and name of the ringer. Calendar dates of ringing were transformed into Julian dates with 1 January = day 0. The ringing activity varied annually and we used data from only those years when nestlings in at least nine nests had been ringed. The average number of nests per year was  $80 \pm 12.0$  se for Fieldfares,  $35 \pm 4.9$  for Blackbirds and  $27 \pm 4.4$  for Song Thrushes. The total quantity of data counts 25 638 nestlings ringed in 5787 nests (3371 nests for Fieldfares, 1472 for Blackbirds, 944 for Song Thrushes). In an earlier study on an open-nesting species we showed that phenological data obtained from ringing records match well with the seasonal progress of phenology (Hušek & Adamík 2006). This is because there is a relatively short time window when chicks in the nests can be safely ringed.

For each year and species we calculated the mean brood size, the 5th percentile, median, 95th percentile, and inter-quantile range (IQR, defined here as a span between the 5th and 95th percentiles) of ringing dates. We evaluated each phenological variable for trends by fitting first a quadratic regression and if the quadratic term was not significant, we assessed the significance of the linear trends.

### Climatic data

To test for the influence of climatic predictors on bird phenology we used climatic data from both wintering and breeding areas. For both areas we used monthly temperature anomalies from the Global Historical Climatology Network (GHCN) Land Surface Data (<http://www.ncdc.noaa.gov/gcag/index.jsp>). Temperature anomalies are given as differences from average temperatures during 1961–1990 (see Saino & Ambrosini 2008). For the wintering area we used the mean from the temperature anomalies during December–February ( $T_{\text{WIN}}$ ). The wintering area was defined by a grid with longitudinal boundaries of 1°W–6°E; and latitudinal boundaries of 50°N–43°N. This area roughly covers the majority of winter recoveries of all three thrushes from the Czech Republic and western Slovakia (Formánek 1958, Cepák *et al.* 2008). For the breeding area climate we used the April temperature anomalies ( $T_{\text{BREED}}$ ) calculated within a grid with longitudinal boundaries of 12°E–19°E; and latitudinal boundaries of 48°N–51°N. Data for both areas were available for the period 1964–2005. There was no significant correlation between  $T_{\text{WIN}}$  and  $T_{\text{BREED}}$  ( $r = 0.24$ ,  $n = 42$ ,  $P = 0.126$ ).

### Urbanization effects

To compare urban and rural populations of Blackbirds and Song Thrushes we chose only those nests where it was possible to recognize clearly whether the nest was found in urban or rural habitat. As the yardstick for an urban area we considered only towns with more than 10 000 inhabitants. The data on numbers of inhabitants were collated from the 1980 edition of the Statistical Yearbook (Czechoslovak Bureau of Statistics 1980). As rural habitats we considered localities close to small villages or in remote areas. We tried to be very cautious in categorizing nests. This resulted in a substantial reduction of sample sizes, which precluded separate estimates of phenological trends in these two habitat types. To compare phenology between urban and rural populations we used mean values of brood size and ringing dates. To control for trends in phenology, we entered the year as a covariate in all models.

## RESULTS

### Trends in breeding phenology

Both Blackbirds and Song Thrushes showed the same trend in the onset of breeding (the 5th percentiles) – a partial delay prior to the 1980s and since then advancement towards earlier dates. In Fieldfares there was a significant linear advancement over the study period (Table 1, Fig. 1). For the medians, both Blackbirds and Song Thrushes showed a tendency toward linear delay, while in the Fieldfares there was first a delay and then a shift toward earlier dates (Fig. 2). In Fieldfares the end of the breeding season (the 95th percentiles) showed a similar pattern to the medians of breeding, i.e. first a delay and then advancement. In contrast, both Song Thrushes and Blackbirds first advanced and then delayed the end of their breeding seasons (Table 1, Fig. 3). As a consequence, the length of the breeding seasons shortened in Fieldfares but extended in both Song Thrushes and Blackbirds (Table 1). Concerning brood size, a significant decrease in mean numbers of ringed nestlings per nest was found in Song Thrushes and a trend towards increase in Fieldfares since 1964 (Table 1).

### Climatic effects

During 1964–2005 there was a trend towards increases in  $T_{WIN}$  ( $b = 0.025 \pm 0.013$ ,  $F = 3.85$ ,  $P = 0.0567$ , Fig. 4). Similarly,  $T_{BREED}$  rose over the studied period which seems to be most pronounced after the late 1970s ( $y = 9110.4 - 9.2233 \times \text{year} + 0.0023 (\pm 0.0012) \times \text{year}^2$ ; year:  $F = 9.95$ ,  $P = 0.0031$ ; year<sup>2</sup>:  $F = 3.67$ ,  $P = 0.0627$ ; Fig. 4).

For both climatic factors,  $T_{WIN}$  and  $T_{BREED}$ , there was generally a negative relationship with onset of breeding (5th percentiles) in all three species. In Fieldfares both  $T_{WIN}$  and  $T_{BREED}$  had a significant effect, while in Song Thrushes and Blackbirds, only  $T_{BREED}$  had significant influence. Except for the effect of  $T_{BREED}$  in Fieldfares, there was no statistically significant effect of climatic factors on medians or the 95th percentiles of breeding dates (Table 2).

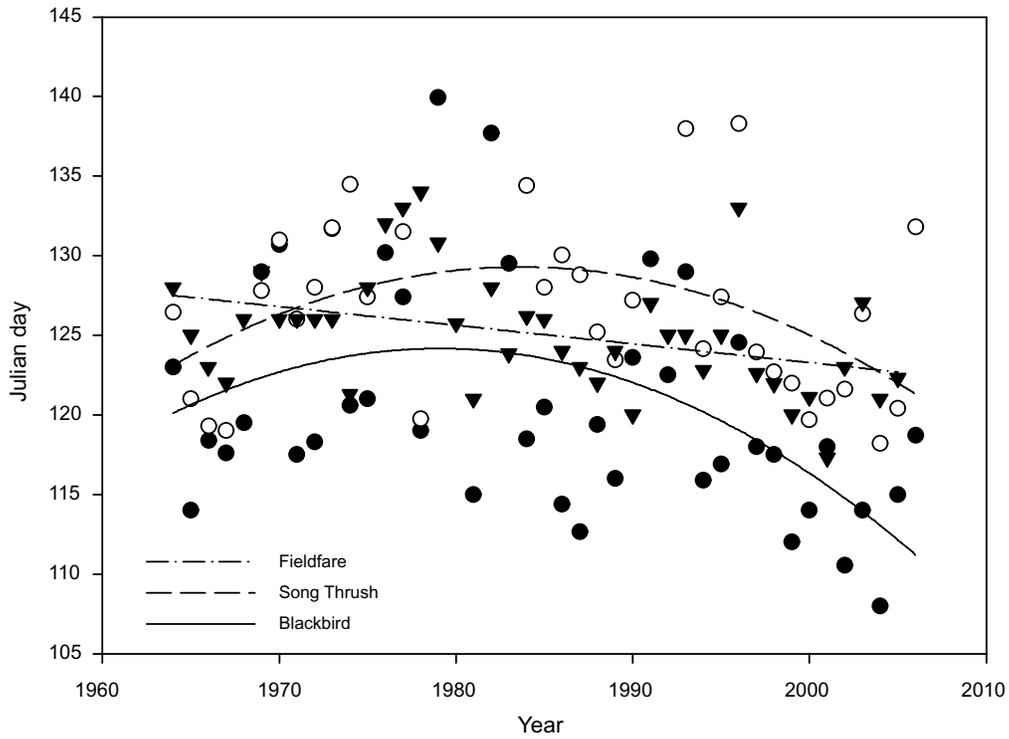
### Urban vs. rural populations

Urban Blackbirds bred on average 7 days earlier than their rural conspecifics (mean<sub>URBAN</sub>  $\pm$  se =  $148.2 \pm 0.92$ ,  $n = 665$ , mean<sub>RURAL</sub> =  $155.1 \pm 1.10$ ,  $n = 485$ ; habitat:  $F = 26.31$ ,  $P < 0.001$ ; year:  $F = 10.38$ ,  $P = 0.001$ ).

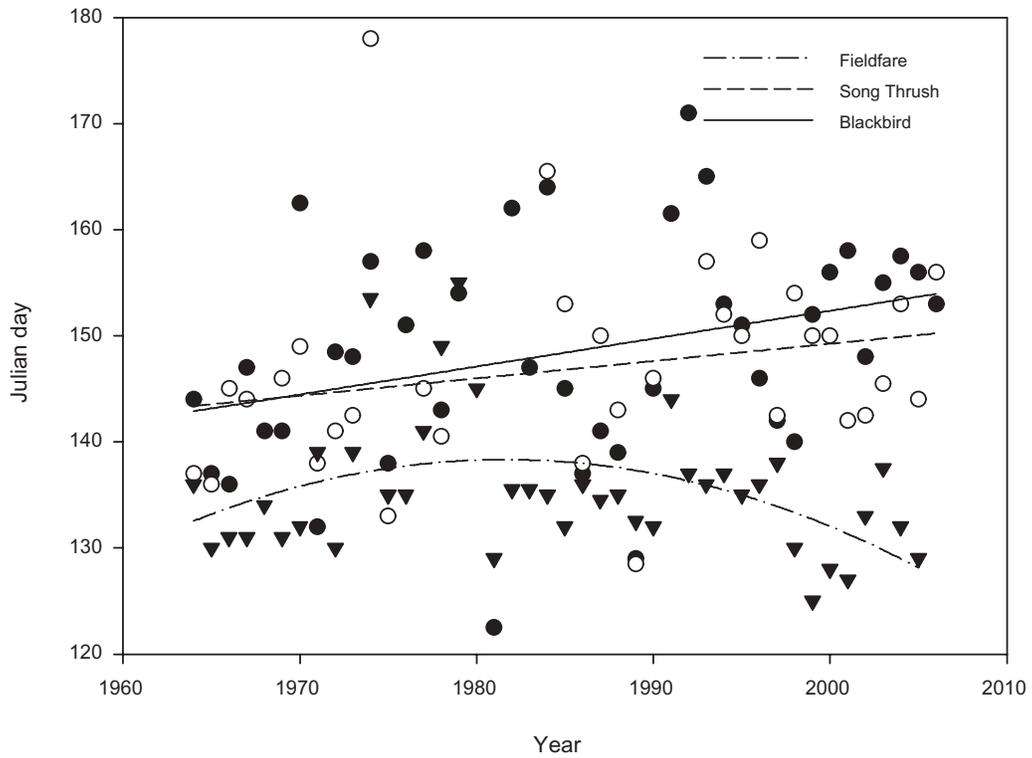
**Table 1.** Long-term trends in selected phenological aspects of the breeding phenology of three European thrushes in the Czech Republic and Slovakia, 1964–2006.

Variable	Equation	Year <sup>a</sup>		Year <sup>2</sup>		R <sup>2</sup>
		F	P	F	P	
<b>Fieldfare</b>						
5th percentile	$y = 358 - 0.1173 (\pm 0.0448) \times \text{year}$	6.84	<b>0.013</b>	–	–	0.146
Median	$y = -73022 + 73.84 \times \text{year} - 0.0186 (\pm 0.0068) \times \text{year}^2$	2.07	0.158	7.31	<b>0.010</b>	0.194
95th percentile	$y = -149668 + 151.22 \times \text{year} - 0.0382 (\pm 0.0104) \times \text{year}^2$	3.19	0.082	13.52	<b>&lt; 0.001</b>	0.300
IQR <sup>b</sup>	$y = -125442 + 126.56 \times \text{year} - 0.0319 (\pm 0.0106) \times \text{year}^2$	0.53	0.473	8.99	<b>0.005</b>	0.196
Brood size	$y = -5.93 + 0.0052 (\pm 0.0030) \times \text{year}$	3.01	0.090	–	–	0.070
<b>Song Thrush</b>						
5th percentile	$y = -62844 + 63.49 \times \text{year} - 0.0160 (\pm 0.0063) \times \text{year}^2$	0.42	0.521	6.52	<b>0.016</b>	0.183
Median	$y = -176.96 + 0.1631 (\pm 0.1199) \times \text{year}$	1.85	0.184	–	–	0.055
95th percentile	$y = 144511 - 145.40 \times \text{year} + 0.0366 (\pm 0.0137) \times \text{year}^2$	0.04	0.849	7.18	<b>0.012</b>	0.189
IQR	$y = 207355 - 208.89 \times \text{year} + 0.0526 (\pm 0.0130) \times \text{year}^2$	0.01	0.912	16.32	<b>&lt; 0.001</b>	0.345
Brood size	$y = 17.69 - 0.00697 (\pm 0.0034) \times \text{year}$	4.25	<b>0.047</b>	–	–	0.117
<b>Blackbird</b>						
5th percentile	$y = -69860 + 70.73 \times \text{year} - 0.0179 (\pm 0.0071) \times \text{year}^2$	7.23	<b>0.011</b>	6.31	<b>0.016</b>	0.258
Median	$y = -374.38 + 0.2634 (\pm 0.1233) \times \text{year}$	4.56	<b>0.039</b>	–	–	0.102
95th percentile	$y = -367.26 + 0.2779 (\pm 0.1420) \times \text{year}$	4.03	0.051	–	–	0.156
IQR	$y = 157725 - 159.35 \times \text{year} + 0.0403 (\pm 0.0125) \times \text{year}^2$	12.53	<b>0.001</b>	10.31	<b>0.003</b>	0.369
Brood size	$y = 12.24 - 0.0044 (\pm 0.0038) \times \text{year}$	1.32	0.258	–	–	0.032

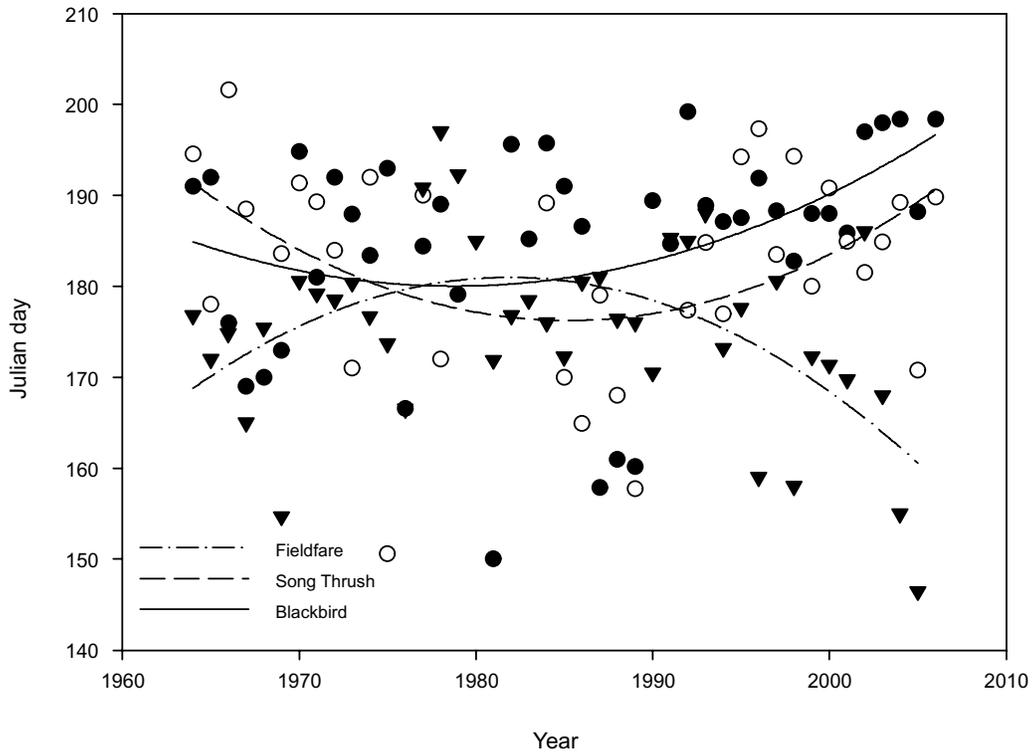
<sup>a</sup>Type I test. Regressions were run on annual means during 1964–2006. Number of years with available data: 42 (Fieldfare), 34 (Song Thrush) and 42 (Blackbird). IQR, inter-quantile range – the span between the 5th and 95th percentiles of ringing dates; significant values ( $P < 0.05$ ) are shown in bold type.



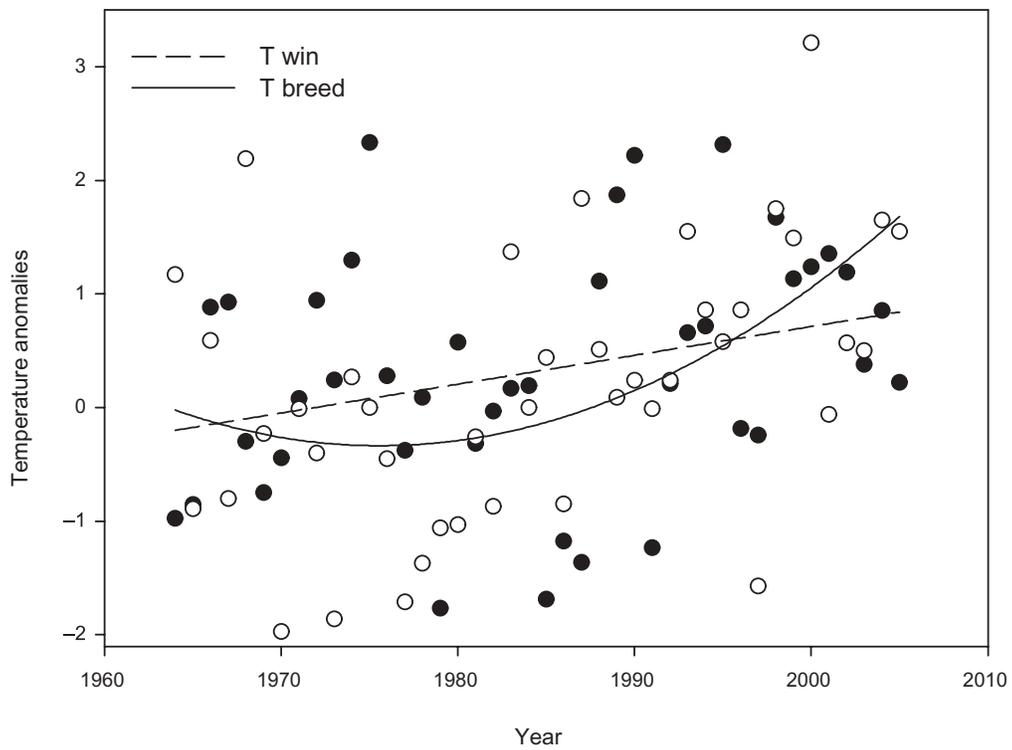
**Figure 1.** Changes in the onset of breeding represented by the 5th percentiles in Song Thrushes (○), Blackbirds (●) and Fieldfares (△), 1964–2006.



**Figure 2.** Changes in the medians of breeding dates in Song Thrushes (○), Blackbirds (●) and Fieldfares (△), 1964–2006.



**Figure 3.** Changes in the 95th percentiles of ringing dates in Song Thrushes (O), Blackbirds (●) and Fieldfares (△), 1964–2006.



**Figure 4.** Trends in temperature anomalies at wintering grounds (●) and breeding grounds (O). For further details on these climatic data see 'Methods'.

**Table 2.** Multiple regression models of breeding phenology in three European thrushes on climatic predictors (temperature in the wintering and breeding grounds) during 1964–2005.

	<i>b</i>	se	<i>F</i>	<i>P</i>	<i>R</i> <sup>2</sup>
<b>Fieldfare</b>					
5th percentile					
<i>T</i> <sub>WIN</sub>	-1.25	0.51	6.09	<b>0.018</b>	0.269
<i>T</i> <sub>BREED</sub>	-0.99	0.45	4.84	<b>0.033</b>	
Median					
<i>T</i> <sub>WIN</sub>	-1.15	0.91	1.60	0.213	0.177
<i>T</i> <sub>BREED</sub>	-1.80	0.81	4.95	<b>0.032</b>	
95th percentile					
<i>T</i> <sub>WIN</sub>	-1.14	1.47	0.61	0.441	0.172
<i>T</i> <sub>BREED</sub>	-3.25	1.3	6.10	<b>0.018</b>	
<b>Song Thrush</b>					
5th percentile					
<i>T</i> <sub>WIN</sub>	-1.28	0.86	2.21	0.149	0.235
<i>T</i> <sub>BREED</sub>	-1.78	0.77	5.35	<b>0.029</b>	
Median					
<i>T</i> <sub>WIN</sub>	-0.63	1.17	0.13	0.721	0.034
<i>T</i> <sub>BREED</sub>	-1.34	1.56	0.74	0.399	
95th percentile					
<i>T</i> <sub>WIN</sub>	-1.27	2.14	0.35	0.557	0.020
<i>T</i> <sub>BREED</sub>	0.89	1.92	0.22	0.644	
<b>Blackbird</b>					
5th percentile					
<i>T</i> <sub>WIN</sub>	-1.59	1.01	2.49	0.122	0.228
<i>T</i> <sub>BREED</sub>	-2.25	0.91	6.09	<b>0.018</b>	
Median					
<i>T</i> <sub>WIN</sub>	-0.15	1.66	0.01	0.929	0.001
<i>T</i> <sub>BREED</sub>	0.27	1.51	0.03	0.856	
95th percentile					
<i>T</i> <sub>WIN</sub>	1.03	1.86	0.31	0.583	0.011
<i>T</i> <sub>BREED</sub>	-0.77	1.69	0.21	0.651	

Significant values ( $P < 0.05$ ) are shown in bold type.

Similarly, urban Song Thrushes bred 4 days earlier than rural birds (mean<sub>URBAN</sub> = 147.8 ± 1.10,  $n = 324$ , mean<sub>RURAL</sub> = 151.7 ± 1.19,  $n = 339$ ; habitat:  $F = 5.55$ ,  $P = 0.019$ ; year:  $F = 3.27$ ,  $P = 0.071$ ). After controlling for the year effect, there were no significant differences in brood sizes between urban and rural populations either for Blackbirds (mean<sub>URBAN</sub> = 3.51 ± 0.04, mean<sub>RURAL</sub> = 3.54 ± 0.04; habitat:  $F = 0.05$ ,  $P = 0.821$ ; year:  $F = 8.46$ ,  $P = 0.004$ ) or Song Thrushes (mean<sub>URBAN</sub> = 3.76 ± 0.06, mean<sub>RURAL</sub> = 3.79 ± 0.06; habitat:  $F = 0.17$ ,  $P = 0.679$ ; year:  $F = 1.74$ ,  $P = 0.188$ ).

## DISCUSSION

### Trends in breeding and climate

We found that all three thrushes shifted their breeding phenology over the 43-year period. The 5th percentiles

first delayed until the late 1970s and then started to advance (Song Thrush and Blackbird) or they shifted linearly towards earlier dates (Fieldfare). The shifts in early phases of phenology were negatively associated with temperatures at both breeding and wintering quarters which suggests that the observed changes in phenology were temperature-dependent. Many bird species start laying earlier in years with higher spring-time temperatures (Myres 1955, Dunn 2004) and our data are in line with this. The breeding ground temperature first cooled, and since the early 1980s it started to rise. This agrees with earlier findings from both the central European region (Weidinger & Král 2007) and the globe (IPCC 2007). The medians in breeding dates were weakly, though still negatively, associated with temperatures. Only in Fieldfares did we find a significant association between temperatures at breeding grounds and the later phenological characteristics. We suggest that in single-brooders it might be much easier to detect climatic effects even in later phenological phases than in multiple-brooders. This is because in the latter group subsequent breeding attempts are likely to conceal true shifts in phenology.

For the later phenological phases we found a contrasting pattern. While in Fieldfares both the medians and 95th percentiles corresponded with the previously described non-linear trends, in Song Thrushes and Blackbirds the medians tended to delay over the whole study period. Moreover, in these two species the 95th percentiles showed exactly the opposite trend to the 5th percentiles, leading to extension of breeding seasons after the late 1970s. In contrast, in Fieldfares the slope of 95th percentiles was much steeper, causing the breeding season to shorten. With respect to brood size, we found that it tended to increase in Fieldfares and significantly decreased in Song Thrushes. Given that there is a strong within-season decline in clutch size among bird species (Crick *et al.* 1993), our data suggest that the Fieldfares' increase in mean brood size is caused by shifting its entire breeding season toward earlier dates, while in Song Thrushes the decline is driven by extending its breeding season with many late small-clutched broods. A long-term increase in brood size has been found in other open-nesting species, for example, Red-backed Shrikes *Lanius collurio* (Hušek & Adamík 2008), Eurasian Reed Warblers *Acrocephalus scirpaceus* and Great Reed Warblers *Acrocephalus arundinaceus* (Schaefer *et al.* 2006, but see Halupka *et al.* 2008).

To date there has been limited evidence that breeding seasons extend in response to climate change. Crick

& Sparks (1999) examined long-term trends in the timing of breeding of 20 British bird species and they found that only European Robins *Erithacus rubecula* extended their breeding season. While in a German population of Eurasian Reed Warblers there was a shortening of their breeding season (Schaefer *et al.* 2006), the Polish population did not shift its end, causing an extension of the breeding season (Halupka *et al.* 2008). A different pattern was reported by Weatherhead (2005) in a study on Red-winged Blackbirds *Agelaius phoeniceus*. The onset of breeding did not shift but the nesting ended later, causing the breeding season to be extended.

In a large-scale study of Great Tits and Blue Tits, Visser *et al.* (2003) found that the rising spring-time temperatures were associated with a reduction in the frequency of second broods. To add to the complexity of climate-driven responses, in a Danish population of Barn Swallows *Hirundo rustica*, the frequency of second clutches did not change over the period 1971–2005, but the interval between the nesting attempts significantly increased (Møller 2006). Unfortunately, data from ringing or nest record schemes do not allow one to distinguish first broods from the subsequent ones, therefore we can not exclude the possibility that the observed extensions of breeding seasons in Song Thrushes and Blackbirds are because of an extending interval between first and subsequent clutches. However, given the high rate of brood losses in thrushes (Weidinger 2002), it seems more likely that selection would favour short intervals between subsequent nesting attempts. As a consequence, the observed extensions of breeding seasons are more likely to be driven by a higher proportion of pairs with second or replacement clutches.

### Urbanization effect

We found that both Blackbirds and Song Thrushes bred significantly earlier in urban than in rural areas of the Czech Republic and Slovakia. This confirms the earlier field studies from central Europe (Havlín 1963, Pikula 1973). The higher thermal conditions, better food supplies and artificial light in urban environment are among the main factors explaining this difference (Luniak *et al.* 1990).

### Methodological constraints

Spatial and temporal distribution of ringing records depends on ringing effort of volunteers. Thus, if

ringers are more active in certain parts of the breeding cycle, this might easily bias the derived estimates of breeding phenology. This bias is likely to be similar to that described for estimates of laying dates and clutch sizes of songbirds collected by volunteer ornithologists (Weidinger 2001). However, given that several hundreds of ringers collected these records over the past four decades, it seems very likely that any such biases would be cancelled out. Ringing records have already been used to document changes in phenology in several studies (Beintema *et al.* 1985, Møller *et al.* 2006, Hušek & Adamík 2008) and we encourage their further use from other national schemes to document long-term changes in birds' breeding phenology.

### Conclusions

We have shown that two multiple-brooded species have extended their breeding seasons, while one single-brooded species has shifted its entire breeding period toward earlier dates, with a steeper trend at the end of the distribution causing a contraction of the breeding season. The available studies on timing of breeding show a variety of phenological responses rather than a clear and uniform pattern. Therefore, we urge field ornithologists to explore in more detail the phenological responses of multiple-brooded species to variation in climate.

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## Studie 5

Adamík, P. & Král, M. 2008: Climate and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds. *Journal of Zoology, London* 275: 209–215.

# Climate- and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds

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## Keywords

*Glis glis*; indirect effects; nest predation; population trends; pulsed resources.

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## Abstract

Global climate change has been shown to cause variable shifts in phenology in a variety of animals and unexpected outcomes across food chains are to be found. Here we examined how rising annual spring temperatures affected the interactions between seed masting, cavity nesting birds and dormice using long-term data from Eastern Czech Republic. We have shown that climate change was associated with unequal shifts in the phenology of two cavity-breeding groups: dormice and birds. Rising spring temperatures have progressively advanced the termination of hibernation for the edible dormouse *Glis glis*, a common bird predator, leading to an increasing overlap in the use of nesting boxes between dormice and birds. In contrast, only the collared flycatcher *Ficedula albicollis*, of the four cavity-nesting bird species, advanced its breeding dates in response to rising temperatures. At the same time, favourable weather conditions, coupled with good seed masting years, have been associated with a substantial rise in dormice numbers. Concurrent with the increasing dormice abundance, the number of bird nests destroyed significantly increased in three out of four bird species. We showed that while there was a significant change in the date that the dormice emerged from hibernation during the course of the study, it did not significantly contribute to predation levels when controlling for their abundance and timing of breeding in birds. We found that the increasing dormice abundance was the main factor causing high brood losses in birds, while the timing of breeding in birds had a variable effect between bird species. This study illustrates how changes in climate might affect organisms at various trophic levels with often unexpected outcomes. Limited evidence from other study organisms suggests that species most at risk are those at different trophic levels that do not shift at the same rate or in the same direction as their food resources, predators or competitors.

## Introduction

In light of the accumulating evidence for the impact of global climate change on biota, the focus in biological studies has shifted from simply documenting changes towards a more complex understanding of the effects of climatic factors on animal and plant populations (Stenseth *et al.*, 2002; Walther *et al.*, 2002). Despite the well-documented shifts in phenology in a variety of animal species (Walther *et al.*, 2002), we are just beginning to learn about the consequences these shifts might have on their populations or other members of their community. Studies on songbirds, which have been examined most frequently in this context, show that climate might often have complex effects within a given ecosystem (Sillett, Holmes & Sherry, 2000; Both & Visser, 2001; Thomas *et al.*, 2001; Jones, Doran & Holmes, 2003). This is because species at different levels of food chains have their own environmental optima

for successful growth and reproduction, which might be easily shifted by sudden climatic changes. In seasonal environments, this may lead to a mismatch between the timing of birds' reproduction and the peak in abundance of their food supply (Both & Visser, 2001; Thomas *et al.*, 2001). As an outcome, the populations of a given species that are out of phase with their food might produce fewer surviving young (Coppack & Pulido, 2004; Visser, Both & Lambrechts, 2004), have lower adult survival (Thomas *et al.*, 2001) or their populations may decline (Both *et al.*, 2006). However, due to the shifts in phenology in a variety of organisms, there are likely to be many less known and unexpected impacts of climate change. For example, the shifts in phenology may lead to an overlap between species that did not interact or compete over some limited resources in the past. In this respect, studies on mistiming due to climate change have been mostly about mistiming with respect to food, while little is known about shifts with

respect to predation risk. Similarly, our understanding of the climatic effects on bird phenology has advanced considerably, but equivalent studies on mammalian phenology are scarce. For example, as a response to increased temperatures, yellow-bellied marmots *Marmota flaviventris* have advanced termination of hibernation (Inouye *et al.*, 2000), and red squirrels *Tamiasciurus hudsonicus* have shifted their breeding period towards earlier dates (Réale *et al.*, 2003) but, in contrast, no evidence for a shift in breeding dates was found in deer mice *Peromyscus maniculatus* breeding in northern latitudes (Millar & Herdman, 2004).

Here we extend earlier climatic studies and illustrate how climate affects both mammals and birds within a Central European temperate deciduous woodland, where several species of rodent (dormice *Gliridae*, *Rodentia*) and birds share the same resource for breeding – cavities in trees or nest boxes. Dormice are traditionally considered to be frugivorous, but accumulating evidence across their distributional range shows that in early spring, shortly after their emergence from hibernation, they represent a serious threat to cavity nesting birds (Juškaitis, 1995; Koppmann-Rumpf, Heberer & Schmidt, 2003; Juškaitis, 2006). We show that in the past, they had a distinct temporal pattern of cavity use, but due to a changing climate this is no longer true. In this study, we examined how rising annual spring temperatures affected the interactions between seed masting, cavity nesting birds and the dormice using a long-term dataset from Eastern Czech Republic.

## Materials and methods

The data were collected near Dlouhá Loučka, Czech Republic (49°49'N, 17°12'E), in a mixed deciduous woodland where an ongoing study of hole-nesting birds breeding in nest boxes was initiated in 1973 (Král & Bičík, 1990; Saetre, Post & Král, 1999). For this study, we used data from 1980 to 2005, because before 1980 there were very few dormice recorded, and in addition, the temperature started to increase after 1980 (IPCC, 2001; Weidinger & Král, 2007). The annual mean number of provided nest boxes was  $174 \pm 16$  s.d. The nest boxes were provided at a constant density of 6 nest boxes  $\text{ha}^{-1}$  in clusters across an area covering c. 2 km<sup>2</sup>. The collared flycatchers *Ficedula albicollis* occupied on average 22% of nest boxes, great tits *Parus major* 16%, blue tits *Parus caeruleus* 8% and nuthatches *Sitta europaea* 7% (data on first broods only). Each year, from April to early July, nest boxes were checked daily or nearly so to record the breeding biology of birds. If a given nest was predated, detailed notes on marks of the predator were taken. The nest failures due to dormice were easily recognized either by their presence in the nest box or indirect cues, for example, excreta inside the nest box, the way they killed the birds or the dormouse nest built from the birds' nest material. During the day, the dormice commonly rest inside the nest boxes, making their identification unmistakable. Three dormice species occur in our study area: the edible dormouse *Glis glis*, forest dormouse *Dryomys nitedula* and common dormouse *Muscardinus avellanarius*. Owing to

insufficient data samples for the other two species, we restricted our analyses to the edible dormouse because it is the dominant species in the area, covering 70% of all dormice observations. Only predation events that could unambiguously be assigned to edible dormice were considered here. If the nest was predated and more than 2 days elapsed between successive nest checks, the mid-day in the time interval was chosen to represent the day of predation.

Data on seed production in the region of Northern Moravia were obtained from the Forests of the Czech Republic and the Forestry and Game Management Research Institute. Seed production was estimated by experienced foresters for both beech *Fagus sylvatica* and oak (including both pedunculate *Quercus robur* and sessile oak *Quercus petraea*) on a scale from 0 to 5, and the sum of these two estimates yielded the annual level of seed production. The annual masting of oak and beech was strongly correlated ( $r = 0.92$ ,  $P < 0.001$ ). A comparison with another available dataset on seed years from the nearby region in southern Poland (Kantorowicz, 2000) for the period 1980–1999 shows highly correlated estimates ( $r = 0.69$ ,  $n = 20$ ,  $P < 0.001$ ). Weather data (mean monthly temperatures) were obtained from a local meteorological station in Paseka located 2 km from the study area. Animal abundance is expressed either as a number of breeding pairs per hectare (for birds) or proportions of occupied nest boxes (dormice). The dormice were not individually marked in all years. Therefore, we used the highest proportion of occupied nest boxes by dormice during a single visit in a 2-week interval in mid June for estimating their abundance. Dormice nest-box occupancy is used here only as a proxy of real population abundance. Results from an intensive dormice-marking study during the last 3 years show that spring nest-box occupancy rates match well with the summer population density estimates (P. Adamík, unpubl. data). This is because by mid June, almost all individuals are already active and they move from belowground into nest boxes or tree cavities.

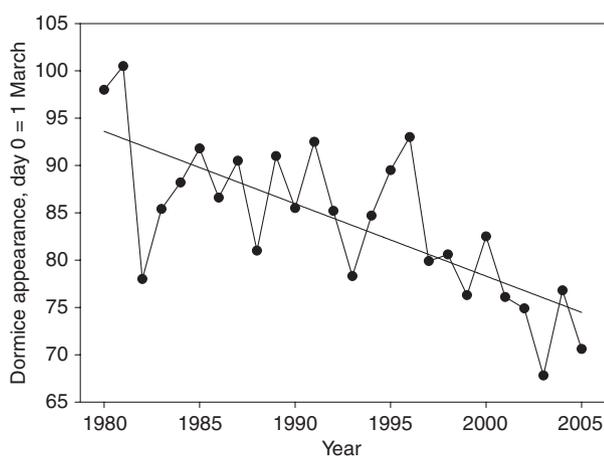
To evaluate the relationship between animal phenology (dormouse nest-box appearance dates and bird mean first egg-laying dates) and mean monthly temperatures, we ran simple linear regressions. We chose mean monthly temperatures in April and May as they cover the main period of either egg laying in birds (April) or the termination of hibernation in edible dormouse (May). The annual means of both first egg-laying dates (birds) and first sighting dates (dormice) were used as response variables. General linear models (GLM) were used for modelling the relationship among dormouse abundance (response variable), mean temperature in May and seed crop (summed values for both oak and beech). Originally, we fitted seed abundance estimates from both the previous and the current calendar year. Owing to the non-significant effect of seed crop of the previous year on dormice population, we excluded this variable from further models (for details, see 'Discussion'). To analyse whether predation rates differed among years (treated as a continuous variable) and bird species, a binomial model for analysis of variance with logit link (Proc

Genmod, SAS Institute, 2004) was used. The response variable was the proportion of predated nests (events) of all nests where at least one egg was laid (trials). Originally, we fitted an interaction between year and bird species, but due to its insignificant effect we excluded it from the results. In further analysis, we tested the role of animal phenology (dormouse nest-box appearance dates and bird mean first egg-laying dates) and dormice numbers in annual predation rates by fitting GLM with a binomial error distribution and logit link. First, we fitted a model with dormice nest-box appearance dates as a single predictor of bird predation rates. Then we fitted a more complex model with dormouse nest-box appearance dates, dormouse abundance and mean first egg-laying dates (to account for annual changes in breeding phenology) as explanatory variables. The response variable was the number of predated nests/the number of all nests where at least one egg was laid (event/trial). We restricted this analysis to collared flycatchers and great tits because these are the only two bird species for which we have sufficient sample sizes. In all models, we checked for any non-linear effects, normality of residuals and homogeneity of variances. Where it was necessary, the variables were appropriately transformed. For all statistical analyses, we used two-tailed  $P$ -values.

## Results

### Shifts in phenology

During the study period, the mean nest-box appearance date advanced significantly for the edible dormouse ( $\beta = -0.765 \pm 0.149$  SE,  $r = -0.72$ ,  $n = 26$ ,  $P < 0.001$ ). The dormouse advanced its phenology by *c.* 8 days decade<sup>-1</sup> (Fig. 1). In hole-nesting birds, the egg-laying dates advanced by 3.5 days decade<sup>-1</sup> in the migratory collared flycatcher ( $\beta = -0.345 \pm 0.068$ ,  $r = -0.72$ ,  $n = 26$ ,  $P < 0.001$ ); however, non-significant advancement was observed in the resident species: great tit ( $\beta = -0.196 \pm 0.115$ ,  $r = -0.33$ ,  $n = 26$ ,  $P = 0.10$ ), blue tit ( $\beta = -0.173 \pm 0.107$ ,  $r = -0.32$ ,  $n = 26$ ,



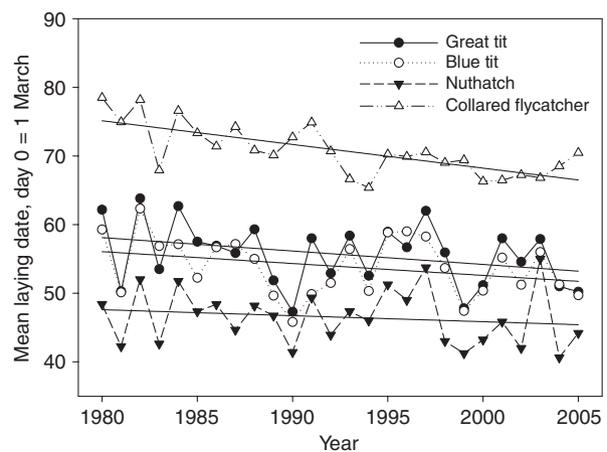
**Figure 1** Mean nest-box appearance dates for the edible dormouse *Glis glis* in Eastern Czech Republic, 1980–2005.

$P = 0.12$ ) and nuthatch ( $\beta = -0.088 \pm 0.107$ ,  $r = -0.16$ ,  $n = 26$ ,  $P = 0.42$ ; Fig. 2).

We found that during the same period, the mean monthly temperatures remained stable in March ( $\beta = -0.011 \pm 0.055$  SE,  $r = -0.02$ ,  $n = 26$ ,  $P = 0.92$ ) but increased in April ( $\beta = 0.125 \pm 0.045$ ,  $r = 0.50$ ,  $n = 26$ ,  $P = 0.01$ ), May ( $\beta = 0.111 \pm 0.055$ ,  $r = 0.38$ ,  $n = 26$ ,  $P = 0.05$ ) and June ( $\beta = 0.141 \pm 0.038$ ,  $r = 0.60$ ,  $n = 26$ ,  $P < 0.01$ ). The mean monthly temperatures during April and May were negatively related to phenology. The mean April temperature influenced the phenology for all four bird species, while in the edible dormouse, May temperature had a stronger effect (Table 1).

### Population densities and predation

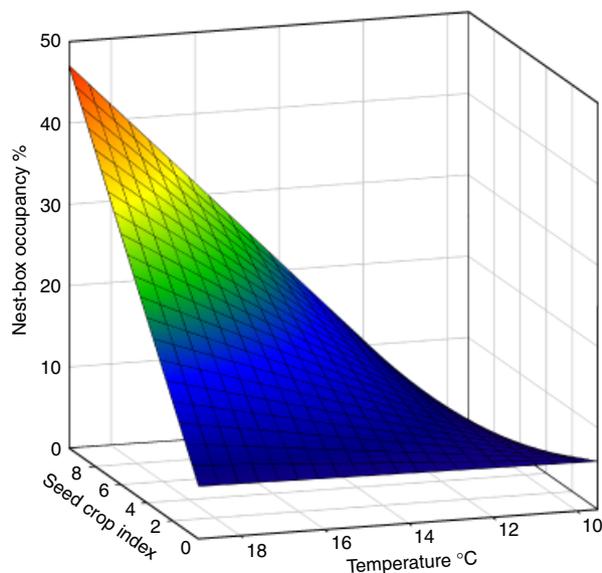
We found a significant increase in the abundance of the edible dormouse (annual proportions of occupied nest boxes:  $\beta = 0.716 \pm 0.134$ ,  $r = 0.74$ ,  $n = 26$ ,  $P < 0.001$ ). While only 2.7% of nest boxes were occupied by dormice in the first 5 study years, the occupancy rates increased to 19.1% in the last 5 years. The mean temperature in May and seed crop estimates of acorns and beechnuts have an interacting positive and significant effect on dormice numbers (GLM, interaction:  $F_{1,22} = 5.87$ ,  $P = 0.024$ ; Fig. 3). Concurrent with the increasing dormice abundance, the number of bird nests destroyed by the edible dormouse significantly increased in three species: collared flycatcher ( $r = 0.78$ ,  $n = 26$ ,  $P < 0.001$ ), great tit ( $r = 0.40$ ,  $n = 26$ ,  $P = 0.04$ ), nuthatch ( $r = 0.42$ ,  $n = 26$ ,  $P = 0.03$ ) and no change in the blue tit ( $r = 0.20$ ,  $n = 26$ ,  $P = 0.33$ ). The binomial model confirmed these results, when the predation rate was significantly influenced by both year ( $F_{1,99} = 44.96$ ,  $P < 0.001$ ) and bird species ( $F_{3,99} = 12.25$ ,  $P < 0.001$ ). The highest brood losses occurred in the collared flycatcher, and the lowest in the blue tit (Fig. 4). A possible link between the timing of breeding and predation pressure might be seen between the bird species. Breeding is earliest in the nuthatch (Fig. 2; median



**Figure 2** Mean first egg-laying dates in four hole-nesting passerines in Eastern Czech Republic, 1980–2005. For each species, separate linear regression lines are shown.

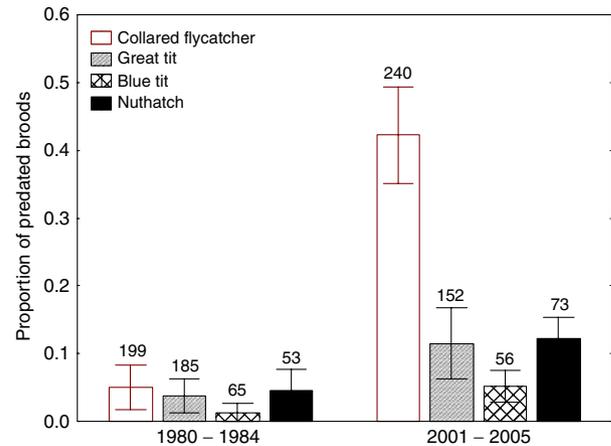
**Table 1** Linear regressions of mean monthly temperatures on bird mean first egg-laying dates and dormouse mean nest-box appearance days during 1980–2005

Variable	Slope	SE	<i>r</i>	<i>P</i>
<i>T</i> <sub>April</sub>				
Edible dormouse	-1.571	0.789	-0.38	0.055
Great tit	-1.266	0.405	-0.54	0.004
Blue tit	-0.836	0.408	-0.39	0.051
Nuthatch	-0.982	0.377	-0.47	0.015
Collared flycatcher	-1.289	0.283	-0.68	0.001
<i>T</i> <sub>May</sub>				
Edible dormouse	-1.839	0.639	-0.51	0.008
Great tit	-0.242	0.414	-0.11	0.565
Blue tit	-0.210	0.382	-0.11	0.591
Nuthatch	-0.098	0.371	-0.05	0.799
Collared flycatcher	-0.887	0.283	-0.54	0.008

**Figure 3** Relationship among edible dormouse *Glis glis* abundance, seed crop (combined values for oak and beech) and mean May temperature.

of first egg-laying date<sub>1980–2005</sub>: 14 April), followed by the blue (23 April) and great tit (25 April), and collared flycatcher (10 May). Predation by edible dormouse occurred on relatively older nests in nuthatch and tits than in the collared flycatcher. The mean age in days (date of first egg laid for a given nest = day 1) for predated nests<sub>1980–2005</sub>: collared flycatcher  $19.69 \pm 1.34$  (95% CI); great tit  $24.88 \pm 3.40$ ; blue tit  $34.83 \pm 6.76$ ; and nuthatch  $32.77 \pm 4.59$ .

The single-factor binomial models of predation rates on the collared flycatcher and great tit nests in relation to dormouse nest-box appearance dates showed, for both species, a negative effect of the timing of dormouse above-ground appearance on bird brood losses (model 1, Table 2). However, when dormouse abundance and bird phenology

**Figure 4** Comparison of annual predation rates on bird nests (means  $\pm$  SE,  $n=5$ ) by the edible dormouse on four hole-nesting songbirds from two 5-year periods: one at the beginning (1980–1984) and one at the end (2000–2005) of the study. The total number of nests is shown above the error bars.**Table 2** Models of predation rates on the collared flycatcher *Ficedula albicollis* and great tit *Parus major* nests in relation to the timing of dormouse appearance in nest boxes, dormouse abundance and birds' timing of breeding (mean first egg-laying dates)

Species/variable	Estimate	SE	$\chi^2$	<i>P</i>
Collared flycatcher				
I. Dormouse appearance	-0.1194	0.0136	95.32	0.001
II. Dormouse appearance	-0.0211	0.0216	0.96	0.327
Dormouse abundance	0.0932	0.0187	26.37	0.001
Mean bird laying date	-0.0713	0.0385	3.56	0.059
Great tit				
I. Dormouse appearance	-0.0937	0.0260	15.09	0.001
II. Dormouse appearance	0.0340	0.0374	0.83	0.363
Dormouse abundance	0.1349	0.0327	20.57	0.001
Mean bird laying date	0.1518	0.0524	9.32	0.002

were added to this model, they showed, for both species, that dormouse abundance has the strongest effect on nest predation (model 2, Table 2). In the great tit, there is a positive effect of the timing of breeding. Between years, the later they breed, the more likely they are to be predated by dormice. However, for the collared flycatcher a marginally non-significant effect of its breeding phenology indicates an opposite effect (Table 2).

Despite the increasing predation pressure, the breeding densities did not show a significant trend for any of the four bird species (great tit  $r=-0.24$ ,  $n=26$ ,  $P=0.23$ ; blue tit  $r=-0.21$ ,  $n=26$ ,  $P=0.31$ ; nuthatch  $r=0.08$ ,  $n=26$ ,  $P=0.68$ ; collared flycatcher  $r=0.15$ ,  $n=26$ ,  $P=0.45$ ).

## Discussion

We found strong shifts in the spring phenology of the edible dormouse and collared flycatcher. We found that these changes in phenology were related to spring temperatures,

which increased over the period of study, in all five studied species. A similar trend in dormice phenology found in a German locality about *c.* 550 km away suggests synchronous advancement across Central Europe (Koppmann-Rumpf *et al.*, 2003). The advancement in nest-box appearance is likely associated with the termination of hibernation. The dormice, which are arboreal rodents that are active at night, spend 7–8 months hibernating each year (Bieber & Ruf, 2004). In spring, after leaving the underground hibernaculum sites, they move into tree cavities or nest boxes using them as dens, and later during the summer for reproduction. Temperature plays an important role in the termination of hibernation (Vietinghoff-Riesch, 1960; Jallageas, Mas & Assenmacher, 1989), and it also affects their sexual activity, which in turn positively correlates with reproductive success (Fietz *et al.*, 2004). For example, in male edible dormice, hypothermia and the development of gonads are mutually exclusive (Jallageas & Assenmacher, 1984; Fietz *et al.*, 2004). Thus, favourable weather conditions in spring may advance the termination of hibernation and/or incur lower energetic costs for the maintenance of body temperature that enables the development of sexual organs.

We also found a considerable increase in dormice numbers during the period of study. We found that this increase was associated with the combination of favourable spring weather and a good seed crop. Mild weather might either incur lower energetic requirements in dormice or advance the onset of foliage development in plant buds that are their main source of food at this time of year. Both these factors might have a positive effect on reproduction and survival, causing an increase in population numbers. It is also possible that the rising spring temperatures triggered seed productivity (Piovesan & Adams, 2001; Kelly & Sork, 2002; van der Meer, Jorritsma & Kramer, 2002; Réale *et al.*, 2003), and this in turn affected the dormice populations. Similar increases in dormice numbers were reported from southern Germany (Gatter & Schütt, 1999). This suggests that the dormice populations are, in some habitat types, responding in a similar way across a scale of several hundred kilometres.

Changes in forest management could also influence the availability of natural cavities. However, at our study sites the forestry practices remained unchanged at least during the past 60 years. Therefore, we believe that changes in habitat structure are unlikely to have an influence on dormice in our study system.

The reproduction and consequent population densities in the edible dormouse were already shown to depend strongly on the mast seeding of oaks *Quercus* spp. and beech *F. sylvatica* (Schlund, Scharfe & Ganzhorn, 2002; Pilastro, Tavecchia & Marin, 2003; Ruf *et al.*, 2006). Heavy seed production is well known to influence rodent populations positively, with a profound impact on other trophic levels (Pucek *et al.*, 1993; Jędrzejewska & Jędrzejewski, 1998). Consequently, abundant rodent populations cause high predation on bird nests, which might affect the bird population levels (McShea, 2000; Schmidt, 2003; Schmidt & Ostfeld, 2003). In contrast to other rodent species, in edible

dormouse the seed crop is known to influence the population numbers, sexual activity and reproduction in the masting year and not in the subsequent or the previous year (Bieber, 1998; Schlund *et al.*, 2002). What is not clear is how, in early spring, the animals assess the future availability of food. A possible role of secondary plant components is one of the most frequently proposed hypotheses (Bieber, 1998; Schlund *et al.*, 2002; Fietz *et al.*, 2004).

We found that the growth of dormouse numbers was positively associated with the increasing number of predated bird nests. The dormice destroy and consume eggs, and kill both nestlings and incubating parents. The predation itself is a controversial issue because dormice are considered to feed mainly on fruits, young leaves and shoots (Vietinghoff-Riesch, 1960; Fietz *et al.*, 2005), but apparently in some populations they become carnivorous (Juškaitis, 1995; Koppmann-Rumpf *et al.*, 2003; Juškaitis, 2006; present study). It seems that interspecific differences in brood losses are a consequence of the timing of a birds' breeding period. The collared flycatcher, seasonally the latest breeding species, experienced the highest brood losses among the four bird species. We found that the high dormice numbers rather than their early phenology have a positive effect on predation rates. In comparison with an earlier study by Koppmann-Rumpf *et al.* (2003), we show, by simultaneous tests of all predictors, that dormice abundance is the primary factor responsible for high brood losses. What we do not know is whether preying just on one nest provides the dormice with a sufficient source of energy or whether they predate repeatedly. If they predate just on one nest, then it is obvious why dormouse abundance is a much better predictor of brood losses than the timing of their emergence. In addition, for the great tit we show that in the years when they started breeding relatively late they suffered higher nest losses due to dormice predation. In contrast, we did not find a similar effect in the collared flycatcher. It might be the case that they are already breeding so late that there is no way to escape the dormice. Field studies from other geographical areas confirm our findings. In Germany and Lithuania, the pied flycatcher *Ficedula hypoleuca*, the latest breeding bird species within the community, suffered the highest brood losses due to edible dormouse predation (29 and 17%), while the great tit nests were predated at much lower rates (8 and 10%; Koppmann-Rumpf *et al.*, 2003; Juškaitis, 2006).

We have shown that both climate change and seed masting affect dormice populations, and when coupled with the late breeding of some bird species, the dormice pose a predation threat to the hole-nesting bird community. Of the four bird species, only the collared flycatcher advanced its breeding dates (its arrival dates remained unchanged, Weidinger & Král, 2007). However, this shift in breeding is not sufficient to escape predation by dormice. In contrast, in the much earlier breeding great tit, we found that in those years when tits nested early, they suffered lower predation rates. It is clear that if the ongoing increase in their numbers continues, it will affect bird nestling productivity negatively, leading possibly to population declines in some of the cavity

nesting bird species. This study shows how climate affects organisms at different trophic levels with often unexpected outcomes. Possibly most at risk are those systems where species from different trophic levels do not shift at the same rate or in the same direction. This variability in responses may decouple the relationships across trophic levels, leading to changes in the predator–prey interaction rates that might have unexpected consequences for the organisms involved. Limited evidence from other study organisms (i.e. amphibians, molluscs, birds) suggests (Beebee, 1997; Philippart *et al.*, 2003; Visser & Both, 2005) that unequal shifts in phenology may be quite common, resulting in negative effects for some species.

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## Studie 6

Kolářová, E. & Adamík, P. 2015: Bird arrival dates in Central Europe based on one of the earliest phenological networks. *Climate Research* 63: 91–98.

# Bird arrival dates in Central Europe based on one of the earliest phenological networks

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**ABSTRACT:** Recording arrival dates of migratory birds to their breeding grounds has been one of the most popular activities among naturalists for more than 2 centuries. However, we know extremely little about the timing of birds' annual cycles when systematic field observations were still in their infancy, before the current warming period. Here we aim at filling this gap for bird arrival dates of 35 species for one of the earliest phenological networks, run by the Bohemian Patriotic-Economic Society during 1828–1847 in the present day Czech Republic. We retrieved station-based archival data and present the arrival dates correlated with local temperature prior to species-specific arrival. The mean slope of arrival advancement with monthly temperature across all species was  $-1.4 \text{ d } ^\circ\text{C}^{-1}$  in our study, which is remarkably similar to a recent dataset from the same region. The strength of this relationship depended on species-specific timing of migration. Early migrating species showed stronger negative relationships with temperature than later arriving, long-distance migrants. Cross-correlations in arrival dates among stations were positive and high for well-known species such as skylark, common quail and common cuckoo. Station-based data also showed strong relationships with temperature. For most species, comparisons with recent arrivals (1991–2010) show later arrivals in recent years, and we suggest that changes in population sizes might also play a role in explaining bird phenology.

**KEY WORDS:** Bird arrival · Long-distance migrant · Phenology · Short-distance migrant · Temperature

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## 1. INTRODUCTION

The 18th century was a period of great interest in endeavouring to explain natural phenomena. In an atmosphere of the development of natural sciences, many academic institutions were established and the foundations of numerous scientific disciplines were laid (Inkster & Morrell 2007, Alcoforado et al. 2012). This was also the case for phenological observations. The first organised networks for observing plants, birds and insects were established across the European continent. The Swedish and Finnish phenological networks were initiated by von Linné and Leche in the 1750s (von Haartman & Söderholm-Tana 1983, Terhivuo et al. 2009). Beginning in 1846, the Finnish

Society of Sciences and Letters set up a regular phenological network which is still running (Lehikoinen et al. 2004, Kubin et al. 2008). Another phenological series originated from Norfolk in the UK. Here the Marsham family recorded the phenological events of over 20 plants and animals over a period of more than 200 yr during 1736 to 1947 (Sparks & Carey 1995). The oldest systematic European network was operated by the Societas Meteorologica Palatina in Mannheim between 1781 and 1792 (Menzel 2003). As well as meteorological data, they also collected phenological records on plants and animals. The data regarding avian phenology consisted of arrivals and departures, and included migratory species such as white stork *Ciconia ciconia*, barn swallow *Hirundo*

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*rustica*, common nightingale *Luscinia megarhynchos*, and common cuckoo *Cuculus canorus*. After the first International Ornithological Congress in 1884, interest in avian phenology was awakened in other countries, and especially during the 20th century many national phenological networks were established (Menzel 2003, Nekovář et al. 2008).

The first sporadic notes on avian phenology in the Czech lands were made by J. Stepling, A. Strnad, T. Haenke and M. David in the second half of the 18th century (Nekovář & Hájková 2010). However, the first regular network was created by members of the Imperial Royal Patriotic-Economic Society of Bohemia. This society was originally established as the Society of Agriculture and Liberal Arts in the Kingdom of Bohemia (Gesellschaft des Ackerbaues und den freien Künste im Königreich Böhmen) by Empress Maria Theresa in 1767. The main aim of this society was to enhance the agricultural and industrial production in the Czech lands (Krška & Šamaj 2001). In 1789 the society was reorganised and renamed as the Imperial Royal Patriotic-Economic Society of Bohemia (K. K. Patriotisch-ökonomische Gesellschaft im Königreich Böhmen) (Volf 1967). Among other topics, the members focussed on meteorology, plant and animal phenology. In 1835, a series of books about the topography of Moravia (Die Markgrafschaft Mähren, topographisch, statistisch und historisch geschildert) was published by the Benedictine T. Wolný (Wolný 1835, Krška 2003). As well as plant phenology, he also described the usual arrival of some common bird species such as skylark *Alauda arvensis*, white wagtail *Motacilla alba* and corncrake *Crex crex* (Wolný 1835). In 1861 the Natural Science Society in Brno (Naturforschender Verein in Brünn) was established (Krška 2003). The society organised meteorological and phenological observations in the areas of Moravia and Silesia. The phenological records of birds were published regularly until 1906. Since 1853 phenological observations, including bird arrival data, were organised from Vienna by the newly established Zentralanstalt für Meteorologie und Geodynamik. Another network based on observations, initiated by Rudolf, the Crown Prince of Austria, was temporarily run by Comité für Ornithologische Beobachtungs-Stationen in Österreich during the 1880s. Since 1923, a national scheme of phenological stations has been run by the present-day Czech Hydrometeorological Institute.

During the last 2 decades a renaissance in phenological research has occurred as a consequence of ongoing climatic changes, which have affected plants and animals at different trophic levels and in

various ecosystems (Rosenzweig et al. 2008). Changes in the timing of bird migration have been reviewed by Lehikoinen et al. (2004), Rubolini et al. (2007), Knudsen et al. 2011, Pearce-Higgins & Green (2014). However, nearly all the studies use time series of no more than a few recent decades (for rare exceptions see Sparks & Carey 1995, Ahas 1999, Lehikoinen et al. 2004, Ellwood et al. 2010, Gordo et al. 2013). This is in contrast to climatology or plant phenology where detailed studies on the reconstruction of past events are widely available. Here we aim to fill this gap for bird arrival dates for one of the earliest phenological networks which ran during 1828 to 1847 in Bohemia, Austrian Empire (nowadays the western part of the Czech Republic). We present an analysis of the archival records, link them to local climate and assess the reliability of data, both from a local, station-based, and regional perspective.

## 2. DATA AND METHODS

### 2.1. Historical data

During 1828 to 1847 the members of the Imperial Royal Bohemian Patriotic-Economic Society contributed their phenological observations to annual reports in the society's journal *Neue Schriften*. The final 2 years appeared in *Verhandlungen und Mittheilungen*. Both migratory and resident bird species were recorded. The data were restricted to Bohemia and involved 33 phenological stations (see Fig. 1, see Table S1 in the Supplement at [www.int-res.com/articles/suppl/c063p091\\_supp.pdf](http://www.int-res.com/articles/suppl/c063p091_supp.pdf)). They consisted of records on the first arrival and the last departure dates of 35 bird species (3594 arrival and 2174 departure records). The reports distinguished between true migratory species (i.e. those with non-overlapping distributions during breeding and wintering periods) and resident species for which peaks in spring and autumn movements were observed (e.g. tits, treecreepers and crossbills). In this study we considered arrival data only.

We expressed the dates of observations as days of the year (DOY; where January 1 = Day 1). The original scientific names were converted into present-day form (see Table 1) and the data were then checked for outliers and incorrect dates caused by mistakes in the original printed records. All incorrect data and scattered outliers (detected by inspection of boxplots and Cleveland dotplots; Zuur et al. (2010) were excluded from analysis (71 records on arrivals). In those cases where there was a clear mistake in listing

the arrival date as the departure date and vice versa, the data were assigned to the right category. For the sites Klášterec nad Ohří, Český Krumlov and Želiv there were 2 first arrivals of birds observed: one at low and another at high altitudes. In these cases, the earlier arrival was chosen and included in the analyses. In a few cases where a range of dates was provided, the earlier date was considered as the first arrival. For the fieldfare *Turdus pilaris* and pine grosbeak *Pinicola enucleator* the autumn arrival data to central Europe actually represented their arrival to wintering sites. In the 19th century the fieldfare was still spreading south from northern Europe and it was only later when it extended its breeding range into the central European region.

For each species we set a lower limit of 50 records for inclusion in analyses (see Table 2); 27 species met this criterion. For each of these 27 species we reconstructed the Bohemian arrival time series with linear mixed-effect models where Site was taken as a random effect and Year as a fixed effect (Häkkinen et al. 1995, Schaber et al. 2010). Species-specific multi-site combined arrival time series were estimated in the R-package ‘pheno’ (Schaber 2012; see Table S5 in the Supplement at [www.int-res.com/articles/suppl/c063p091\\_supp.pdf](http://www.int-res.com/articles/suppl/c063p091_supp.pdf)). Annual predicted values of arrivals from the fixed part of the model were then used to explain the relationship with climate using linear regressions and Pearson correlations. Species-specific arrivals were compared to mean temperature of the month of arrival or to the month preceding the mean arrival (depending on the temporal overlap of arrivals and the focal month; see Table S2 in the Supplement at [www.int-res.com/articles/suppl/c063p091\\_supp.pdf](http://www.int-res.com/articles/suppl/c063p091_supp.pdf)). Mean monthly temperatures are widely used in avian phenological studies (Gordo 2007). The mean monthly temperature data were obtained from a reconstructed homogenized temperature series (1800–2010) for the Czech Republic (Brázdil et al. 2012a,b).

For those sites where reliable time series ( $\geq 14$  yr of data) were available for particular bird species (Hradec Králové, Loket, Velké Dvorce and Vyšší Brod), we assessed the local relationship between arrivals and temperature. For an assessment of

between-site similarity in annual first arrivals, we cross-correlated the time series of these 4 stations. Paired *t*-tests were used to compare the slopes of arrival–climate relationships both at a regional (Bohemian) and site scale.

## 2.2. Recent data

To compare the historical arrivals with recent data we used a dataset for the period 1991–2010. We collected data on bird arrivals from various sources, but the majority of the records were collected from the phenological network of the Czech Society for Ornithology and supplemented by data from various personal diaries and grey literature. We tried to match the observations to spatially overlap with those of the Bohemian Patriotic-Economic Society. For some species (e.g. *Ardea cinerea*, *Upupa epops*, etc.) we did not have enough records to reconstruct the arrival dates. Therefore the recent dataset consisted of only 17 species: true migrants for which we had sufficiently large sample sizes. We checked for outliers and used mixed effect modelling as for the historical times series.

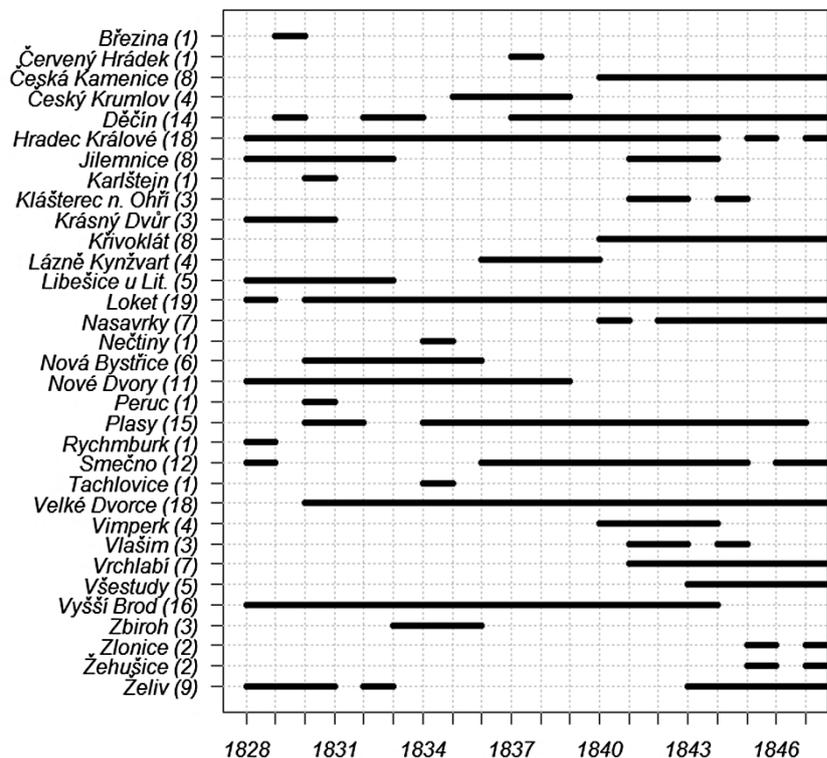


Fig. 1. Overview of available station-based arrival data from the network of the Bohemian Patriotic-Economic Society, 1828–1847. In parentheses: number of years with data for each site

Table 1. Bird species recorded by the members of the Bohemian Patriotic-Economic Society and current valid classification of species names

Original scientific name	Original German name	Current valid scientific name	Common English name
<i>Alauda arvensis</i>	Feldlerche	<i>Alauda arvensis</i>	Common skylark
<i>Anas anser canorus</i>	Wildgans	<i>Anser</i> spp. <sup>a</sup>	Geese
<i>Anas anser ferus</i>	Wildgans	<i>Anser</i> spp.	Geese
<i>Ardea cinerea</i>	Fischreiher	<i>Ardea cinerea</i>	Grey heron
<i>Ardea minuta</i>	Kleine Rohrdommel	<i>Ixobrychus minutus</i>	Little bittern
<i>Ardea stellaris</i>	Gemeine Rohrdommel	<i>Botaurus stellaris</i>	Great bittern
<i>Certhia familiaris</i>	Baumkletterer	<i>Certhia</i> spp. <sup>b</sup>	Treecreeper
<i>Ciconia alba</i>	Gemeiner Storch	<i>Ciconia ciconia</i>	White stork
<i>Columba oenas</i>	Holztaube	<i>Columba oenas</i>	Stock dove
<i>Columba palumbus</i>	Ringeltaube	<i>Columba palumbus</i>	Wood pigeon
<i>Columba turtur</i>	Turteltaube	<i>Streptopelia turtur</i>	Turtle dove
<i>Colymbus cristatus</i>	Großer Haubentaucher	<i>Podiceps cristatus</i>	Great crested grebe
<i>Cuculus canorus</i>	Kukuck	<i>Cuculus canorus</i>	Common cuckoo
<i>Hirundo apus</i>	Mauerschwalbe	<i>Apus apus</i>	Common swift
<i>Hirundo riparia</i>	Uferschwalbe	<i>Riparia riparia</i>	Sand martin
<i>Hirundo urbica</i>	Hausschwalbe	<i>Delichon urbicum</i>	House martin
<i>Larus</i>	Möwen	<i>Larus</i> spp.	Gulls
<i>Loxia coccythraustes</i>	Dickschnabel	<i>Coccothraustes coccythraustes</i>	Hawfinch
<i>Loxia enuncleator</i>	Fichtenkernbeißer	<i>Pinicola enucleator</i>	Pine grosbeak
<i>Motacilla alba</i>	Gemeine Bachstelze	<i>Motacilla alba</i>	White wagtail
<i>Motacilla erithacus</i>	Hausrothschwänzchen	<i>Phoenicurus ochruros</i> <sup>c</sup>	Black redstart
<i>Motacilla hortensis</i>	Grasmücke	<i>Sylvia</i> spp. <sup>d</sup>	–
<i>Motacilla luscini</i>	Nachtigall	<i>Luscinia megarhynchos</i>	Common nightingale
<i>Motacilla phoenicurus</i>	Gartenrothschwänzchen	<i>Phoenicurus phoenicurus</i>	Common redstart
<i>Oriolus galbula</i>	Goldamsel	<i>Oriolus oriolus</i>	Golden oriole
<i>Parus ater</i>	Schwarzmeise	<i>Periparus ater</i>	Coal tit
<i>Parus coeruleus</i>	Blaumeise	<i>Cyanistes caeruleus</i>	Blue tit
<i>Parus major</i>	Kohlmeise	<i>Parus major</i>	Great tit
<i>Scolopax rusticola</i>	Waldschnepfe	<i>Scolopax rusticola</i> <sup>e</sup>	Eurasian woodcock
<i>Sturnus vulgaris</i>	Star	<i>Sturnus vulgaris</i>	Common starling
<i>Tetrao coturnix</i>	Wachtel	<i>Coturnix coturnix</i>	Common quail
<i>Turdus musicus</i>	Singdrossel	<i>Turdus philomelos</i>	Song thrush
<i>Turdus pilaris</i>	Kronowetvogel	<i>Turdus pilaris</i>	Fieldfare
<i>Turdus viscivorus</i>	Misteldrossel	<i>Turdus viscivorus</i>	Mistle thrush
<i>Upupa epops</i>	Wiedehopf	<i>Upupa epops</i>	Eurasian hoopoe
<i>Vanellus cristatus</i>	Kiebitz	<i>Vanellus vanellus</i>	Northern lapwing

<sup>a</sup>Geese were not well recognized to species level at that time. <sup>b</sup>At that time Eurasian treecreeper and short-toed treecreeper were not separately recognized, therefore data may refer to both species. <sup>c</sup>Misidentification of robin and black redstart was very common. <sup>d</sup>*M. hortensis* is now garden warbler but at that time several *Sylvia* warbler species were labelled under this name. <sup>e</sup>This could be any species of the genus *Scolopax*, *Gallinago* and *Lymnocyptes*

### 3. RESULTS

#### 3.1. General pattern of bird arrivals to Bohemia

We retrieved data on 35 bird species (27 species with >50 records) from 33 sites (Fig. 1, Table 1, see Table S1 in the Supplement). For an overview of mean first arrival dates to Bohemia and sample sizes see Table 2. In general the mean first arrival dates correlated negatively with mean monthly temperatures (see Table S2 in the Supplement). The mean

slope of arrival advancement with temperature across all species was  $-1.43 \text{ d } ^\circ\text{C}^{-1}$  for both the 1828–1847 and the 1991–2010 periods. The mean slope of the 17 species for the 1828–1847 period was  $-1.52 \text{ d } ^\circ\text{C}^{-1}$ . Slope estimates for the arrival–temperature relationship between these 2 time periods were highly correlated ( $r = 0.61$ ,  $n = 17$ ,  $p = 0.010$ ). While some early arriving species such as skylark or song thrush showed strong negative responses to temperature ( $-1.8$  to  $-2.5 \text{ d } ^\circ\text{C}^{-1}$ ), other species, especially the later arriving ones, did not. The strength of the

Table 2. List of the 35 species whose arrivals were observed by the members of the Bohemian Patriotic-Economic Society in 1828–1847, and a comparison with recent (1991–2010) arrival dates. Migratory categories (mc): short- (S) or long-distance (L) migrant; n: number of records; Mean first arrival day of the year (DOY) for species with  $n < 50$  was taken as a simple arithmetic mean of all observations (marked with <sup>a</sup>), and for species with  $n > 50$  an arrival time series was reconstructed from a linear mixed-effects model (see 'Data and methods'). Significance of comparisons of arrival dates between the 2 periods (2-tailed  $t$ -test): ns = non-significant difference, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

Species	mc	1828–1847			1991–2010			Difference p-value
		n	DOY	SE	n	DOY	SE	
<i>Alauda arvensis</i>	S	211	50	8.5	480	62	9.8	***
<i>Anser</i> spp.	S	120	66	9.3				
<i>Apus apus</i>	L	113	119	9.3	456	123	5.1	ns
<i>Ardea cinerea</i>	S	83	93	9				
<i>Botaurus stellaris</i> <sup>a</sup>	S	15	94					
<i>Certhia</i> spp.	S	81	77	13.2				
<i>Ciconia ciconia</i> <sup>a</sup>	L	49	98					
<i>Coccothraustes coccothraustes</i> <sup>a</sup>	S	35	78					
<i>Columba oenas</i>	S	166	74	11.8	92	81	7.3	*
<i>Columba palumbus</i>	S	162	78	10.1	343	75	9.9	ns
<i>Coturnix coturnix</i>	L	145	132	10.3	195	134	12	ns
<i>Cuculus canorus</i>	L	197	113	5.5	484	120	6.4	***
<i>Cyanistes caeruleus</i>	S	67	71	9.5				
<i>Delichon urbicum</i>	L	210	106	7.4	391	113	6.5	***
<i>Ixobrychus minutus</i> <sup>a</sup>	L	2	87					
<i>Larus</i> spp. <sup>a</sup>		48	81					
<i>Luscinia megarhynchos</i>	L	58	117	3.5	206	118	4.8	ns
<i>Motacilla alba</i>	S	185	71	7.8	533	76	9	**
<i>Oriolus oriolus</i>	L	69	105	13.9	197	128	6.5	***
<i>Parus major</i>	S	85	72	11.7				
<i>Periparus ater</i>	S	61	68	11.2				
<i>Phoenicurus ochruros</i>	S	116	94	11.2	527	86	8.6	***
<i>Phoenicurus phoenicurus</i>	L	100	96	11.1	270	109	8.5	***
<i>Pinicola enucleator</i> <sup>a</sup>	S	21	289					
<i>Podiceps cristatus</i> <sup>a</sup>	S	14	89					
<i>Riparia riparia</i> <sup>a</sup>	L	2	183					
<i>Scolopax rusticola</i>	S	176	88	10.9				
<i>Streptopelia turtur</i>	L	90	113	11.3	188	119	10.5	***
<i>Sturnus vulgaris</i>	S	139	68	10.6	549	61	9.1	***
<i>Sylvia</i> spp.		127	112	11				
<i>Turdus philomelos</i>	S	151	74	8.8	400	73	8.9	ns
<i>Turdus pilaris</i>	S	101	297	18.9				
<i>Turdus viscivorus</i>	S	88	55	14.3	132	62	10.1	ns
<i>Upupa epops</i>	L	52	104	11.2				
<i>Vanellus vanellus</i>	S	94	76	11.6	380	70	11.8	***

relationship between arrival and temperature was, in part, explained by species-specific arrival dates, i.e. a stronger relationship in early arriving species and vice versa (Fig. 2, linear regression:  $b = 0.016 \pm 0.006$  SE,  $F_{1,24} = 7.09$ ,  $p = 0.013$ ,  $R^2 = 0.23$ ) for the period 1828–1847. For the recent dataset the arrival–temperature relationship was slightly stronger ( $b = 0.029 \pm 0.005$ ,  $F_{1,15} = 32.36$ ,  $p < 0.001$ ,  $R^2 = 0.66$ ). There was no significant relationship between mean arrival day and SE in the datasets for 1828–1847 ( $b = -0.03 \pm 0.02$ ,  $F_{1,24} = 0.94$ ,  $p = 0.178$ ,  $n = 26$  excluding the fieldfare) or 1991–2010 ( $b = -0.03 \pm 0.02$ ,  $F_{1,15} = 3.21$ ,  $p = 0.093$ ,  $n = 17$ ).

### 3.2. Local magnitude of arrivals

Station-based first arrival dates from the 4 sites with the most reliable datasets were generally positively cross-correlated (mean  $r = 0.41 \pm 0.23$  SD,  $n = 33$  pairwise comparisons), with the highest correlation in arrival in the common cuckoo and skylark (see Table S4 in the Supplement at [www.int-res.com/articles/suppl/c063p091\\_supp.pdf](http://www.int-res.com/articles/suppl/c063p091_supp.pdf)).

Comparisons of site-based arrival–temperature slopes with those from Bohemian regional data showed a significantly stronger relationship at the regional scale for Locket and Velké Dvorce, but not for

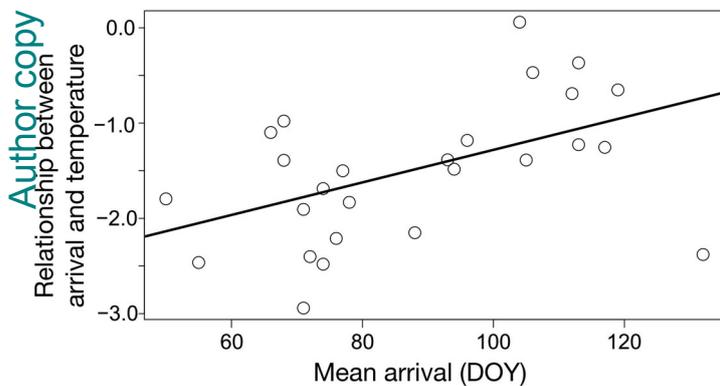


Fig. 2. Relationship between species-specific mean first arrival date and the slopes of the relationship between arrival and mean monthly temperature (1828–1847). Fieldfare data is not included since it represents autumn arrival to wintering sites

Hradec Králové; Bohemia versus Loket (paired  $t$ -test;  $t_{12} = 3.27$ ,  $p = 0.001$ ), Bohemia versus Velké Dvorce ( $t_{10} = 3.29$ ,  $p = 0.008$ ) and Bohemia versus Hradec Králové ( $t_{12} = -2.08$ ,  $p = 0.059$ ). Mean slope estimates with monthly temperature were  $-2.40$  in Loket ( $n = 13$ ),  $-2.04$  in Velké Dvorce ( $n = 11$ ),  $-0.91$  in Hradec Králové ( $n = 13$ ), and  $-1.16$  in Vyšší Brod ( $n = 3$ ; see Table S3 in the Supplement at [www.int-res.com/articles/suppl/c063p091\\_supp.pdf](http://www.int-res.com/articles/suppl/c063p091_supp.pdf)).

#### 4. DISCUSSION

The Bohemian Patriotic-Economic Society organised a network of observations of bird arrivals for 20 yr. This is one of the earliest and most comprehensive networks on avian phenology in central Europe. We confirmed with more recent datasets that warmer weather was associated with earlier spring arrivals. The mean slope of arrival advancement with temperature across all species was  $-1.43 \text{ d } ^\circ\text{C}^{-1}$  for both periods in our study. But the strength of this relationship depended on species-specific timing of migration. Early migrating species showed much stronger and negative relationship with temperature than later arriving (mostly long-distance) migrants. This is in line with the comprehensive overviews of Lehikoinen et al. (2004) and Pearce-Higgins & Green (2014). The mean response fits into the range ( $-1.11 \text{ d } ^\circ\text{C}^{-1}$  for long-distance and  $-1.87 \text{ d } ^\circ\text{C}^{-1}$  for short-distance migrants, see Table S2 in the Supplement for source data) based on studies from the second half of the 20th century ( $-2.9 \text{ d } ^\circ\text{C}^{-1}$  in Lehikoinen et al. 2004; and ca.  $-0.35$  and  $-1.3 \text{ d } ^\circ\text{C}^{-1}$  in long- and short-distance migrants, respectively, in Pearce-

Higgins & Green 2014). Few studies have analyzed 18th and 19th century time series on bird arrivals. Data on 3 species from Finland show responses between  $-1.02$  to  $-2.34 \text{ d } ^\circ\text{C}^{-1}$  in 1749–1762 (Lehikoinen et al. 2004). The Marsham family records from the east of England and 2 other shorter British time series show a slightly stronger relationship with temperature; e.g. the common cuckoo:  $-1.5$  to  $-2.8 \text{ d } ^\circ\text{C}^{-1}$ , which in our study was  $-1.2 \text{ d } ^\circ\text{C}^{-1}$  in the regional dataset (but see also the variable station-based data, Sparks & Carey 1995, Sparks 1999). Spatial heterogeneity in local adaptations could result in this pattern (Sparks et al. 2007). The Bohemian Patriotic-Economic Society also recorded data on plant phenology. An assessment of these records shows very strong negative relationships with local temperature (Brázdil et al. 2011). Although, the members of the Society were mostly professionals, e.g. foresters and teachers, it is possible that their knowledge on identification of species was not sufficient. For example, some well-known species such as white wagtail, skylark, wood pigeon *Columba palumbus* or common cuckoo show reasonable associations with temperature. In contrast, the song of starlings *Sturnus vulgaris* was likely confused with that of the golden oriole *Oriolus oriolus* since there are several records of golden oriole from February and March (very unlikely arrival dates for a long-distance migrant that is among the latest species to appear in central Europe). This suggests that arrivals for well-known and easily recognized species are more reliable than for the less well-known ones. Judging from the magnitude of temperature–arrival relationships of the 2 Czech datasets, we conclude that these historical records are as reliable as the recent arrival data.

The period 1828–1847 in Bohemia was characterized by a monthly temperature in March and April that was  $\sim 2^\circ\text{C}$  lower than in the 1991–2010 period (Brázdil et al. 2012a). We know extremely little on how birds tuned their timing of migration at times when climate was cooler (cf. Sparks 1999, Lehikoinen et al. 2004). Studies on plants show much later onset of phenophases in the first half of the 19th century than today (Brázdil et al. 2011, Možný et al. 2012, Kolářová et al. 2014). In contrast, comparison with the more recent data on bird arrivals to Bohemia shows that timing of migration was in general earlier by 4.1 d (2.9 d when excluding the golden oriole) in 1828–1847. Of the 17 species available for comparisons, 12 arrived later in the recent period. We do not know why so many species in the 19th century dataset arrived earlier than today. The temperature–arrival relationships are similar in these 2 datasets,

indicating their reliability. From 1983 to 2003, arrival dates to western Poland were on average 2.3 d earlier (for 12 species in common) than our historical dataset. When excluding the golden oriole the difference is 4.9 d (Tryjanowski et al. 2005). This discrepancy could be attributed to changes in population sizes, which in declining species may result in apparent delayed arrival (Tryjanowski & Sparks 2001, Miller-Rushing et al. 2008). Especially farmland species such as skylark or quail are currently suffering from severe population declines (Reif et al. 2008). On the other hand, a wide range of species were hunted for food (e.g. skylark, starling, thrushes and tits) or trapped for their song (e.g. blackcap, nightingale), which could locally lead to significant declines of their populations at that time (Baum 1955). We cannot rule out also the possible role of dynamic changes in migratory routes or wintering areas that could be also mirrored in different timing of arrivals (Berthold et al. 1992, Sutherland 1998).

We also showed that station-based first arrival dates were positively cross-correlated. Given the high variability in first arrival dates, which makes this variable often criticized for its stochastic component (Moussus et al. 2010), we perceive this as a sign of reliability of these records. A detailed view on station-based associations with climate shows a much stronger relationship than at regional scales for 2 stations, and a tendency towards weaker a relationship at 1 station. It might be that the observer effect plays a major role in the quality of station-based data. For this reason we suggest that the regional reconstructions provide more reliable estimates of arrival dates than the station-based data. The latter may be confounded by the observer effect, population trends, predation pressure and skills of individual observers, or the length of the time series might be too short to detect a true relationship with climate (von Haartman & Söderholm-Tana 1983, Sparks 1999, Hušek et al. 2009, 2012, Lehikoinen & Sparks 2010).

Phenological data are a good indicator of the response of biota to climate change (Parmesan 2007). Therefore, reconstructing historical time series broadens our understanding of how both plants and animals reacted to climate at times that preceded the current warming period (Amano et al. 2010, Naef-Daenzer et al. 2012, Primack & Miller-Rushing 2012, this study).

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## Studie 7

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# Changes in spring arrival dates and temperature sensitivity of migratory birds over two centuries

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**Abstract** Long-term phenological data have been crucial at documenting the effects of climate change in organisms. However, in most animal taxa, time series length seldom exceeds 35 years. Therefore, we have limited evidence on animal responses to climate prior to the recent warm period. To fill in this gap, we present time series of mean first arrival dates to Central Europe for 13 bird species spanning 183 years (1828–2010). We found a uniform trend of arrival dates advancing in the most recent decades (since the late 1970s). Interestingly, birds were arriving earlier during the cooler early part of the nineteenth century than in the recent warm period. Temperature sensitivity was slightly stronger in the warmest 30-year period ( $-1.70 \pm \text{SD } 0.47 \text{ day } ^\circ\text{C}^{-1}$ ) than in the coldest period ( $-1.42 \pm \text{SD } 0.89 \text{ day } ^\circ\text{C}^{-1}$ ); however, the difference was not statistically significant. In the most recent

decades, the temperature sensitivity of both short- and long-distance migrants significantly increased. Our results demonstrate how centennial time series can provide a much more comprehensive perspective on avian responses to climate change.

**Keywords** First arrival date · Migratory birds · Phenology · Temperature · Temperature sensitivity

## Introduction

Given the rapidity of current climatic changes, long-term observational time series are highly valuable. They can document phenological responses to contrasting climate conditions and provide a broad perspective on the current rapid changes of climate. However, studies with more than a few decades of uninterrupted data are rare, especially for animals. The mean length of published phenological time series is only around 35 years (Bitterlin and van Buskirk 2014; Parmesan and Yohe 2003; Root et al. 2003; Rubolini et al. 2007, but see e.g. Ahas 1999; Askeyev et al. 2009; Lehikoinen et al. 2004; Sparks and Carey 1995) which might bias the detected trends (Hovestadt and Nowicki 2008). Furthermore, several studies already demonstrated spatially variable responses of organisms to temperature (spatial component; Gordo et al. 2007; Parmesan 2007; Saino and Ambrosini 2008). But there is no a priori reason to assume that temperature sensitivity of the species is constant and that the strength of the relationship remains unchanged through time (temporal component). This was proved to be true for plants (Fu et al. 2015; Quansheng et al. 2014; Rutishauser et al. 2008; Rutishauser et al. 2009; Schleip et al. 2008; Wang et al. 2015) and insects (Kharouba et al. 2014). But despite some studies which studied the temperature sensitivity (Askeyev et al. 2009; Gordo

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and Doi 2012; Gordo et al. 2013), a comprehensive long-term study which would investigate the course of temperature sensitivity in vertebrates is still lacking. Yet, an assessment of temporal variability in temperature sensitivity is critical for forecasting their responses to climate change.

The issue of variable temperature sensitivity is especially pressing in organisms at higher trophic levels in which species-specific cues trigger the onset of phenophases (Stenseth and Mysterud 2002; van Ash et al. 2007; Visser and Holleman 2001). In spite of that, temperature is generally accepted to be the main factor driving shifts in phenology (including for example chilling effect and growing degree days), but other mechanisms such as photoperiod, humidity and nutrients were also identified to play a role in triggering of phenophases (Chambers et al. 2013; Ellwood et al. 2012; Heide and Prestrud 2005; Jochner et al. 2013; Körner and Basler 2010; Laube et al. 2014; Tooke and Battey 2010; Zhang et al. 2007). In addition, as the temperature signal pervades from primary producers to top consumers, the number of trophic interactions increases. This results in weaker temperature signals and makes the temporal match of the phenophases less likely (Both et al. 2009; Ellwood et al. 2012; Gordo and Sanz 2005; Naef-Daenzer et al. 2012; Nakazawa and Doi 2012; Schwartzberg et al. 2014). Despite numerous studies about the phenological shifts due to changing climate, it is unclear which mechanisms vertebrates employ to respond to temperature change across a long time period.

Migratory birds represent an ideal system to enlighten this issue. Commonly, they fit into one of two migratory strategies which differ in response to temperature. Short-distance migrants are usually more influenced by temperature due to a strong spatial autocorrelation of climate between the breeding and wintering sites. On the other hand, the onset of long-distance migrants' migration is believed to be under endogenous control (Berthold 1996; Halkka et al. 2011; Lehikoinen et al. 2004; Marra et al. 2005; Mitrus et al. 2005; Sparks et al. 2007; Zalakevicius et al. 2006). Therefore, it is assumed that long-distance migrants are not able to perceive climatic conditions in the distant breeding sites as accurately as short-distance migrants. As a consequence, they are not able to adequately track the speed of the advanced spring phenology (Both and Visser 2001; Both et al. 2010; Møller et al. 2008; Sanz et al. 2003). In contrast to this, only two studies have shown that especially in the last decades the long-distance migrants have advanced their arrivals more than short-distance migrants, which might imply a strong evolutionary pressure on them (Jonzén et al. 2006; Stervander et al. 2005). However, other authors hypothesised that such as rapid advancement could be attributed to improved conditions en route and due to mixture of birds which come from different populations with different timing of migration (Both 2007). In addition, because birds represent top consumers, they are

under strong selection to optimise the timing of their arrival to breeding grounds and the onset of nesting with the phenophases of insects (Jonzén et al. 2007). Several multi-trophic-level studies showed that the response of birds to temperature is less strong than their prey and that this can lead to temporal phenological mismatch across the food chain (Both et al. 2009; Thackeray et al. 2010).

To address these issues, we present one of the longest time series of bird arrivals ever analysed dating back to the beginning of the nineteenth century and spanning 183 years. First, we reconstruct the historical avian first arrivals and assess their temporal shifts. Next, we investigate the strength of the relationship between arrival and temperature and how it has been changing throughout such an extensive time period. Finally, we examine the hypothesis that short- and long-distance migrants show different patterns in the strength of the response to the changing temperature (Knudsen et al. 2011).

## Materials and methods

### Phenological data

We compiled first arrival dates (FAD) of birds in the Czech Republic for the period 1828–2010. Data on FAD from the Czech Hydrometeorological Institute, which covered most of the database, were supplemented by data from various societies, networks and grey literature. For a detailed overview of the data sources and their time spans, see Table S1 and Fig. S1. Archival records were converted into digital format as day of the year (where January 1 = day 1), and all nomenclature was updated (see Kolářová and Adamík 2015). Due to the discrepancy between the calendar and astronomical year, we expressed arrival dates in each year as deviations from the vernal equinox (Sagarin 2001). When more than one record of the same species from the same locality was available in a given year, the earliest record was retained in the database.

We visualised the data distribution and detected outliers (mostly mistyped values in old printed records) by inspection of Cleveland dotplots and boxplots; Zuur et al. 2009), and they were subsequently excluded from the analyses. We restricted this study to species for which we had  $n \geq 900$  records spanning the period 1828–2010. Barn swallow *Hirundo rustica* arrivals spanned a shorter time period (1853–2010), but its observations were very numerous and had a balanced distribution through time. Three other species (chiffchaff *Phylloscopus collybita*, serin *Serinus serinus*, blackcap *Sylvia atricapilla*) had  $\geq 900$  records, but their data distribution was markedly imbalanced through time which would have hampered data analysis and therefore were omitted from analyses. We ended up with 13 species with 80,489 observations of FAD from 3480 sites across the Czech Republic (Fig. 1).



**Fig. 1** Map of the Czech Republic with the sites ( $n = 3480$ ) where first arrival dates were recorded

Out of the 13 species, 7 were short-distance migrants (winter grounds in Europe or Northern Africa) and 6 were long-distance migrants which winter in sub-Saharan Africa (see Table 1).

### Reconstruction of arrival dates

For each of the 13 species, we reconstructed annual mean FAD time series within a mixed-effects modelling framework with year as fixed effect and site as random effect (Häkkinen et al. 1995; Schaber et al. 2010; Table S2). Multi-site combined arrival time series were estimated in R-package “pheno” for each species. This package provides functions

which enable to deal with estimations of combined phenological time series (Schaber 2012). We used linear mixed effects model (LMM, R-package “lme4”) to compare timing of arrivals during the first and last 30-year period with year and species as random effects. Barn swallow arrivals were not included in this model as records of its arrival start later.

Temporal trends in reconstructed arrivals were assessed by generalised additive models (GAM) for the period 1828–2010 and by weighted linear regressions for the period 1978–2010. As weights for linear regression, we used the square root of the number of observations per year and species (Table S3). Similarly, weighted linear regression was used to assess temperature sensitivity. Mean FADs were associated to Czech

**Table 1** Weighted linear regression estimates of the relationship between mean first arrival date (FAD) and mean monthly temperature during 1828–2010

Species name	Common name	ms	Arrival	Month	Number	TS (d °C <sup>-1</sup> )	SE	<i>t</i>	<i>R</i> <sup>2</sup>	<i>P</i>
<i>Alauda arvensis</i>	Skylark	S	Mar 1	Feb	156	-1.424	0.161	-8.87	0.34	<b>&lt;0.001</b>
<i>Sturnus vulgaris</i>	Starling	S	Mar 6	Feb	155	-1.145	0.135	-8.49	0.32	<b>&lt;0.001</b>
<i>Vanellus vanellus</i>	Lapwing	S	Mar 13	Mar	131	-2.008	0.265	-7.58	0.31	<b>&lt;0.001</b>
<i>Motacilla alba</i>	White wagtail	S	Mar 14	Mar	166	-1.162	0.197	-5.89	0.17	<b>&lt;0.001</b>
<i>Columba palumbus</i>	Woodpigeon	S	Mar 19	Mar	127	-1.411	0.329	-4.28	0.13	<b>&lt;0.001</b>
<i>Turdus philomelos</i>	Song thrush	S	Mar 23	Mar	151	-0.856	0.389	-2.20	0.03	<b>0.029</b>
<i>Phoenicurus ochruros</i>	Black redstart	S	Mar 28	Mar	143	-1.503	0.190	-7.93	0.31	<b>&lt;0.001</b>
<i>Phoenicurus phoenicurus</i>	Common redstart	L	Apr 11	Apr	153	0.871	0.390	2.23	0.03	<b>0.027</b>
<i>Hirundo rustica</i>	Barn swallow	L	Apr 16	Apr	140	-1.066	0.192	-5.55	0.18	<b>&lt;0.001</b>
<i>Delichon urbicum</i>	House martin	L	Apr 22	Apr	155	-0.713	0.224	-3.19	0.06	<b>0.002</b>
<i>Cuculus canorus</i>	Cuckoo	L	Apr 26	Apr	167	-0.833	0.172	-4.86	0.13	<b>&lt;0.001</b>
<i>Apus apus</i>	Swift	L	May 3	Apr	149	-0.801	0.206	-3.88	0.09	<b>&lt;0.001</b>
<i>Coturnix coturnix</i>	Quail	L	May 15	Apr	148	-1.384	0.377	-3.67	0.08	<b>&lt;0.001</b>

Species are listed in ascending order according to their mean FAD

*ms* migratory strategy (*S* short-distance migrant, *L* long-distance migrant), *Month* focal month used for temperature-arrival relationship, *Number* number of years with available data, *TS* temperature sensitivity, regression estimates of mean FAD against mean monthly temperature, *SE* standard error of the TS estimate, significant *P* values ( $\leq 0.05$ ) are in bold

mean monthly temperature series spanning 1828–2010 (Fig. S2) reconstructed from station-based meteorological observations (Brázdil et al. 2012) and weighted by the square root of the number of observations per year (Table 1). The focal month for temperature was selected individually for each species based on the temporal overlap with its arrival. To describe the temporal changes in temperature-arrival relationship, we estimated linear regressions as 30-year moving windows with the shift by 1 year starting in 1828 (for barn swallow in 1853). Again, all regressions were weighted by the square root of the number of observations per year. We chose a period of 30 years since this was the most commonly reported length of published time series with FAD (see “Introduction” section).

Next, we assessed whether the species’ temperature-arrival relationship differed during cold and warm periods. For that, we detected the warmest and the coldest periods by averaging the mean monthly temperature of the focal month for arbitrarily set 30-year time intervals (the last one having 33 years) 1828–1857, 1858–1887, 1888–1917, 1918–1947, 1948–1977 and 1978–2010. The 1978–2010 period was the warmest for all the months, while the coldest periods were 1828–1857 for February and March and 1888–1917 for April. Species-specific differences in slopes of the temperature-arrival relationship between the warmest and coldest periods were assessed according to Zar (1999; slope test).

For an assessment of temporal changes in the mean temperature sensitivity between short- and long-distance migrants, we averaged the species-specific estimates of temperature sensitivity weighted by the square root of the number of observations per year for 30-year moving windows at the beginning (1857–1886), in the middle (1919–1948) and at the end (1981–2010) of the 1828–2010 time series. Differences in mean responses (average temperature sensitivity estimates) were assessed by GLM where we used a model that included interaction between the three time periods and migratory strategy.

## Results

### Bird arrival dates 1828–2010

The temporal trends for majority of the species showed strong non-linearity in arrivals during the period 1828–2010 (Fig. S3). Usually, the arrivals were most pronounced at the beginning of the nineteenth century. Between beginning and ca. second half of the nineteenth century, the arrivals were delaying and then again advancing which lasted until the first half of the twentieth century. From then, the arrivals were constantly delaying until the 1970s. Afterwards, there is a

clear pattern in rapid advancement which lasts up to now (Figs. 2 and S3).

During the most recent period, 1978–2010, all species advanced their arrivals (mean advancement was  $-0.35$  day year<sup>-1</sup>, SD = 0.27; Table S3). The mean shift for short-distance migrants was  $-0.35$  day year<sup>-1</sup> (SD = 0.36) and for long-distance migrants  $-0.35$  day year<sup>-1</sup> (SD = 0.15). Despite these advancements, most species are still arriving later today (LMM effect for period  $5.25 \pm 1.32$  days,  $t = 3.9$ ,  $P < 0.001$ ) than in the early half of the nineteenth century (e.g. house martin *Delichon urbicum* and cuckoo *Cuculus canorus*, Figs. 2 and S3).

### Relationship between arrival and temperature

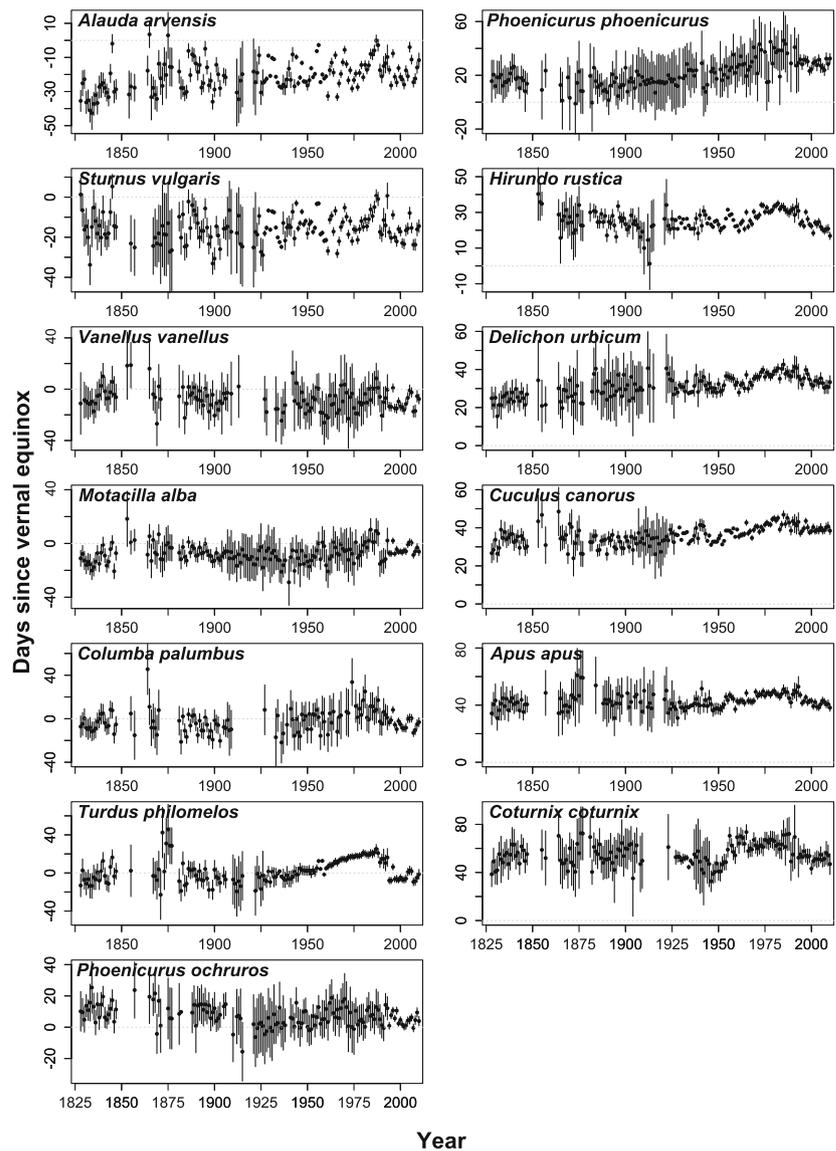
Across all species (except for the common redstart *Phoenicurus phoenicurus*), mean FADs were negatively associated with temperature during the period 1828–2010 (mean response for all 13 species  $-1.03$  day °C<sup>-1</sup>, SD = 0.68, without common redstart  $-1.19$  day °C<sup>-1</sup>, SD = 0.37, Table 1). The mean response to temperature was  $-1.36$  day °C<sup>-1</sup> (SD = 0.36) in short-distance migrants and  $-0.65$  day °C<sup>-1</sup> (SD = 0.79) in long-distance migrants (without common redstart  $-0.96$  day °C<sup>-1</sup>, SD = 0.27). The positive temperature responses were rare and appeared in periods with poor data coverage, i.e. early part of the twentieth century (Fig. 3). The strongest variation in responses was detected in lapwing *Vanellus vanellus*. Early arriving species such as skylark *Alauda arvensis* and starling *Sturnus vulgaris* had very similar patterns of the temperature-arrival relationship. Strong temperature sensitivity in the second half of the nineteenth century was followed by a moderate relationship from the late 1920s onwards. Four long-distance migrants (barn swallow, house martin, cuckoo and swift *Apus apus*) showed, with various intensities, a strengthening of the relationship around the 1950s and then a steep weakening prior to 2000 followed by a slight strengthening in the last decade. In contrast to other species, common redstart showed an unusually long period of strengthening of the temperature-arrival relationship from the 1920s until today (Fig. 3).

The mean temperature sensitivity across all species was slightly stronger in the warmest period ( $-1.70$  day °C<sup>-1</sup>, SD = 0.47) than in the coldest period ( $-1.42$  day °C<sup>-1</sup>, SD = 0.89; Table 2). However, the species-specific differences in the temperature-arrival relationship between these two contrasting periods were significant only for common redstart (Table 2).

### Differences between short- and long-distance migrants in variation of temperature sensitivity

Temperature sensitivity of short- and long-distance migrants varied considerably during the study period, but the responses

**Fig. 2** Reconstructed mean first arrival dates with 95% confidence intervals in the Czech Republic for the period 1828–2010. The arrivals are expressed as annual deviations relative to vernal equinox (zero line). Species are ordered according to their mean first arrival date (FAD). *Left column*: short-distance migrants, *right column*: long-distance migrants



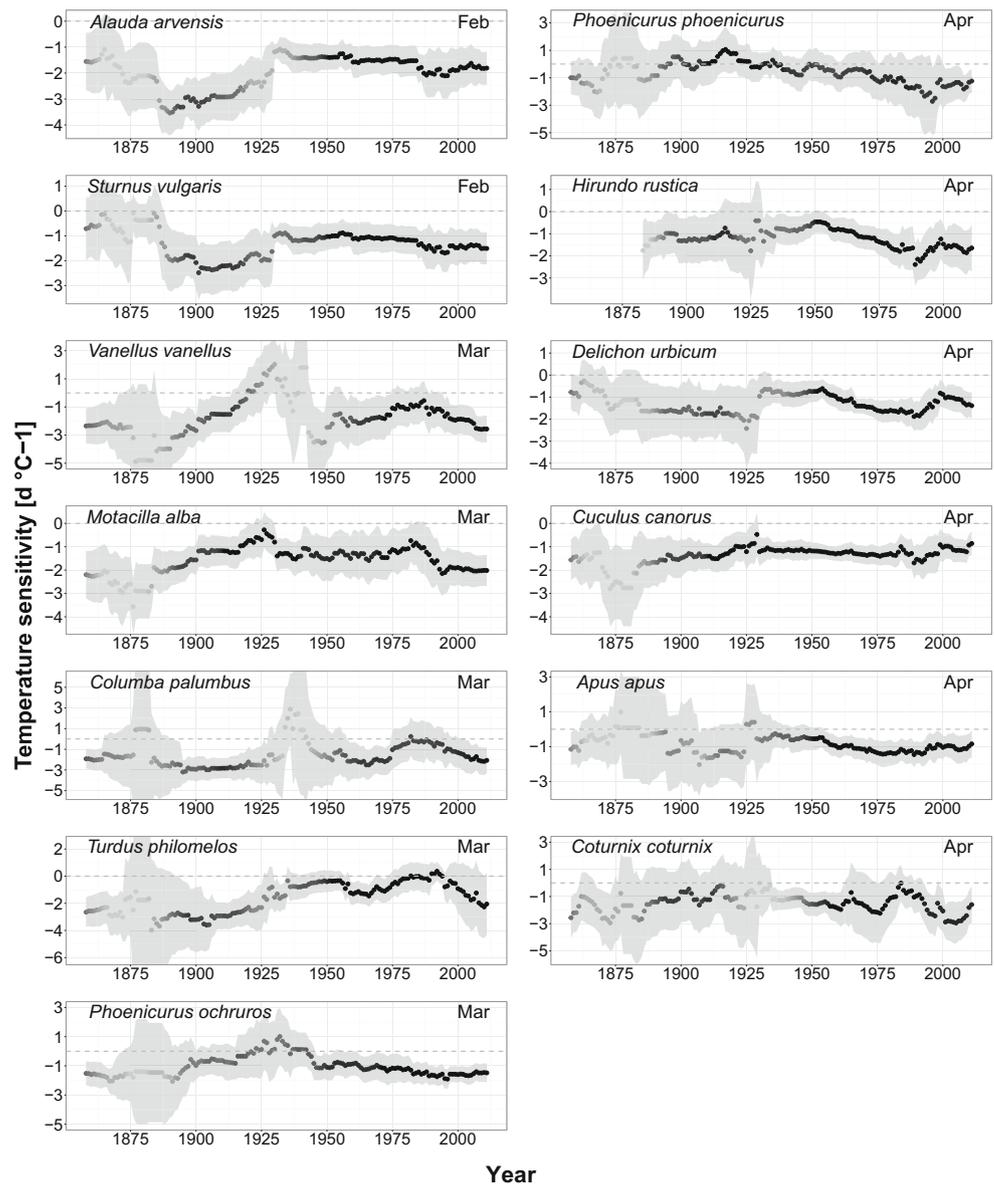
of the two migratory groups did not differ statistically (GLM, factor period  $F_{2,35} = 6.00$ ,  $P = 0.006$ , factor migratory strategy  $F_{1,35} = 1.59$ ,  $P = 0.216$ ; Fig. 4). While in the first decades (1828–1857) short-distance migrants reacted more strongly to temperature ( $-1.93$  day  $^{\circ}\text{C}^{-1}$ ) than long-distance migrants ( $-1.22$  day  $^{\circ}\text{C}^{-1}$ ), there was no significant difference between these two groups over the three time periods (GLM with period by migratory strategy interaction  $F_{2,33} = 1.52$ ,  $P = 0.233$ ).

## Discussion

To the best of our knowledge, we present one of the longest comprehensive time series of mean first arrivals of 13 bird species. We found that birds arrived earlier at the beginning

of the nineteenth century than today, although at that time the climate was cooler and more humid (Brázdil et al. 2011). The later arrivals compared to the beginning of the nineteenth century persisted despite an ongoing advancement of arrival dates in recent decades. The sensitivity of bird arrivals to temperature varied considerably throughout the two centuries. However, it did not differ significantly between the coldest and warmest periods (except for common redstart). In accordance with other studies (reviewed in Pearce-Higgins and Green 2014; Rainio 2008; Usui et al. 2016), short-distance migrants responded more strongly to temperature. But in recent decades, long-distance migrants showed similar or even stronger responses than short-distance migrants, although there was no evidence of significant difference. Since the late 1970s, the short-distance migrants showed a clear strengthening of the temperature-arrival relationship, while the

**Fig. 3** Temporal changes in temperature sensitivity. Regression slopes of mean first arrival date (FAD) against mean monthly temperature (focal month indicated in the *upper right corner*) based on the estimates of 30-year moving windows during the period 1828–2010. Each data point represents the end-year of the 30-year moving window (starting in 1828) for which the linear regression was estimated. Grey areas show 95% confidence intervals. Dot colour intensity indicates the number of missing values in the 30-year period from low (black) to high (grey). Species are ordered based on their mean first arrival dates. *Left column*: short-distance migrants, *right column*: long-distance migrants



relationship for long-distance migrants did not show any directional shift.

At the beginning of the time series, some species were arriving earlier compared to the long-term mean (Fig. 2). This is in contrast to the findings of Brázdil et al. (2011) who found a later onset of plant phenology in Bohemia during the cooler and humid period 1828–1848 compared to the warmer period 1993–2009. One possibility for the past earlier arrivals might be that in the nineteenth century birds were under stronger selection due to more common unfavourable weather events. For example, barn swallows regularly die in large numbers during fall migration in the Alps with consequences for their phenology (Newton 2007). Hence, only the strongest individuals could have survived which were likely to arrive earlier. It could also be the case that our set of species might have been more common in the past than today. Under such scenario,

there could be a better detectability of arriving individuals and also a stronger selection for early arriving males. Earlier arrivals in historical datasets were also recorded by Ahas (1999) for white wagtail *Motacilla alba* in Estonia. While other long-term studies showed usually the opposite (Askeyev et al. 2009; Kullberg et al. 2015; Lehikoinen et al. 2004).

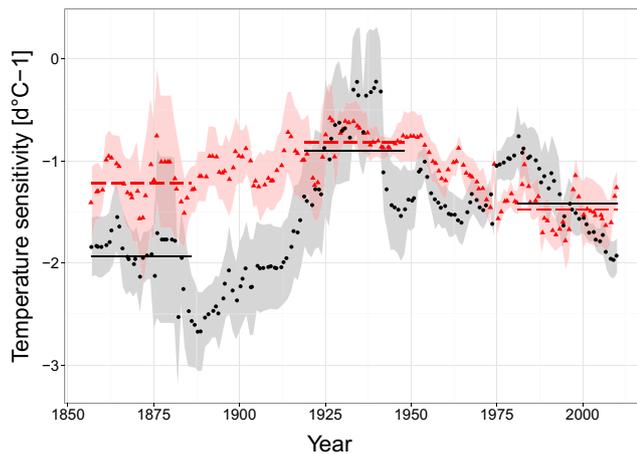
The trends in arrivals during the last decades agreed with the general advancement found by other authors (e.g. Gordo 2007; Knudsen et al. 2011; Pearce-Higgins and Green 2014). The advancement of the late-arriving species might be explained by the strong recent increase of April and May mean temperatures in the area of the Czech Republic. The mean temperature in the dataset of Brázdil et al. (2012) increased by  $0.08 \text{ } ^\circ\text{C year}^{-1}$  ( $P < 0.001$ ) in April and by  $0.06 \text{ } ^\circ\text{C year}^{-1}$  ( $P = 0.005$ ) in May, respectively, during 1970–2010 (Fig. S2). But the lack of significant difference in temperature sensitivity

**Table 2** Weighted linear regression statistics of the relationship between mean first arrival dates (FAD) and monthly temperature for the coldest and the warmest 30-year periods

Species	Coldest period						Warmest period									
	Month	Period	Number	TS (d °C <sup>-1</sup> )	SE	<i>t</i>	R <sup>2</sup>	<i>P</i>	Period	Number	TS (d °C <sup>-1</sup> )	SE	<i>t</i>	R <sup>2</sup>	<i>P</i>	<i>P</i> diff
<i>Alauda arvensis</i>	Feb	1828–1857	23	-1.554	0.569	-2.73	0.26	<b>0.013</b>	1978–2010	33	-1.749	0.317	-5.53	0.50	< <b>0.001</b>	0.884
<i>Sturnus vulgaris</i>	Feb	1828–1857	22	-0.709	0.657	-1.08	0.06	0.293	1978–2010	33	-1.453	0.311	-4.67	0.41	< <b>0.001</b>	0.242
<i>Vanellus vanellus</i>	Mar	1828–1857	21	-2.350	0.638	-3.68	0.42	<b>0.002</b>	1978–2010	33	-2.543	0.466	-5.46	0.49	< <b>0.001</b>	0.886
<i>Motacilla alba</i>	Mar	1828–1857	23	-2.196	0.516	-4.25	0.46	< <b>0.001</b>	1978–2010	33	-2.028	0.323	-6.29	0.56	< <b>0.001</b>	0.918
<i>Columba palumbus</i>	Mar	1828–1857	22	-1.923	0.479	-4.01	0.45	<b>0.001</b>	1978–2010	33	-2.126	0.656	-3.24	0.25	<b>0.003</b>	0.765
<i>Turdus philomelos</i>	Mar	1828–1857	21	-2.653	0.555	-4.78	0.55	< <b>0.001</b>	1978–2010	33	-2.072	1.188	-1.75	0.09	0.091	0.615
<i>Phoenicurus ochruros</i>	Mar	1828–1857	21	-1.520	0.411	-3.70	0.42	<b>0.002</b>	1978–2010	33	-1.461	0.309	-4.73	0.42	< <b>0.001</b>	0.958
<i>Phoenicurus phoenicurus</i>	Apr	1888–1917	30	0.898	0.801	1.12	0.04	0.272	1978–2010	31	-1.411	0.434	-3.25	0.27	<b>0.003</b>	<b>0.006</b>
<i>Hirundo rustica</i>	Apr	1888–1917	27	-1.160	0.788	-1.47	0.08	0.153	1978–2010	33	-1.794	0.463	-3.88	0.33	< <b>0.001</b>	0.449
<i>Delichon urbicum</i>	Apr	1888–1917	25	-1.728	0.657	-2.63	0.23	<b>0.015</b>	1978–2010	33	-1.263	0.265	-4.76	0.42	< <b>0.001</b>	0.576
<i>Cuculus canorus</i>	Apr	1888–1917	30	-1.285	0.370	-3.48	0.30	<b>0.002</b>	1978–2010	33	-0.966	0.226	-4.28	0.37	< <b>0.001</b>	0.362
<i>Apus apus</i>	Apr	1888–1917	23	-1.251	0.785	-1.59	0.11	0.126	1978–2010	33	-1.084	0.355	-3.06	0.23	<b>0.005</b>	0.949
<i>Coturnix coturnix</i>	Apr	1888–1917	21	-1.037	1.317	-0.79	0.03	0.441	1978–2010	32	-2.187	0.640	-3.42	0.28	<b>0.002</b>	0.605

Species are listed in ascending order according to their mean FAD

*Month* the focal month linked to the bird arrival, *Number* number of years with available data in the 30-year period, *TS* temperature sensitivity, estimate of FAD against mean monthly temperature, *SE* standard error of the estimate, *P* *diff* significance of comparisons of the slopes of temperature sensitivity between the coldest and the warmest periods, significant *P* values (≤0.05) are in bold



**Fig. 4** Averaged linear regression estimates of mean first arrival date (FAD) against monthly temperatures during 1828–2010 for short- (black dots) and long-distance (red triangles) migrants (for classification see Table 1). Each data point represents the end-year of the 30-year moving window (starting in 1828) for which the linear regression was estimated. The shadow area shows  $\pm 1$ SE of the regression estimate. The horizontal lines indicate the mean of the regression coefficients for a given 30-year period for short- (solid line) and long-distance migrants (dashed line, colour figure online)

between the coldest and warmest periods precludes us from a conclusion that the migratory strategy matters more than the need to adjust the species' arrival during specific climatic conditions. Spatial replicates of arrival times series from other areas outside of Central Europe would help to reach a definitive conclusion on this topic.

According to several studies, population density affects the ability to detect the first arrived individuals. Thus, higher population densities can overestimate the real shift in arrivals (Dunn and Møller 2014; Miller-Rushing et al. 2008; Sparks 1999). This might be the case also for this study since some species were likely to be much more numerous in the nineteenth century than today (for a detailed discussion, see Kolářová and Adamík 2015). We are also aware of potential biases caused by the use of FADs which might be sensitive to outliers (Goodenough et al. 2015; Tryjanowski et al. 2005). On the other hand, we used mean FADs across multiple sites which are likely to reduce any potential bias. We also would like to emphasise that FADs are often the only available data for old time series. For the common redstart, we got positive temperature-arrival relationship which does not match the conventional negative pattern. We do not know whether this could be a result of misinterpreted observations with black redstart *Phoenicurus ochruros*, especially in the nineteenth century. For the most recent period, the relationship was in line with the other species (Table 2). Another potential source of bias might come from different source of data over time. Obviously, the knowledge on bird life histories and identification skills was different in 1828 and 2010. Also, spatial variability in locations could lead to different estimates. To overcome this issue, we collated data from throughout

Czechia. However, for the earliest period, 1828–1847, we only have data from Bohemia, i.e. the western area (Kolářová and Adamík 2015). But due to the landscape configuration and spatial scale of the study area, there is little latitudinal and longitudinal variation in arrival dates (Beklová 1975; Beklová et al. 1983).

It is usually assumed that long-distance migrants are unable to shift their timing of arrival to breeding sites sufficiently due to constraints of their migratory triggers (especially photoperiod; Berthold 1996; Gwinner 1996). However, we showed that during the last decades long-distance migrants strengthened the temperature-arrival relationship equally to short-distance migrants (Fig. 4). This has led to advanced arrivals in both migratory groups. Among the numerous phenological studies, only Stervander et al. (2005) and Jonzén et al. (2006) found markedly stronger responses in the arrivals of long-distance compared to short-distance migrants. They both suggested that microevolution can play a role in the mechanism of changing migration. But as Both (2007) argued, the advanced arrival can be caused by faster migration due to better conditions en route and that the birds can come from mixed populations which differ in onset of migration. In our study, we cannot fully exclude the issue of mixed origin of populations even though our data were intentionally collected as arrivals to breeding grounds. In addition, climatic teleconnections between breeding and non-breeding grounds or improved environmental conditions north of the Sahara Desert might also lead to shorter stopovers and advanced arrivals (Finch et al. 2014; Saino and Ambrosini 2008).

Short-distance migrants have consistently strengthened the temperature-arrival relationship since the late 1970s (Fig. 4). We hypothesise that this might be a consequence of changed environmental conditions which result in rapid modifications of migratory routes such as decreasing migratory distances between breeding and non-breeding residency grounds (Berthold et al. 1992; Sutherland 1998). This was recently documented for several short-distance migrants (Pulido and Berthold 2010; Smallegange et al. 2010; Visser et al. 2009) and a long-distance migrant, the barn swallow (Ambrosini et al. 2011). This probably leads to better climatic teleconnections of residency sites of birds over their annual cycle. One consequence of this might be that short-distance migrants will always show stronger relationship in arrivals when linked to breeding site temperature.

By reconstructing one of the longest avian phenological time series, we analysed the course of temperature sensitivity across nearly two centuries. We showed that the strength of the temperature-arrival relationship has been changing throughout time but independently of cold or warm periods. Our results show that time series of sufficient length provide a more complex perspective on avian responses to climatic variability than studies with short time series. Centennial time series with bird arrivals are rare (e.g. Ahas 1999; Ellwood

et al. 2010; Lehikoinen et al. 2004; Sparks and Carey 1995; Sparks 1999). Thus, a comprehensive synthesis of such long records from various sites with different patterns of climatic trends would be highly desirable as this would help us to better understand vertebrate responses to climatic variability.

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## Studie 8

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# Long-term temporal changes in central European tree phenology (1946–2010) confirm the recent extension of growing seasons

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**Abstract** One of the ways to assess the impacts of climate change on plants is analysing their long-term phenological data. We studied phenological records of 18 common tree species and their 8 phenological phases, spanning 65 years (1946–2010) and covering the area of the Czech Republic. For each species and phenophase, we assessed the changes in its annual means (for detecting shifts in the timing of the event) and standard deviations (for detecting changes in duration of the phenophases). The prevailing pattern across tree species was that since around the year 1976, there has been a consistent advancement of the onset of spring phenophases (leaf unfolding and flowering) and subsequent acceleration of fruit ripening, and a delay of autumn phenophases (leaf colouring and leaf falling). The most considerable shifts in the timing of spring phenophases were displayed by early-successional short-lived tree species. The most pronounced temporal shifts were found for the beginning of seed ripening in conifers with an advancement in this phenophase of up to 2.2 days year<sup>-1</sup> in Scots Pine (*Pinus sylvestris*). With regards to the change in duration of the phenophases, no consistent patterns were revealed. The growing season has extended on average by 23.8 days during the last 35 years. The most considerable prolongation was found in Pedunculate Oak (*Quercus robur*): 31.6 days (1976–2010). Extended growing season lengths do have the potential to increase growth and

seed productivity, but unequal shifts among species might alter competitive relationships within ecosystems.

**Keywords** Climate change · Flowering · Growing season · Long-term trends · Phenology · Trees

## Introduction

Many countries have a long-standing tradition of observing phenological events. These long-term records have emerged as an essential tool for studying the present phenomenon of global climate change (Schwartz 2003). A variety of temporal shifts in phenological events have been documented across a range of species, communities and trophic levels (Root et al. 2003; Visser and Both 2005; Walther et al. 2002). In general, results suggest an advancement in spring and a delay in autumn phenology for tree species during the last few decades in Europe (Chmielewski and Rötzer 2001, 2002; Menzel et al. 2001; Schwartz et al. 2006; Sparks and Menzel 2002). However, the shifts in phenophases can substantially vary among countries—studies have found an advancement of spring phenophases of up to 4 weeks in Western and Central Europe and a delay of up to 2 weeks in Eastern Europe during the time period 1951–1998 (Ahas et al. 2002). These phenological changes have shown close correlations with increasing mean temperature in several countries (Menzel et al. 2006; Sparks et al. 2009). Accordingly, the growing season assessment coupled with data from International Phenological Gardens for tree species across Europe showed that 1 °C warming in early spring (February–April) caused a 7-day advancement in the beginning of the growing season (Chmielewski and Rötzer 2001). According to Menzel and Fabian (1999), the growing period lengthened by an average of 11 days in Europe during the period of 1959–1993.

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During the last 60 years, the growing season has widened up to 18 days in Spain for 29 perennial species (Gordo and Sanz 2009). Garzía-Mozo et al. (2010) found that the flowering of olive (*Olea europea*) has likewise significantly advanced by 40 days in Spain during 1986–2008. In Germany, the shifts in spring phenophases were in the range of 5–20 days between 1951 and 1999 (Schaber and Badeck 2005), and the growing season extended by 5 days on average between 1974 and 1996 in comparison to the period 1951–1973 (Menzel et al. 2001). In Switzerland, one of the oldest plant phenological time series in Europe shows an advancement in the onset of bud burst by 0.23 day year<sup>-1</sup> in Horse Chestnut (*Aesculus hippocastanum*) and by 0.06 day year<sup>-1</sup> for the flowering of Cherry trees (*Prunus avium*) (Defila and Clot 2001). Likewise, advancement in the onset of flowering and the peak of flowering of woodland herbaceous plants was documented by Sparks et al. (2009) in north-eastern Poland. Finally, the bud burst and the flowering of deciduous trees in Finland have advanced at a rate of 3–11 days per century during the last 160 years (Linkosalo et al. 2009).

The origins of phenological observations, including trees, in the Czech Republic can be traced back to the second half of the eighteenth century (Brázdil et al. 2011; Nekovář et al. 2008; Nekovář and Hájková 2010). Most recent studies on plant phenology in the Czech Republic deal with agricultural crops (Hlavinka et al. 2009; Mozny et al. 2009; Trnka et al. 2011a, b, c), but a comprehensive assessment of tree species is still lacking.

This study aims to identify and quantify temporal trends in phenological events of 18 common tree species across the Czech Republic. For this purpose, we evaluated three phenomena for each tree species. First, we evaluated changes in the annual mean values of a given phenophase in order to identify temporal shifts in the timing of their onsets. Secondly, we evaluated changes in the annual standard deviations of a given phenophase in order to explore the changes in duration of each phenophase. Finally, we evaluated the changes in the duration of the growing season.

## Materials and methods

### Phenological data

Data on the timing of particular phenological events were obtained from the archives of the Czech Hydrometeorological Institute. These data were collected from 149 phenological stations under the national phenological network across the entire Czech Republic (Fig. 1, ESM 1). Volunteer observers contribute annually observation data from the same locality. Data from the same individual trees are recorded over the years. For details on the network that runs since 1923, see Nekovář and Hájková (2010). The archive keeps records for

many more stations, but we have restricted our analyses only to those stations where there was at least a time series of 20 years of uninterrupted records. Similarly, we included only those tree species with at least 50 years of data. Thus, 18 common European tree species (Table 1) and their 8 phenophases (more than 317,000 records) were chosen for analyses. Because of the lack of data, the phenophases leaf colouring, the beginning of leaf falling and leaf falling could not be included for *Picea abies* and *Pinus sylvestris*. The phenophases were defined as:

Beginning of flowering	<10 % of flowers are in blossom
Flowering	>50 % of flowers are in blossom
Beginning of leaf unfolding	<10 % of leaves have already appeared
Leaf unfolding	>50 % of leaves have already appeared
Leaf colouring	>50 % of leaves have already coloured
Beginning of leaf falling	<10 % of leaves have already fallen
Leaf falling	>50 % of leaves have already fallen
Beginning of fruit ripening	<10 % of seeds /fruits have ripened.

### Data processing and analysis

First, it was necessary to check the database for mistaken values or outliers. All outliers were identified by the visual inspection of box-plots of records for each species and phenophase in a given year. Some of the mistakes could arise during the digitalisation of the original paper records or during data processing. In all cases when the records seemed to be clearly incorrect or suspicious, they were removed from the final dataset. The phenological observations by volunteers are standardised according to the published methodology and supervised by regional professional meteorologists.

We set a limit of a minimum of 10 observations for each phenophase in each year for a given tree species for inclusion into the analyses. All year-specific phenophases that did not meet this criterion were excluded from further analyses. All dates were expressed as days of the year (DOY), where January 1 was set as 1. However, some phenophases started in the second half of the calendar year (after September) and continuously overran to the following year. In those cases, the DOY had a value 365 (366 in leap years)+the number of days that overran to the next year. This was the case for leaf falling in *Fagus sylvatica* and *Larix decidua*, and beginning of fruit ripening in *Alnus glutinosa*, *L. decidua*, *Picea abies* and *Pinus sylvestris*.

In order to evaluate the temporal trends, mean and standard deviation were calculated for each phenophase of a given tree

**Fig. 1** Map of locations of 149 phenological stations in the Czech Republic involved in this study. Only stations with long-term continuous data were included



species in a given year from all available phenological stations. The mean gives us the information about the position of the phenophase in the calendar, whereas standard deviation illustrates the variability in the duration of the phenophase. In other words, as a consequence of the change in mean values, the plants delay or advance the onset of the phenophase. However, the shift in standard deviation values implies that the duration of the phenophase is either compressed or extended. For detailed explanation, see Gordo and Sanz (2009).

To evaluate long-term trends in phenology, multiple regression models were used with year and the quadratic effect of year as explanatory variables. First, quadratic regressions for the mean and the standard deviation for each phenophase and

species were examined for the period 1946–2010. In the case of non-significance of the quadratic term ( $P < 0.05$ ), only linear regression was calculated (ESM 2). Given that the quadratic regression fit was appropriate, we determined the turn-point of the curve—the year when the recent linear trend starts. This was a local maximum or minimum of each quadratic function, i.e. the point when derivatives of the quadratic functions were equal to 0. By simply averaging all of the turn-points for mean and standard deviation, we arrived at the global turn-point (in this case, the year 1976). Our aim here was to set a common year from which phenophases of all tree species showed a rather consistent linear temporal pattern. The curves that approached the shape of straight lines or the turn-points whose data series were short (minimum set at 50 years) were not included in calculation of the global turn-point (ESM 2).

Next, the linear regressions for all phenophases of each species were evaluated again for the period 1976–2010 to get the slope of the straight line. This represents the change of phenophase in the time span (ESM 3). Mean values and values of standard deviation of all species whose time series were minimally 30 years long (ESM 3) were used to compare the variability of data for each phenophase.

The length of growing season was defined as the time span between leaf unfolding and leaf colouring. For each species for which we had data for both phenophases, we calculated the change in the length of growing season. This was calculated from the differences of slopes for leaf unfolding and leaf colouring, multiplied by 35 (i.e. the number of years in the period 1976–2010).

Phenological data collected by volunteers might be biased by uneven effort during the week as a result of the observers preferentially making their phenological observations over the weekend (Menzel et al. 2001). To check for this bias, the day of the week for all observations was calculated (see ESM 4). We found a slight bias towards Sunday (14.80 %), while the day with the lowest number of records was Wednesday (13.97 %). This range fits within the values found in similar

**Table 1** Plant species included in this study ( $n$  number of observations per particular species)

	Scientific name	Common name	$n$
1.	<i>Sambucus nigra</i> L.	Black Elder	17.054
2.	<i>Pinus sylvestris</i> L.	Scots Pine	7.924
3.	<i>Betula pendula</i> Roth	Silver Birch	24.854
4.	<i>Fagus sylvatica</i> L.	European Beech	17.750
5.	<i>Quercus robur</i> L.	Pedunculate Oak	24.673
6.	<i>Crataegus laevigata</i> (Poir.) DC.	Midland Hawthorn	15.345
7.	<i>Acer pseudoplatanus</i> L.	Sycamore	19.249
8.	<i>Acer platanoides</i> L.	Norway Maple	21.539
9.	<i>Sorbus aucuparia</i> L.	Rowan	24.725
10.	<i>Tilia cordata</i> Miller	Small-leaved Lime	21.995
11.	<i>Corylus avellana</i> L.	Common Hazel	15.690
12.	<i>Larix decidua</i> Miller	European Larch	16.048
13.	<i>Alnus glutinosa</i> (L.) Gaertn	Common Alder	16.578
14.	<i>Prunus spinosa</i> L.	Blackthorn	20.480
15.	<i>Picea abies</i> (L.) Karsten	Norway Spruce	7.269
16.	<i>Cornus sanguinea</i> L.	Common Dogwood	5.975
17.	<i>Robinia pseudoacacia</i> L.	Black Locust	20.006
18.	<i>Salix caprea</i> L.	Goat Willow	20.593

studies (Gordo and Sanz 2009; Menzel et al. 2001). We consider the observers' effort very stable during the week, and thus, the influence of biased data is negligible and should not have a significant impact on the findings. All data were analysed using JMP (SAS Institute) and R (R Development Core Team 2012).

## Results

Temporal trends of plant phenology for the period 1946–2010

### Shifts in timing of phenophases

Out of 115 phenophases, 92 showed significant trends spanning the period of 65 years (ESM 2). With a closer look at the phenophases, 15 out of 18 species have significantly changed the beginning of flowering. Among them, three species showed a linear advancement, while in 12 others, there was a delay, followed by an advancement, beginning around the 1970s.

For flowering, changes in 11 out of 18 phenophases were significant. Three species showed linear advancement, and one species showed a linear delay. Non-linear response was found in six species with a delay followed by an advancement. Only one species, *Alnus glutinosa*, showed an advancement initially and then, beginning in 1985, a delay in onset of this phenophase. The beginning of leaf unfolding phenophase showed a high proportion of significant trends (16 out of 18). Five species showed significant linear advancement, while non-linear trends were found in 11 species. In 10 species, there was first a delay and a subsequent advancement. In *Cornus sanguinea*, there was initially no change and an advancement after 1968. For the leaf unfolding phenophase, eight out of 16 species showed significant change. Among them, *Crataegus laevigata* and *Sambucus nigra* showed a linear advancement. Non-linear changes, with a delay and subsequent advancement were found in four species. In two species (*Cornus sanguinea* and *Prunus spinosa*), the curves were flat first and later showed advancement. All 11 species' phenophase, leaf colouring showed significant non-linear change of an advancement in the initial period and later a delay. Similarly, all 11 considered species showed significant trends in beginning of leaf falling. Six species showed a linear trend of earlier leaf falling and five species showed a non-linear trend. These non-linear trends had the shape of a shallow convex function. For leaf falling, 10 out of 12 species showed a significant change. Three species linearly delayed the onset of this phenophase. Seven species showed a non-linear delaying change. In the case of beginning fruit ripening, nine out of 11 species displayed significant shifts. *Quercus robur* and *Sorbus aucuparia* showed a linear advancement in timing. In *Betula pendula*, *Crataegus laevigata*, *Prunus*

*spinosa* and *Sambucus nigra*, there was a non-linear concave advancement, while in *Robinia pseudoacacia*, *Corylus avellana* and *F. sylvatica*, there was initially a delay followed by an advancement.

### Changes in the duration of phenophases

Out of 115 studied phenophases, 73 were significant (ESM 2). The shifts in mean values were usually accompanied by shifts in standard deviations (49 cases). For beginning of flowering, 13 species out of 18 have significantly increased variability in the length of the phenophase. Four linear and nine non-linear trends were detected, with the latter showing a consistent pattern of expansion at the beginning of the period and compression since 1980s. For flowering, three species showed significant linear trends (two prolongations and one compression) and 10 non-linear significant trends. In all of the non-linear trends, there was first a compression followed by an expansion. The only exception was *Prunus spinosa*, which showed an opposite trend. Only two species (*Cornus sanguinea* and *Picea abies*) displayed significant non-linear shifts in the duration of beginning of leaf unfolding. Among 10 species with linear changes in duration, 9 showed a compressed phenophase and only *Robinia pseudoacacia* showed an extended phenophase. For leaf unfolding, nine significant trends were found; three linear (two compressions represented by *Salix caprea* and *Q. robur*, and one expansion found for *Sorbus aucuparia*) and six non-linear trends. For *Acer pseudoplatanus*, *F. sylvatica* and *Robinia pseudoacacia*, compression was found until the 1980s, and subsequently, the phenophase extended its duration. In contrast, for *Cornus sanguinea*, *Crataegus laevigata* and *Prunus spinosa*, the function had a convex shape. For leaf colouring, only four species (out of 11) showed significant change in duration. Linear extension was found for *Sorbus aucuparia*. Non-linear trends with compression followed by an expansion were found for *Acer platanoides* and *F. sylvatica*. For *Prunus spinosa*, the function had a shallow concave shape. The highest proportion of changes was found for the beginning of leaf falling (10 out of 11). All of them showed linear expansion. For the leaf falling, four linear expansions and two non-linear changes were found. The curves for *F. sylvatica* and *Q. robur* had a very similar shape with no change until 1967, respectively 1974, and then followed by considerable extension of the phenophase. For fruit ripening, seven species showed significant shifts in duration of the event. *Acer platanoides* linearly shortened the period, whereas *Robinia pseudoacacia* prolonged it. Non-linear trends for *Acer pseudoplatanus* revealed a very fast expansion and after 1981 a compression, while the function for *Corylus avellana*, *Prunus spinosa*, *Sambucus nigra* and *Sorbus aucuparia* had a rather shallow convex shape.

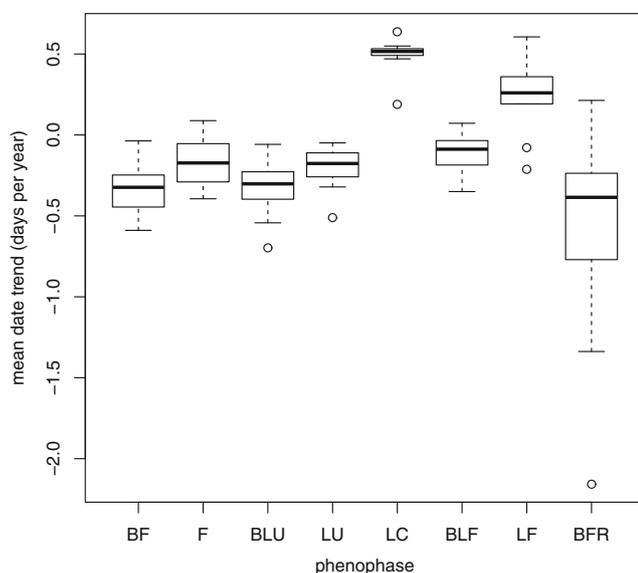
## Temporal trends in plant phenology 1976–2010

## Shifts in timing of phenophases

Out of 118 time series, 81 showed significant trends over the 35-year period (ESM 3). Overall, all spring phenophases (beginning of flowering, flowering, beginning of leaf unfolding and leaf unfolding) uniformly advanced the onset, whereas the autumn phenophases' shifts (leaf colouring, beginning of leaf falling, leaf falling and beginning of fruit ripening) were less uniform (Fig. 2). The phenophase leaf colouring had the smallest variability and was the most delayed phenophase. The phenophase beginning of leaf falling slightly advanced the onset contrary to leaf falling, which was delayed. The event beginning of fruit ripening advanced its onset but displayed the highest variance.

Looking closely at the beginning of flowering, all species showed an advancing pattern. For 13 species, this trend was significant. The largest shifts were documented in *Cornus sanguinea* ( $b=-0.590$  day year<sup>-1</sup>) and in *Tilia cordata* ( $b=-0.495$  day year<sup>-1</sup>).

Similarly, a coherent pattern of advancement was found across species (16 out of 18) for flowering. Out of 18 species, the trend was significant in 7. The most considerable shifts were found in *Cornus sanguinea* ( $b=-0.394$  day year<sup>-1</sup>) and in *Prunus spinosa* ( $b=-0.334$  day year<sup>-1</sup>). The highest proportion of significant changes for spring phenophases was found for beginning of leaf unfolding (16 out of 18), and all of them showed advancement. As in the previous cases, *Cornus sanguinea* showed the most markedly advanced position in



**Fig. 2** Box plot of mean temporal trends for each phenophase during the period 1976–2010. Beginning of flowering (BF), flowering (F), beginning of leaf unfolding (BLU), leaf unfolding (LU), leaf colouring (LC), beginning of leaf falling (BLF), leaf falling (LF) and beginning of fruit ripening (BFR) are shown

the calendar ( $b=-0.697$  day year<sup>-1</sup>), but *Robinia pseudoacacia* also displayed a noticeable shift ( $b=-0.543$  day year<sup>-1</sup>). In the case of leaf unfolding, the result was analogous to the above-mentioned phenophases—all species advanced the onset of the phenophase, and for eight species, this trend was significant. Again *Cornus sanguinea* ( $b=-0.511$  day year<sup>-1</sup>) and *Prunus spinosa* ( $b=-0.321$  day year<sup>-1</sup>) showed the most pronounced shifts. Leaf colouring was the first evaluated autumn phenophase, and all tree species showed a significant delay. The most considerable shift was found in *Q. robur* with a delay of 0.638 day year<sup>-1</sup>, but nearly all other species delayed leaf colouring by approximately half a day per year.

Beginning of leaf falling advanced in 9 out of 11 considered species, and for 4 of them, the trend was significant. The most pronounced shift was found in *Sorbus aucuparia* ( $b=-0.350$  day year<sup>-1</sup>). For leaf falling 10 out of 12 species delayed the onset of the phenophase. For all 10 species, this shift was significant. The most pronounced delays were found in *Q. robur* ( $b=0.606$  day year<sup>-1</sup>) and *L. decidua* ( $b=0.568$  day year<sup>-1</sup>).

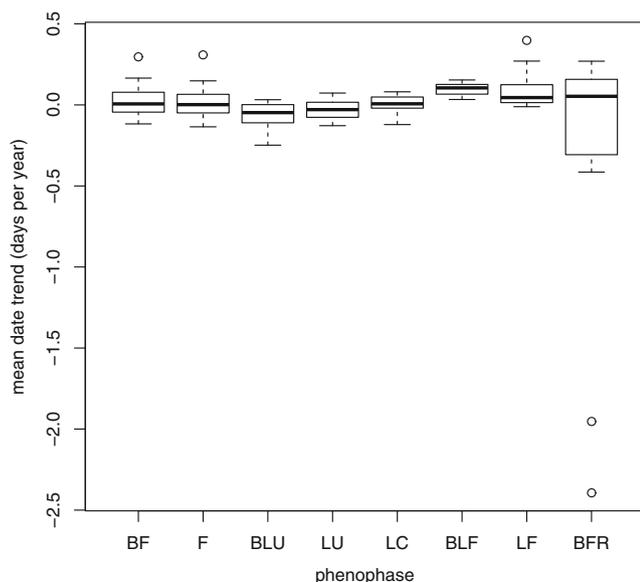
For the beginning of fruit ripening, 12 species showed significant shifts. Except for *Acer pseudoplatanus*, which delayed the seed ripening by 0.213 day year<sup>-1</sup>, all of the remaining species advanced this phenophase. Interestingly, the most advanced beginning of ripening was found in coniferous trees: *Pinus sylvestris* ( $b=-2.157$  day year<sup>-1</sup>) and *Picea abies* ( $b=-1.338$  day year<sup>-1</sup>). Among deciduous species, the most marked shift was found in *Prunus spinosa* ( $b=-0.823$  day year<sup>-1</sup>).

## Changes in the duration of phenophases

Overall, the trends in the durations of the phenophases were less coherent in comparison with the mean values. Out of 118 phenophases, there were significant trends in 46 species. The detected shifts were rather small, and no particular trend for spring or autumn phenophases was obvious (Fig. 3).

The first evaluated phenophase—beginning of flowering—showed five significant expansions and two compressions in data distribution. Whereas the onset of flowering in *Picea abies* has shortened by 0.117 day year<sup>-1</sup>, in contrast, *Alnus glutinosa* extended the time period of beginning of flowering by 0.296 day year<sup>-1</sup>.

Only six species showed significant change in flowering data distribution: Four species showed extension of the phenophase duration while two species showed contraction. The largest positive slope was found for *Alnus glutinosa* ( $b=0.308$  day year<sup>-1</sup>), while the largest negative trend was found in *Prunus spinosa* ( $b=-0.135$  day year<sup>-1</sup>). In the case of beginning of leaf unfolding, seven species displayed significant change, and in all cases, they shortened the duration of



**Fig. 3** Box plot of temporal trends in standard deviation for each phenophase during the period 1976–2010. Abbreviations as in Fig. 2

this phenophase. The most marked shift was found in *Cornus sanguinea* ( $b=-0.248$  day year<sup>-1</sup>). Five species showed significant shifts in leaf unfolding; four of them compressed and one, *Robinia pseudoacacia*, prolonged the duration of this phenophase by 0.073 day year<sup>-1</sup>. For leaf colouring, only 2 out of 11 time series showed a significant trend. *L. decidua* extended the duration of the phenophase by 0.081 day year<sup>-1</sup>, while *Prunus spinosa* contracted the duration by 0.121 day year<sup>-1</sup>. In the case of beginning of leaf falling, all 6 out of 11 species significantly prolonged the duration of the onset of leaf falling. The largest expansion was found in *Salix caprea* ( $b=0.154$  day year<sup>-1</sup>). Similarly, the phenophase leaf falling showed overall prolongation of duration. In four species, this trend was significant. The largest effect was found in *F. sylvatica* ( $b=0.398$  day year<sup>-1</sup>). A high proportion of significant shifts (9 species out of 14) was found for beginning of fruit ripening. This phenophase also displayed the highest variance in data distribution. The most extreme cases for contraction of timing of ripening were found in *Picea abies* by 2.393 day year<sup>-1</sup> and prolongation in *Prunus spinosa* ( $b=0.270$  day year<sup>-1</sup>).

#### Temporal changes in the growing season

Across 11 tree species, the growing season has extended by an average of 23.81 days during the period 1976–2010 (Table 2). The prolongation substantially varied among species from 10.55 days for *Sorbus aucuparia* to 31.57 days for *Q. robur*. Only rarely were the shifts in the timing of spring and autumn phenophases of similar magnitude. More often, the magnitude in shifts in the onset of leaf colouring exceeded the shifts in leaf unfolding.

**Table 2** Temporal trends of the growing season for the period 1976–2010

Species	LU (days year <sup>-1</sup> )	LU 35 (days)	LC (days year <sup>-1</sup> )	LC 35 (days)	GS 35 (days)
<i>Acer platanoides</i>	-0.080	-2.82	0.491	17.18	20.00
<i>Acer pseudoplatanus</i>	-0.160	-5.61	0.549	19.22	24.83
<i>Betula pendula</i>	-0.109	-3.81	0.503	17.62	21.43
<i>Fagus sylvatica</i>	-0.234	-8.17	0.516	18.50	26.67
<i>Larix decidua</i>	-0.206	-7.22	0.470	16.45	23.67
<i>Prunus spinosa</i>	-0.321	-11.24	0.520	18.19	29.43
<i>Quercus robur</i>	-0.264	-9.25	0.638	22.32	31.57
<i>Robinia pseudoacacia</i>	-0.290	-10.16	0.491	17.18	27.34
<i>Salix caprea</i>	-0.068	-2.40	0.542	18.97	21.37
<i>Sorbus aucuparia</i>	-0.113	-3.95	0.189	6.60	10.55
<i>Tilia cordata</i>	-0.193	-6.74	0.523	18.32	25.06

The change in timing of leaf unfolding (LU) and leaf colouring (LC) per 1 and per 35 years, and the extension of the growing season (GS) per 35 years are shown

#### Discussion

##### Shifts in timing of phenophases

Our results indicate a general trend in an advancement of spring phenophases, which has been widely described by other authors (Chmielewski and Rötzer 2001; Gordo and Sanz 2009; Menzel et al. 2006; Schwartz et al. 2006). For fruit ripening, we also found strong evidence for advancement, a pattern which has been rarely described to date (Menzel et al. 2006). For autumn phenophases, we found an overall delaying trend, but the effect was not as strong and uniform as in spring phenophases.

We found 1976 to be the mean break-point year. This is close to the global turn-point for Spain (1973) found by Gordo and Sanz (2009). Additionally, this is in accordance with the claim that two main time warm periods have been taking place in the twentieth century—between 1910 and 1945 and from 1976 onwards (Easterling 2002; Kunkel et al. 2004; Walther et al. 2002).

The primary force driving the onset of the spring phenophases is air temperature (Fitter and Fitter 2002; García-Mozo et al. 2010; Chmielewski and Rötzer 2002). However, it is sometimes overlooked that, in temperate zones, plants employ another two factors controlling the end of dormancy—chilling and photoperiod (Estrella et al. 2009; Harrington et al. 1999; Körner and Basler 2010; Tooke and Battey 2010). It is generally assumed that long-lived, late successional species (e.g. *Fagus* spp.) that become dominant in mature forests are sensitive to photoperiod, whereas shorter-lived, early successional and pioneer species, such as *Corylus* spp., *Populus* spp., and *Betula* spp., are photoperiod

insensitive (Körner and Basler 2010). Theoretically, those plants whose spring phenophases are triggered only by temperature might have a competitive advantage in comparison with those plants, which also require completion of chilling and photoperiod for the breaking of dormancy (Körner and Basler 2010). A rigorous evaluation of this hypothesis is hampered by a lack of studies dealing with the physiological demands of particular tree species, but some partial findings are in concordance with this assumption. While *Picea abies* is a photoperiod sensitive species (Partanen et al. 1998; Partanen et al. 2001), apple, pear and some other species of the Rosaceae family are not (Heide and Prestrud 2005). *B. pendula* and *B. pubescens* seem to be stimulated by photoperiod only to a limited extent (Myking and Heide 1995). Stříž and Nekovář (2010) also pointed out that the onset of generative phenophases (e.g. flowering, fruit ripening) might depend on the inner energy balance and accumulated energy of the plant, whereas vegetative phenophases (e.g. leaf unfolding, leaf colouring, leaf falling) are more influenced by climatic conditions.

Likewise, in this study, the most considerable shifts in timing of spring phases (beginning of flowering, flowering, beginning of leaf unfolding and leaf unfolding) were found for more or less shorter-lived early-successional species *Cornus sanguinea*, *Crataegus laevigata*, *Prunus spinosa*, *Robinia pseudoacacia* and *Tilia cordata*, and hence, the findings were in concordance with the above-mentioned hypothesis. However, another early-successional species expected to display this trend showed no or only slight changes. Specifically, *Alnus glutinosa* showed negative but non-significant change in the timing of beginning of flowering ( $b = -0.173 \text{ day year}^{-1}$ ), but data from the Alpine region (Ziello et al. 2009) proved a significant advancement by  $0.41 \text{ day year}^{-1}$  during the period 1971–2000. This discrepancy could be attributable to local environmental factors. Conversely, the trend of beginning of flowering for *Sorbus aucuparia* ( $b = -0.267 \text{ day year}^{-1}$ ) fitted the map of phenological trends found across Europe (Schleip et al. 2009). For the late-successional species *Q. robur*, the shift of leaf unfolding was only slight ( $b = -0.264 \text{ day year}^{-1}$ ), but in a close concordance with the findings from Germany ( $b = -0.23 \text{ day year}^{-1}$ ) for the periods 1951–1980 and 1967–1996 (Menzel et al. 2001). Similarly, the shifts of leaf unfolding for *F. sylvatica* by  $0.234 \text{ day year}^{-1}$  strongly agreed with the finding from Germany where an advancement by  $0.23 \text{ day year}^{-1}$  for the periods 1951–1973 and 1951–1980 was found (Menzel et al. 2001).

Another interesting pattern related to spring phenophases is that early flowering species (such as *Corylus* and *Betula*) show a much stronger response to warming than late flowering species (Ahas et al. 2002; Fitter and Fitter 2002; Menzel et al. 2006; Schleip et al. 2009). In contrast, our study did not find the largest responses in early flowering species. Therefore, this hypothesis cannot adequately clarify our findings.

While the spring phenophases are easily to recognise, the autumn phenophases are harder to define and detect. Furthermore, while there is a consensus on air temperature being the primary driving force of onsets of spring phenophases (Chmielewski and Rötzer 2002; Larcher 2006; Linkosalo et al. 2009; Menzel et al. 2006), the explanation of autumn forces is less straightforward (Menzel et al. 2006; Sparks and Menzel 2002). The activation of autumn phenophases seems to be more complex than just a simple temperature weighted function, and they are triggered by several factors in tandem (Chmielewski and Rötzer 2001; Menzel et al. 2001; Menzel et al. 2006; Rötzer and Chmielewski 2001; Sparks and Menzel 2002). Estrella and Menzel (2006) tested the influence of meteorological parameters on onset of leaf colouring. They included such parameters as monthly mean temperatures, threshold temperatures, sum of precipitation and number of dry days. They found that warm Septembers and Augusts delayed leaf colouring, whereas warm Junes and Mays advanced it.

The largest shifts in autumn phenophases (leaf colouring, beginning of leaf falling, leaf falling and beginning of fruit ripening) were displayed by a wider range of species compared with spring phenophases. Shifts in leaf colouring oscillated in many species around the value of  $0.5 \text{ day year}^{-1}$ . *Q. robur* showed largest delay in leaf colouring ( $b = 0.638 \text{ day year}^{-1}$ ), which exceeded the value from Germany ( $b = 0.23 \text{ day year}^{-1}$ ). Similarly, the delay of *F. sylvatica* ( $b = 0.516 \text{ day year}^{-1}$ ) was well over the finding from Germany ( $b = 0.07 \text{ day year}^{-1}$ ) during the periods 1951–1980 and 1967–1996 (Menzel et al. 2001). *Acer platanoides* significantly delayed leaf colouring by  $0.491 \text{ day year}^{-1}$ , while it has significantly advanced by  $0.63 \text{ day year}^{-1}$  in Latvia and between  $0.39$  and  $0.57 \text{ day year}^{-1}$  in Lithuania (Kalvāne et al. 2009). The shift of leaf colouring of *B. pendula* ( $b = 0.503 \text{ day year}^{-1}$ ) was in accordance with a delay of up to  $0.44 \text{ day year}^{-1}$  of this species in Germany (Menzel et al. 2001). However, it was partly inconsistent with the trend from Latvia where it has delayed in the eastern region ( $b = 0.33 \text{ day year}^{-1}$ ) and advanced in the western region ( $b = -0.27 \text{ day year}^{-1}$ ). In addition, in Lithuania, a uniform advancement was detected of up to  $0.80 \text{ day year}^{-1}$  (Kalvāne et al. 2009). In contrast to fruit trees or those with readily observable seeds such as *Quercus* spp. or *Acer* spp., the observation of conifers' fruit ripening is rather difficult even for experienced observers. This may explain the lower number of records in comparison to other species. Except for *Acer pseudoplatanus*, all significant shifts represented an advancement of beginning of fruit ripening. This might be attributed to the fact that fruit ripening is closely related to the flowering, and therefore, the accelerated flowering consecutively influenced the onset of fruit ripening.

An intriguing finding is the pronounced advancement of seed ripening in two coniferous species when compared to

deciduous species. The shifts of *Pinus sylvestris* ( $b = -2.157$  day year<sup>-1</sup>) and *Picea abies* ( $b = -1.338$  day year<sup>-1</sup>) are remarkable, while the most pronounced advancement among deciduous trees was displayed by *Prunus spinosa* ( $b = -0.823$  day year<sup>-1</sup>). The hygroscopic movements of conifers cones depend on air humidity. The cones open when it is dry and close when it is wet (Reyssat and Mahadevan 2009). There is a significant increase in air humidity in the autumn months of October–December during the period 1961–2005 in the Czech Republic (Brázdil et al. 2008). Thereby, the conifers might be forced to shed seed sooner during dry periods. Among other species where comparable published data exists, *Sambucus nigra* significantly advanced fruit ripening by 0.458 day year<sup>-1</sup>, which is similar to the finding from Germany where the advancement was 0.30 day year<sup>-1</sup> during 1951–1996 (Menzel et al. 2001).

#### Temporal trends in duration of phenophases

No apparent trend in shifts of standard deviation was found. Among the species that have changed the duration of the phenophases, the majority were shorter-lived trees such as *Alnus glutinosa*, *Cornus mas*, *Cornus sanguinea*, *Prunus spinosa* and *Salix caprea*. Because all of them are short-lived, early-successional species, the change in the duration of the phenophase could be only a different form of the same phenomenon, which was described above—pioneer species are more adapted to a risky life and thus probably more adaptable to changing climate (Körner and Basler 2010). The marked shifts of *Alnus glutinosa* and *Salix caprea* support the widely assumed prediction that early flowering plants react more sensitively and rapidly to warming than later flowering plants (Ahas et al. 2002; Fitter and Fitter 2002; Menzel et al. 2006; Schleip et al. 2009). Further research is needed to test this hypothesis with a larger sample of species at different sites.

#### Temporal trends in the length of the growing season

Growing season is considered to be the time between spring and autumn phenophases (Rötzer and Chmielewski 2001; Schwartz et al. 2006; Menzel et al. 2006). The length mainly depends on the beginning of spring phenophases, which vary more than those in autumn (Chmielewski and Rötzer 2001). As a result of the acceleration of spring events and postponement of autumn events, the winter is squeezed, and thus, the growing season gets longer (Schaber and Badeck 2005). An average length of the growing season is related to the annual air temperature, and an increase in temperature by 1 °C prolongs the growing season by approximately 5 days (Chmielewski and Rötzer 2001). According to Menzel and Fabian (1999), the growing season has lengthened by nearly 11 days in Europe since the early 1960s. Almost the same figure was

found for Germany—about 10 days for the time period 1951–1999 (Schaber and Badeck 2005). In Latvia and Lithuania, the growing season extended by an average of 7 days during 1971–2000 (Kalvāne et al. 2009).

Our results show a lengthening of the growing season for a sample of 11 species by nearly 24 days on average during the period 1976–2010. The smallest change was found in *Sorbus aucuparia* (10.55 days), while the largest change was found in *Q. robur* (31.57 days). The range of variability in the length of the growing season was documented by Rötzer and Chmielewski (2001). They showed that, in comparison with the long-term mean, the growing season lengthened by 12 days in the warm year of 1990, while in the cold year of 1970, it shortened by 10 days. Our results for particular species were in line with other studies. The prolongation of the growing season of *B. pendula* by 0.61 day year<sup>-1</sup> in our dataset (1976–2010) slightly exceeded the values of 0.44 day year<sup>-1</sup> found in Germany for the period 1951–1996 (Menzel et al. 2001). The differences among other species were of similar magnitudes—the growing season of *F. sylvatica* in our dataset was prolonged by 0.76 day year<sup>-1</sup>, whereas in Germany, it was prolonged by 0.33 day year<sup>-1</sup> (Menzel et al. 2001). For *Q. robur*, the season was prolonged by 0.90 day year<sup>-1</sup> in the Czech Republic vs. by 0.49 day year<sup>-1</sup> in Germany (Menzel et al. 2001). The growing season of *Robinia pseudoacacia* has considerably extended as well—all the more significant because it is an important invasive species in the Czech Republic. The timing of phenophases is a very complex phenomenon, which is driven and influenced by many exogenous and endogenous factors. The dataset presented here covers the entire Czech Republic. Therefore, the influence of local climatic conditions might be substantial. Factors such as slope and altitude of the locality are known to considerably influence the findings (Rötzer and Chmielewski 2001). For example, Ziello et al. (2009) showed that beginning of flowering of *Corylus avellana* can be delayed up to 5 days per 100 m of altitude. On the other hand, *Picea abies* from the Alpine region, included in the same study showed the delay of beginning of flowering only by 1 day per 100 m of altitude. Additionally, some phenophases in that study showed no significant correlation with altitude. In our study, the range between the lowest and highest phenological station was almost 1,000 m (Doksany—155 m a.s.l.; Filipova Hut—1,102 m a.s.l.). According to Estrella et al. (2009), higher population densities or size of urban areas are correlated with advancement in onset dates because of the influence of heat islands. Not all stations in this study were further away than 10 km from a settlement larger than 10 km<sup>2</sup>. This area was determined as a limit from which the impact of increased temperature from the settlement is negligible (Zhang et al. 2004), and this effect also should be taken into an account.

## Conclusion

Our results contribute to the coherent pattern of plant phenological responses across Europe. In short, spring phenophases have advanced and those in autumn have delayed. The most substantial shifts in advancement of spring phenophases were revealed for shorter-lived, early-successional species, which might be related to their life histories as pioneer species. This shift could bring an advantage to these species in the form of a better ability to track the changing climate (Körner and Basler 2010). In addition to commonly considered plant phenophases, we provide comprehensive multi-species data on the timing of fruit/seed ripening. Such data are still very rare. An interesting finding of our study is a marked shift in fruit ripening in coniferous species, which largely exceeded values found for deciduous trees. We are not aware of any comparable study dealing with conifers and their fruit ripening phenology, but undoubtedly, this phenomenon merits further attention. Along with the timing, we also analyzed the change in duration of all phenophases. Similarly to the trends in means, rather shorter-lived species prolonged or compressed the duration of phenophases the most, but the trends were not as uniform as in mean values. The species that shifted the duration of phenophase and the mean timing were not always the same. As a consequence of advanced spring and delayed autumn phenophases, the growing season has extended on average by 23.81 days during the 35-year time period.

The timing of phenophases is a crucial mechanism for coexistence of plant species in ecosystems, which leads to reduction of competition for resources (Rathcke and Lacey 1985). Decoupled synchronisation can promote the disruptions of relationships on intra- and interspecific levels through a wide range of species and trophic levels (Adamík and Král 2008; Visser and Holleman 2001).

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## Studie 9

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# Čejka chocholátá

*Vanellus vanellus*

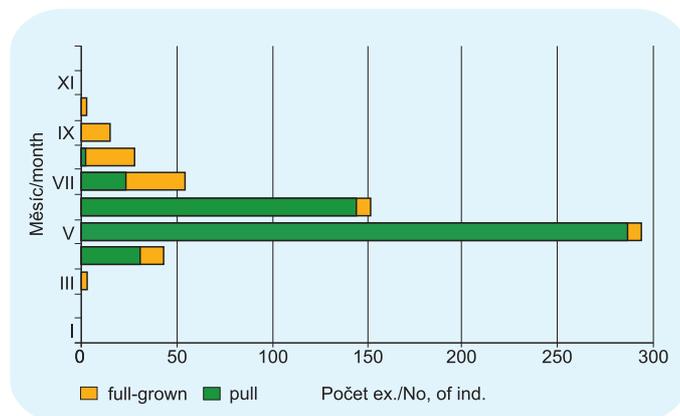
Cíbik chochlatý

Northern Lapwing

Čejka je monotypický druh s palearktickým typem rozšíření. Hnízdní areál se rozkládá od Britských ostrovů napříč Euroasií až k Mongolsku a severní Číně. Jižní hranice hnízdního rozšíření leží v Evropě kolem 40°N, severní hranice ve Skandinávii až k 70°N a 65°N v Rusku. Na našem území je to nejběžnější druh bahňáka a tomu i odpovídá celkový počet okroužkovaných ptáků. Ve srovnání s ostatními druhy bahňáků je jedním s nejnižšími nároky na výběr prostředí. Původně hnízdila více na vlhkých loukách a okrajích rybníků, s rozsáhlými zásahy do krajiny však došlo k výraznějšímu obsazování sušších biotopů, zejména polí (viz např. ŠÁLEK 1994). Ve značné části evropských zemí došlo k poklesům početnosti hnízdicích ptáků a území bývalého Československa není výjimkou (ŠTASTNÝ ET AL. 1996, STROUD ET AL. 2004). K hlavnímu zlomu v počtu okroužkovaných ptáků došlo na přelomu 70. a 80. let. Tento úbytek, který velice pravděpodobně kopíruje počty hnízdicích ptáků, je patrný i z ročních výkazů okroužkovaných ptáků (tab. 1). Na našem území se tradičně kroužkovala nejvíce mláďata. Tomu odpovídá i distribuce míst kroužkování, a to zejména v rybníčních oblastech v jižních a ve východních Čechách. Ve srovnání s ostatními bahňáky je rozložení míst kroužkování mnohem vyrovnanější (mapa 1). Bohužel nápadná absence kroužkování našich dospělých ptáků (graf 1) nebo zpětných odchytů na hnízdištích neumožňuje detailnější analýzu věrnosti hnízdištím. Navíc převážná většina hlášení do 10 km se týkala nálezu mrtvých tohoročních ptáků. U čejek ze severní Anglie bylo zjištěno, že po okroužkování mláďat se v prvních dvou letech vrátilo na jedné

lokalitě 74% a na druhé 37% ptáků do vzdálenosti 5 km od místa kroužkování. Zajímavé je také zjištění, že téměř 70 % ptáků hnízdí ve svém prvním roce života a zbylých 30 % až v letech následujících (THOMSON ET AL. 1994). Obdobně IMBODEN (1974) zjistil při analýze celoevropských zpětných hlášení, že kolem 70 % ptáků se vrací hnízdit do vzdálenosti 19 km od původního místa kroužkování. Kromě relativně vysoké věrnosti hnízdištím je pro čejku také charakteristické, že někteří jedinci přesídlují hnízdit z původních hnízdišť na velké vzdálenosti. Pro naše čejky to dokazuje výskyt některých našich adultních jedinců v hnízdním období v různých částech Evropy (mapa 2). Obdobně byli i někteří původně v Británii hnízdicí kroužkovanci nalezeni na hnízdištích v Rusku (BA).

Největší počet zpětných hlášení připadá na ptáky ulovené člověkem (graf 3). Čejka spolu s bekasinou otavní patří mezi "tradičně" střelené ptáky na zimovištích, a to zejména ve Francii, Španělsku a před rokem 1980 i v Itálii. O intenzitě lovu vypovídá i to, že více než 92 % hlášení z Francie se týká střelených ptáků.



**Graf 1:** Měsíc kroužkování později nalezených ptáků.

**Fig. 1:** Month of ringing of birds later recovered.

Směr podzimního tahu našich čejek je hlavně jihozápadní do Francie a Španělska. Někteří ptáci se vydávají více západněji Německem do Nizozemí, Belgie, na atlantské pobřeží Francie a do Británie. Na počátku migrace je směr tahu více západní (mapa 5). Již FORMÁNEK (1959) si všiml, že mladí ptáci měli větší tendenci táhnout i jihozápadním směrem (zejména do Itálie) než dospělí jedinci. Podrobnější analýza s mnohem větším datovým souborem potvrzuje dřívější závěry. Naše mláďata byla při svém prvním zimování (prosinec - únor) mnohem častěji (21 %) nalezena v jihozápadním směru, zejména v Itálii než mláďata, která byla hlášena již jako adulti z pozdějších zim. Pouze 7 % ptáků přezimovalo v Itálii

	<1960	60-69	70-79	80-89	90-02	Celkem Total
<b>Kroužkováno</b> Ringd (%)	14	13	33	29	11	26387
<b>Nalezeno</b> Recovered						
Naši ptáci (%) CZP-rings	16	26	29	22	7	598
Cizí ptáci (%) Foreign-rings	30	30	20	20	0	10

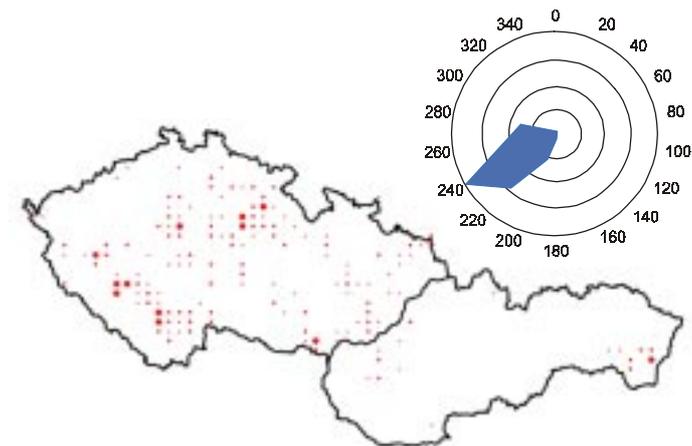
**Tab.1:** Počty okroužkovaných a nalezených ptáků.

**Table 1:** Number of birds ringed and recovered.

ve druhém roce nebo pozdějších letech ( $n=246$ ). Hlavní podíl na tomto věkovém trendu mají mláďata pocházející z jihočeských a jihomoravských hnízdišť. Obdobně lze potvrdit i dřívější zjištění, že čejky z jižnějších oblastí ČR zimují jihojihozápadněji než čejky pocházející ze severnějších hnízdišť; ty dávají přednost více západněji položeným zimovištím. Při arbitrárně stanovené hranici 50° N jako předělu mezi J a S populacemi a směru tahu 225° je rozdíl v počtu zimujících ptáků statisticky průkazný ( $n=178$ ). Zdá se, že vyšší tendence jihomoravských a jihočeských ptáků pro zimování v italských zimovištích je věkově specifická. Pro detailní srovnání tahu se slovenskými kroužkovanci je velmi málo zpětných hlášení. Při srovnání všech hlášení je podíl slovenských kroužkovanců v Itálii průkazně vyšší než českých. Časování tahu může být značně variabilní. IMBODEN (1974) udává, že někteří jedinci stře-

4, 5). Pro zimoviště čejky je charakteristické, že se vyskytují v přímořských oblastech a pokud možno se vyhýbají oblastem s charakteristicky kontinentálním průběhem zimy. Podobně v závislosti na průběhu zimy se zdržují na jihu Pyrenejského poloostrova a v severní Africe. Právě do těchto oblastí dochází k velkým přesunům ze severněji položených zimovišť v západní Evropě a Britských ostrovů. V letech, kdy se vyskytují extrémně silné mrazy, bývá mnohem více zpětných hlášení z těchto oblastí (BA, BWP, LEITAO & PERIS 2004). Do roku 2002 bylo na našem území nalezeno 11 zahraničních kroužkovanců. Všichni byli nalezeni mrtvi - převážně v hnízdním období. Někteří z těchto ptáků byli původně kroužkováni na zimovištích v Nizozemí (2), Belgii (1), Francii (1) a Itálii (1).

Jarní tah začíná již na konci ledna, kdy první ptáci opouštějí zimoviště, a na našem území se první jedinci vyskytují v první polovině února. Zřejmě mezi nimi převažují adulti, kteří obvykle obsazují hnízdiště mnohem dřív než „ložští“ ptáci (BWP). Tah vrcholí na přelomu února a března (Fauna). Někteří jedinci bývají ještě v druhé březnové dekádě zastihnuti v oblastech zimovišť (mapa 2). Nápadně vyšší počty jarních hlášení z Itálie ve srovnání



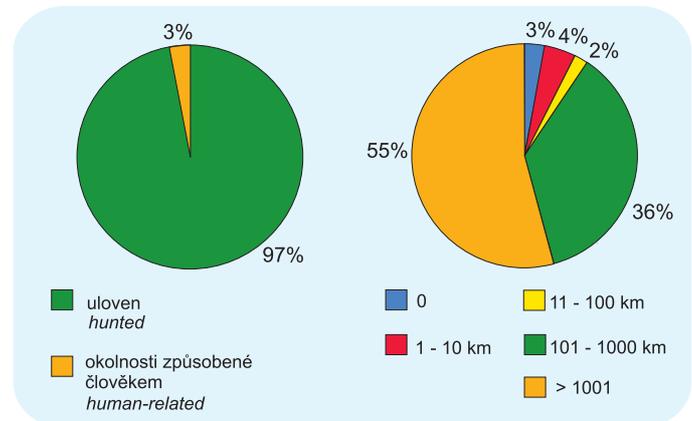
Graf 2: Směr tahu našich ptáků ( $n=116$ ).

Fig. 2: Direction of migration.

Mapa 1: Místa kroužkování později nalezených ptáků.

Map 1: Ringing places of birds later recovered.

doevropských populací opouštějí hnízdiště a vydávají se na tah již v červnu a červenci. Čtyři červencové nálezy našich ptáků z atlantského pobřeží Francie a středozemního Camargue ukazují, že někteří ptáci mohou dosáhnout zimovišť již uprostřed léta. Vrchol podzimního tahu probíhá od září po přelom října a listopadu. Naši ptáci zimují v široké oblasti od jižní Anglie přes Nizozemí, Belgii, atlantskou i středozemní oblast Francie, Španělsko, Portugalsko a jižněji až po severní pobřeží Afriky (Maroko, Alžírsko). Zimní nálezy z Itálie leží při východním okraji oblasti zimního výskytu (mapa



Graf 3: Známé příčiny úhynu ( $n=498$ ).

Ostatní okolnosti nálezu: kontrolován 10, neznámé příčiny úhynu 90

Fig. 3: Known mortality causes.

Other finding circumstances: controlled by ringer 10, unknown causes of death 90

Graf 4: Rozložení nálezů podle vzdálenosti od místa kroužkování.

Fig. 4: Distribution of recoveries according to distance between ringing and recovery place.

<b>Nejstarší pták</b> Oldest bird	<b>16 let, 7 měsíců, 7 dní</b>
H 55931 pull. 15.05.1978 22.12.1994	Praha-Kunratice (AA) Irun, Španělsko
<b>Nejvzdálenější nález</b> Longest recovery	<b>2698 km</b>
H 21935 pull. 02.04.1959 22.01.1962	Horní Měcholupy (AA) Sidi Bennou, Maroko
<b>Hnízdní období</b> Breeding season	<b>V- VI</b>
<b>Početnost CZ / SK</b> Population estimate	<b>7000-10000 / 2500-5000</b>

s Francií naznačují, že část ptáků protahuje jakoby oklikou. Je možné, že k tomu dochází po silných zimách, kdy velká část ptáků z atlantské oblasti je nucena se přesunout více na jih do středozemní oblasti, odkud se pak vrací přes Itálii. Malý počet dat pro naše ptáky neumožňuje detailnější analýzu této domněnky.

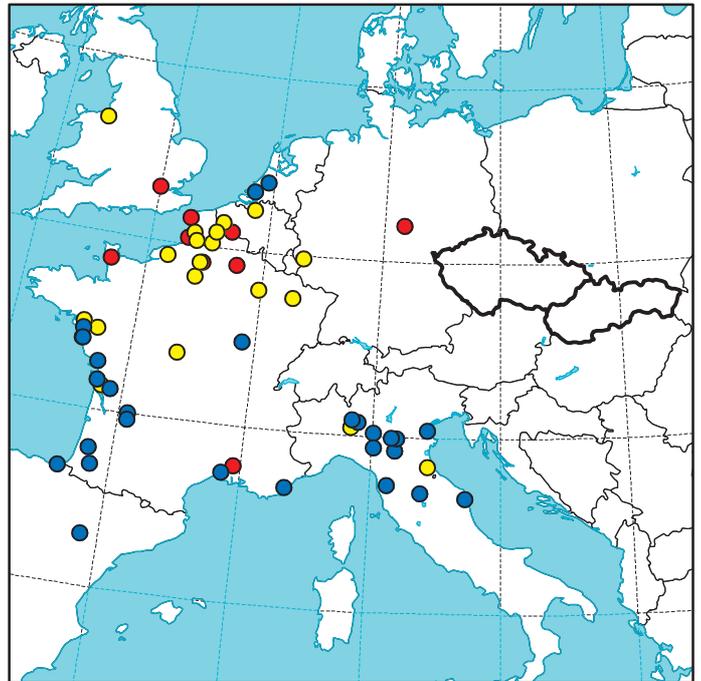
Nejstarším doloženým kroužkovancem v Evropě byl dánský pták, který byl kroužkován jako dospělý a kontrolovaný po 23 letech a 7 měsících (STAAV 1998).

Peter Adamík

## Summary

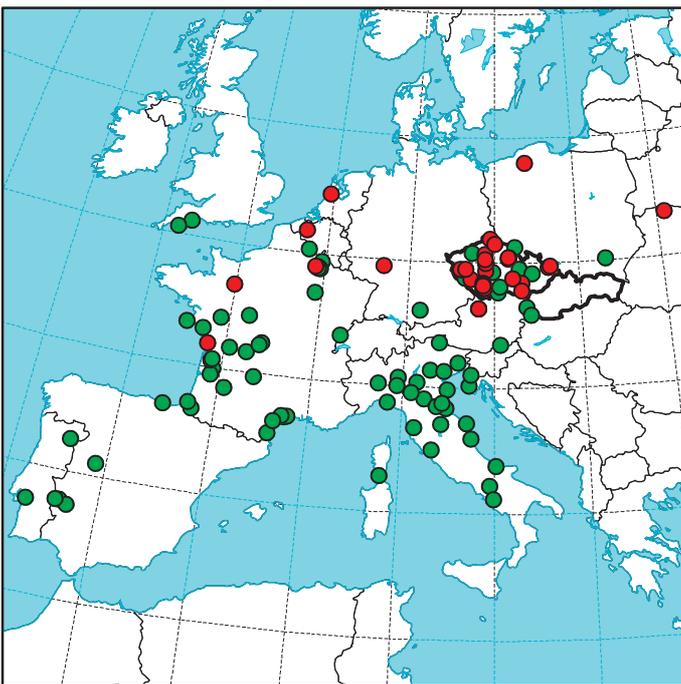
Breeding population of the Lapwing in CS have declined severely during the past two decades. This trend is also mirrored in the annual ringing totals showing the peak in 1978 and then a slow decline. Until the period of this population decline it used to be one of the most commonly ringed wader species. The majority of ringed birds were nestlings and, as a consequence, the number of sites at which they were ringed is much higher than for any other wader. Traditionally, the fishpond areas in southern and eastern Bohemia host the most abundant lapwing populations. The absence of adult recaptures at the breeding sites does not allow for a detailed site fidelity analysis. Moreover, of the few local recoveries (up to 10 km from the ringing place) the majority are first year birds, which were found dead. On the other hand, the high hunting pressure in the wintering areas causes the bulk of the long distance recoveries to be deliberately taken

by man. Although it is well known that the birds are highly site faithful to the breeding areas, the abmigration takes place occasionally. During the autumn migration the birds move mainly in the southwestern direction. However, some birds move west to Germany, the Netherlands, Belgium and the Atlantic coast of France, while others move southeast to Italy. Young birds are more likely to spend their first winter in Italy, while older birds tend to winter in the southwestern areas e.g. in France and Spain. Similarly, Lapwings from the southern regions of the Czech Republic (below 50°N) are more likely to winter in Italy than Lapwings born in the north. In addition, Slovak birds were recovered in Italy in a higher proportion than Czech birds. Four July recoveries of first year birds from both the Atlantic and the Mediterranean coast of France bring evidence for early summer migration. However, the main migration peaks in September/October. CS birds winter in a wide area from northwestern Europe (Belgium, the Netherlands, UK) through the maritime regions of France, in Spain, Portugal to northern Africa (Morocco and Algeria). Recoveries from Italy indicate the eastern limits of winter distribution of CS populations. The spring migration peaks in late February/early March. However, at this time some birds are still found at the wintering grounds. The higher occurrence of spring recoveries from Italy indicates that some birds may move southwest to France or Spain in autumn and later, during the winter, they move east along the Mediterranean coast with spring return through Italy.



**Map 3:** Nálezů našich pull. čejek chocholatých za přímého tahu na podzim (VII-XI, červeně-hnědě). Zobrazeny jsou pouze nálezů nad 100 km.

**Map 3:** Recovery locations (within same season) in autumn (VII-XI, red-brown) of Lapwings ringed in CS as pullus (only movements over 100 km are given).



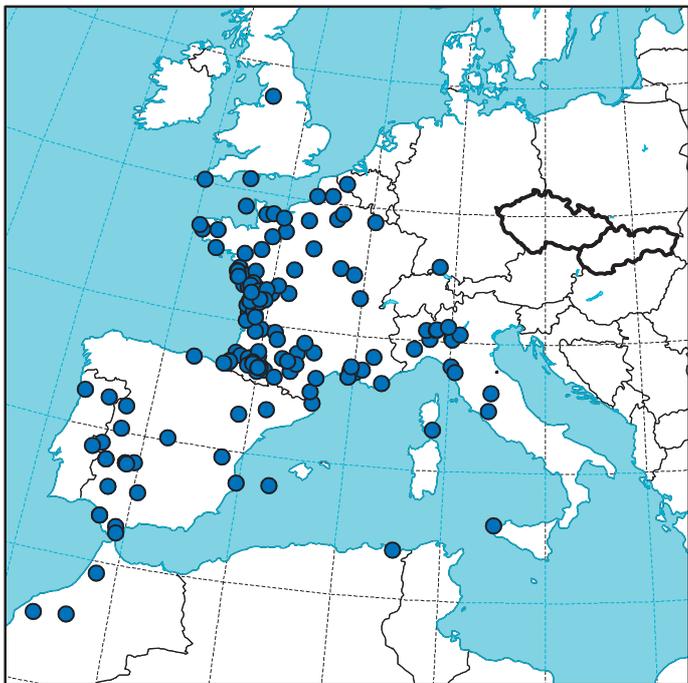
**Map 2:** Nálezů našich pull. čejek chocholatých na jaře (III-IV, zeleně) a v hnízdní době (V-VI, červeně).

**Map 2:** Recovery locations in spring (III-IV, green) and breeding season (V-VI, red) of Lapwings ringed in CS as pulli.



**Map 4:** Nálezů našich čejek chocholatých za přímého tahu v zimě (XII-II).

**Map 4:** Recovery locations (within same season) in winter (XII-II) of Lapwings ringed in CS as pulli.



**Map 5:** Nálezy našich pull. čejek chocholátých v následujících letech po okroužkování v zimě (XII-II).

*Map 5: Recovery locations in subsequent years in winter (XII-II) of Lapwings ringed in CS as pulli.*

# Vodouš bahenní

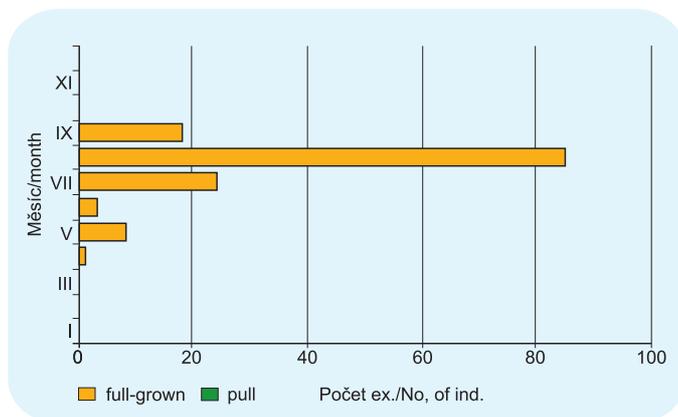
## *Tringa glareola*

### Kalužiak močiarny

### Wood Sandpiper

Hnízdiště vodouše bahenního se rozkládají od boreálních a subarktických oblastí Skandinávie až po Kamčatku. Velmi malé populace hnízdily nebo příležitostně hnízdí ve Skotsku, Dánsku, Německu, Polsku, na Ukrajině a v Pobaltí. Hnízdím biotopem jsou otevřené mokřiny, často pokryté mechem s řídkou zakrslou vegetací, nebo i vlhká vřesoviště a rašeliniště, případně vlhčí nížinné louky. V mimohnízdním období se na rozdíl od ostatních bahňáků vyhýbá mořskému pobřeží, a tak je na tahu u nás ve vnitrozemí jedním z nejpočetnějších druhů. Tady ho nejčastěji nalezneme na rybnících nebo otevřených březích toků, kde je alespoň nepatrný ostrůvek bahna, nízký vodní sloupec a nízká pobřežní vegetace. Podobně jako u řady jiných migrujících bahňáků ve střední Evropě jsou častým místem výskytu odkaliště v cukrovarech, kde eutrofizované bahno bohaté na vodní bezobratlé živočichy je důležitým zdrojem energie pro táhnoucí ptáky. Ekonomické změny v 90. letech, v jejichž důsledku došlo k uzavření provozu celé řady cukrovarů na našem území, výrazně zredukovaly množství odpočinkových míst. Dlouhodobé pozorování na více středoevropských lokalitách poukazuje na sestupný trend v počtu migrujících ptáků (FIALA 1991, OLDEKOP ET AL. 2000, ANTHES ET AL. 2002). Navíc data ze severovýchodních hnízdišť (EA) jsou velice nepřesná pro odhad populačních trendů, a tak doposud nejsou zcela objasněny příčiny tohoto poklesu. Hlavní zimoviště se nacházejí v tropické a subtropické Africe, dále napříč jižní Asii až po jižní Čínu a v menší míře i v Indonésii a Austrálii. Skandinávští ptáci přezimují v

západní Africe, ruští ptáci ve východní a jižní Africe a sibiřští ptáci v Indii (BWP, HVM, OSCHADLEUS 2002). Malé počty ptáků zůstávají také v oblasti Středozeří a pobřežní severní Afriky. Velice vzácně se může stát, že někteří jedinci u nás přezimují (Fauna). Podzimní migrace evropských populací začíná na konci června, kdy dospělci opouštějí severská hnízdiště a vydávají se jižním směrem. Mladí ptáci se vydávají na tah s několikátýdenním zpožděním. V průběhu srpna vrcholí podzimní tah na našem území (graf 1). Afrických zimovišť dosahují v srpnu, září a především v říjnu. Zdá se, že směr tahu přes Evropu je do jisté míry ovlivněn zeměpisnou délkou. Ptáci táhnoucí ze západních hnízdišť ve Skandinávii směřují jihozápadním směrem (ANTHES ET AL. 2002) a s přibývajícím zeměpisnou délkou více ptáků táhne jihovýchodním směrem (např. do Itálie, MEISSNER 1997). Po překonání Alp část ptáků může změnit směr tahu a vydává se více jihozápadním směrem do západní Afriky (DIADICHEVA & MATSIEVSKAYA 2000). Sedm zpětných hlášení našich ptáků ze západní subsaharské Afriky potvrzuje pře-



Graf 1: Měsíc kroužkování později nalezených ptáků.

Fig. 1: Month of ringing of birds later recovered.

vážně skandinávský původ přes naše území protahujících ptáků. Jediný nález našeho ptáka v jižní Africe (a také náš nejvzdálenější nález vodouše bahenního vůbec) naznačuje, že ptáci migrující přes Východoslovenskou nížinu mohou být z východnějších hnízdišť.

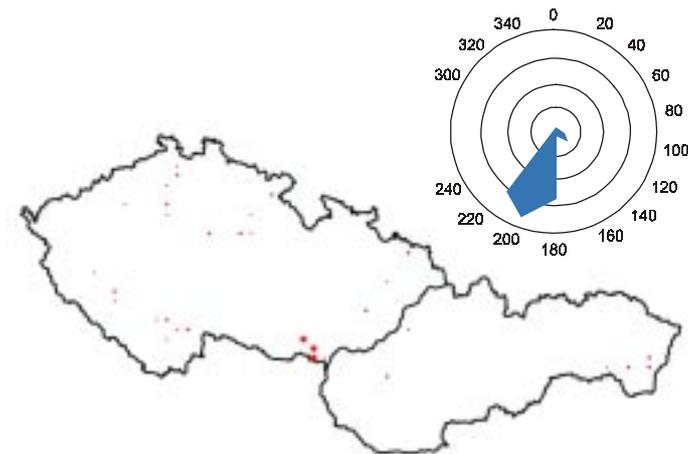
Ptáci pravděpodobně přelétají mediteránní oblast a Saharu na jeden zátah. Velice nízký počet zpětných hlášení z této oblasti (BWP, HVM) a teoretické výpočty maximálního doletu na základě stavu tukových zásob (WICHMANN ET AL. 2004) nahrávají této domněnce. To vyžaduje akumulaci značných tukových rezerv. Čím více se ptáci přesouvají na jih v průběhu podzimního tahu, tím více přibývají na váze, což právě může indikovat přípravu na přelet

	<1960	60-69	70-79	80-89	90-02	Celkem Total
<b>Kroužkováno</b> Ringed (%)	2	14	23	32	29	14099
<b>Nalezeno</b> Recovered						
Naši ptáci (%) CZP-rings	7	26	24	21	22	139
Cizí ptáci (%) Foreign-rings	4	23	15	35	23	26

Tab.1: Počty okroužkovaných a nalezených ptáků.

Table 1: Number of birds ringed and recovered.

Saharou. Na některých jižněji položených odpočinkových místech, např. v Camargue ve Francii se denně zastaví i přes tisíc vodoušů bahenních. Zdá se, že převážná většina ptáků přetahujících přes



**Graf 2:** Směr tahu našich ptáků (n=36).

**Fig. 2:** Direction of migration.

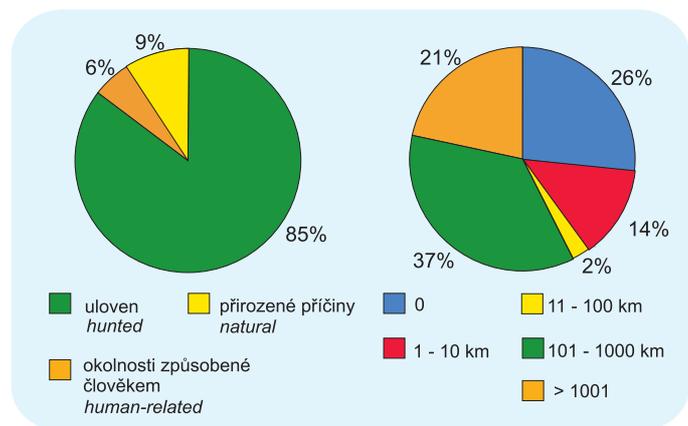
**Mapa 1:** Místa kroužkování později nalezených ptáků.

**Map 1:** Ringing places of birds later recovered.

střední Evropu táhne v malých krocích, jako strategii k doplňování zásob tuku (WICHMANN ET AL. 2004). Podle teoretických výpočtů stejné studie z rakouské lokality Hohenau nejtěžší adultní jedinci měli zásoby tuku postačující na dolet kolem 4200 km a toho-roční ptáci kolem 3400 km.

U nás byly největší počty vodoušů kroužkovány tradičně na Břeclavsku. Mnohem méně ptáků bylo označeno na východním Slovensku (Senné), ve Slezsku, na Českosudějovicku a Pardubicku (mapa 1).

Jarní tah začíná v pozdním březnu a na počátku dubna, kdy ptáci opouštějí zimoviště (malé procento ptáků zůstává na zimovištích i po zbytek roku). Našeho území dosáhnou v polovině dubna a přelety pokračují zejména v průběhu května. Malé počty vodoušů se mohou vyskytovat i v období mezi jarním a podzimním tahem (červen). Z tohoto pohledu je velice zajímavý případ adultního jedince (K307047) kroužkovaného 4. června u Sedlece na Břeclavsku a hlášeného z 24. července téhož roku z jižního Finska. Ptáci migrující přes střední Evropu jsou původem převážně ze Švédska



**Graf 3:** Známé příčiny úhynu (n=53).

Ostatní okolnosti nálezů: kontrolován 72, neznámé příčiny úhynu 14

**Fig. 3:** Known mortality causes.

Other finding circumstances: controlled by ringer 72, unknown causes of death 14

**Graf 4:** Rozložení nálezů podle vzdálenosti od místa kroužkování.

**Fig. 4:** Distribution of recoveries according to distance between ringing and recovery place.

a Finska (MEISSNER 1997, STAWARCZYK 1998, naše kroužkovací data).

Zpětná hlášení našich kroužkovanců naznačují převážně jižní až jihozápadní směr podzimního tahu. Malá část populace může táhnout jihovýchodním směrem (2 nálezy našich ptáků v Maďarsku a po 1 nálezu v Řecku a Turecku). Zpětná hlášení východoslovenských kroužkovanců ukazují, že tito ptáci táhnou zejména přes Itálii, pouze jediný nálezy slovenského ptáka (K302428) ve Francii naznačuje, že část těchto ptáků táhne i jihozápadním směrem. Rozdíly ve směru podzimního tahu mezi slovenskými a českými kroužkovanci nejsou statisticky průkazné. Největší počty nálezů jsou z Itálie (37), Francie (11), Švédska (6), Finska (5) a Polska (4) - mapa 2. Ze subsaharské Afriky je celkově 8 nálezů: 3 z Mali a po jednom ze Zimbabwe, Pobřeží Slonoviny, Ghany, Senegalu a Burkiny Faso (mapa 3). Ze zahraničních kroužkovanců bylo na našem území odchyceno nejvíce ptáků ze Švédska (10), Polska (7), dále z Itálie a Finska (3) a Německa, Rakouska a Francie (1) (mapa 4).

Ze 60 místních kontrolních odchytů našich ptáků bylo 13 v některém z následujících let, avšak vždy na podzim - jarní kontrolní odchyt nebyl evidován žádný. Právě vysoký podíl našich domácích hlášení má za důsledek vyšší podíl kontrolních okolností nálezů. Četnost místních kontrolních odchytů naznačuje, že na rozdíl od podzimního tahu se na jařevodouši bahenní u nás zdržují

#### Nejstarší pták

*Oldest bird*

Z 685752 1K

08.08.1991

09.05.2001

**9 let, 9 měsíců, 1 den**

Vojkovice (ME)

Satopy-Samulewo, Polsko

#### Nejvzdálenější nálezy

*Longest recovery*

Z 679471 1K

03.08.1991

11.01.1992

**7468 km**

Iňačovce (MI)

Chegut, Zimbabwe

#### Početnost CZ / SK

*Population estimate*

nehnízdí

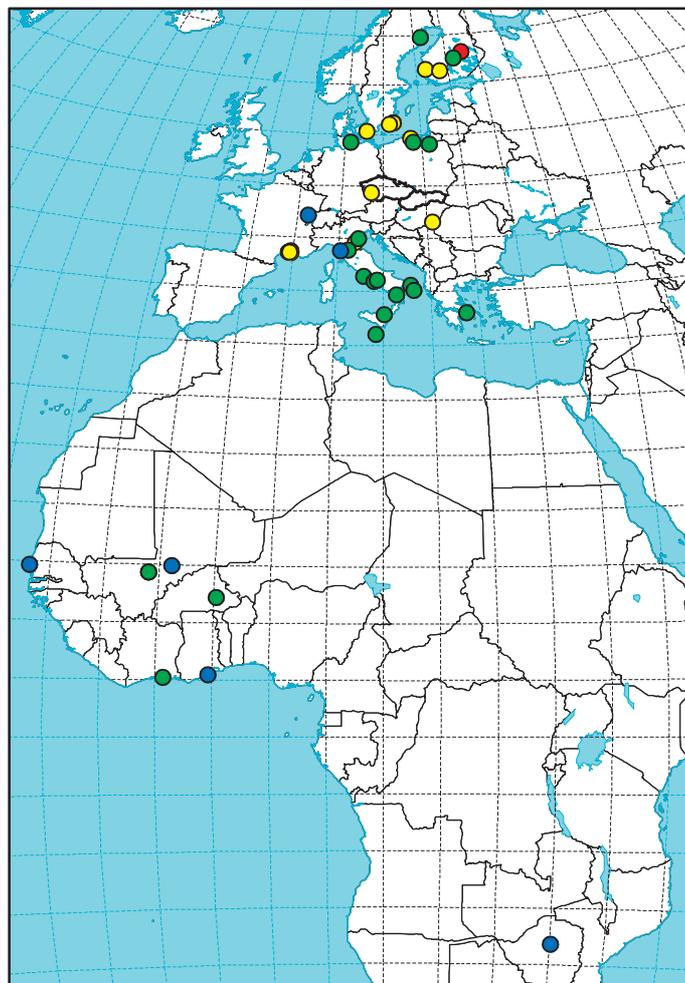
none

jen velice krátkou dobu. Naopak na podzimním tahu může délka pobytu na stejném místě dosáhnout až 37 dní (Z267525, Lednice). Průměrná odstup mezi jednotlivými kontrolními odchty byl 9,9 dní (n=43, medián = 8 dní). Na druhé straně „našim“ rekordmanem v rychlosti přeletu je mladý pták (GDANSK JN 17851) kroužkovaný 25. 7. 1989 v Jastarnii na polském pobřeží Baltiku, který byl následující den kontrolován po 659 km u Mušova na Břeclavsku. Absolutním „vítězem“ dle literárních pramenů bude ale pravděpodobně švédský pták, který byl následující den po okroužkování nalezen po 1075 km v Itálii (BWP). Právě již výše zmíněných 13 kontrolních odchytů z různých let na téže lokalitě naznačuje, že vodouši bahenní mohou být značně věrní jak své tahové cestě, tak i odpočinkovým místům. Příkladem takové věrnosti je např. K248097 kroužkovaný jako mladý pták v srpnu 1964 u Sedlece na Břeclavsku a kontrolován o 4 léta později na podzimním tahu na téže lokalitě, nebo Z673228 kroužkovaný také jako mladý pták v srpnu 1988 u Vojky na východním Slovensku a kontrolován o 5 let později na podzimním tahu také u Trebišova. V kontrastu s těmito nálezy je starý pták kroužkovaný na podzimním tahu v Dolním Sasku a v následujícím roce kontrolován také na podzimním tahu u Senného 921 km východně nebo Z636198 kroužkovaný na jarním tahu v Lednici a ve stejném roce hlášený na podzimním tahu v Camargue ve Francii. Ze zimního období je již výše zmíněno 8 afrických nálezů; možné přezimování několika jedinců ve Středomoří naznačuje nálezy ptáky z 23. 11. ze Sardinie. Zajímavý je také zástřel starého ptáka z 30. 12. ve Francii nedaleko hranic se Švýcarskem.

Peter Adamik

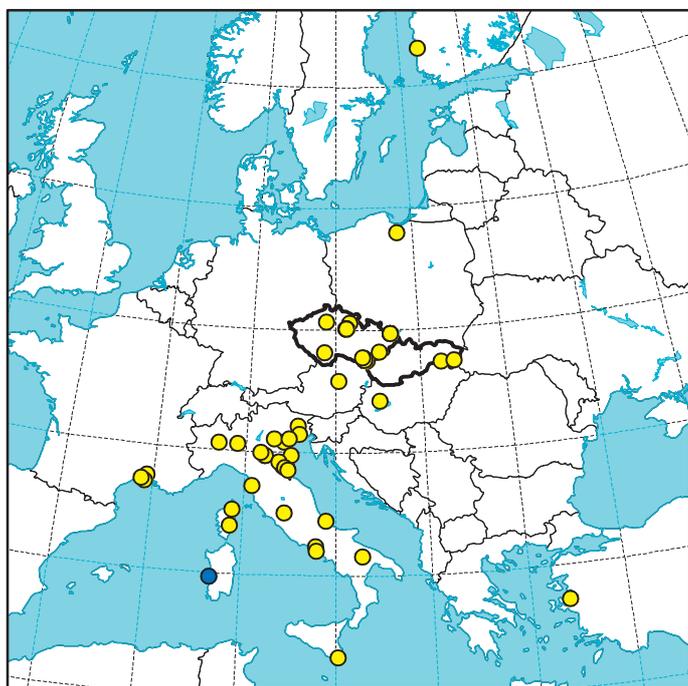
## Summary

The Wood Sandpiper regularly migrates via CS. The spring arrival starts in mid April and peaks in May with a very small number of birds occurring in June. The autumn migration starts in July, peaks in August and continues to decline until mid October. In 1934-2002, 78 birds were reported abroad (Italy 37, France 11, Sweden 6, Finland 5, Poland 4 etc.), 60 cases were local recoveries and 26 foreign-ringed birds were found in CS (Sweden 10, Poland 7, Italy 3, Finland 3, Germany 1, Austria 1 and France 1). The highest numbers of birds have been caught during the autumn migration. The autumn migration via CS takes a southern to southwestern direction. However, a small proportion of the population takes a southeastern direction (2 birds recovered in Hungary, 1 in Greece and 1 in Turkey). Birds migrating via CS winter mostly in western Africa (Mali 3, Ivory Coast 1, Ghana 1, Senegal 1, and Burkina Faso 1). One recovery of a bird ringed in eastern Slovakia from Zimbabwe suggests that a part of the Sandpipers ringed in Slovakia might come from breeding grounds in eastern Europe. A late November recovery of an individual from Sardinia indicates that some birds may winter in the Mediterranean. Birds migrating via CS probably are of Fenno-Scandinavian origin. This is inferred from the fact that all the northernmost recoveries come from Sweden and Finland. Thirteen of the 60 locally recovered birds have been caught at the same site in some of the subsequent years. This indicates that at least some birds might show high fidelity either to their migration route or to the stopover sites. However, there are also recoveries showing the opposite to be the case. An adult ringed in Lower Saxony in Germany during autumn migration has been recaptured 921 km away in eastern Slovakia the next autumn.



**Mapa 3:** Nálezy protahujících vodoušů bahenních v následujících letech: na podzim (VII-X, žlutě), v zimě (XI-II, modře), na jaře (III-V, zeleně) a v hnízdní době (VI, červeně). Zobrazeny jsou pouze nálezy nad 100 km.

**Map 3:** Recovery locations in subsequent years in autumn (VII-X, yellow), winter (XI-II, blue), spring (III-V, green) and breeding season (VI, red) of Wood Sandpipers present in CS during migration (only movements over 100 km are given).

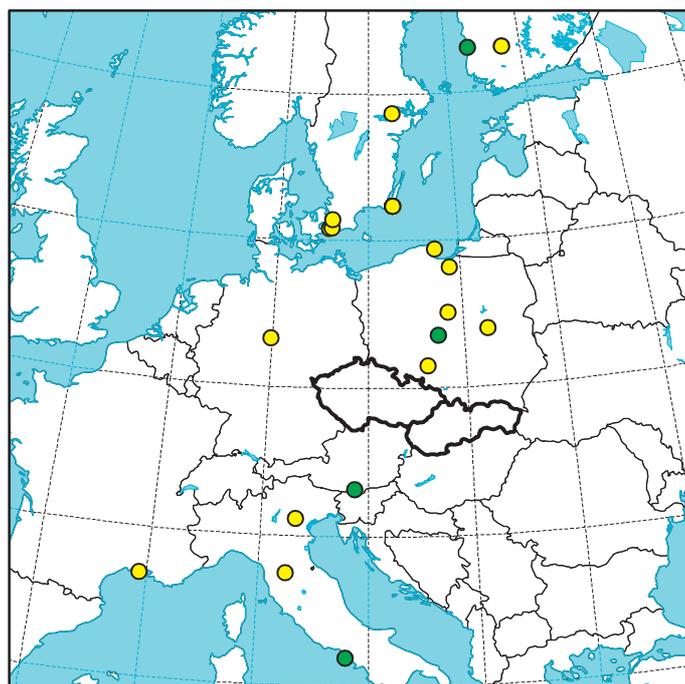


**Mapa 2:** Nálezy protahujících vodoušů bahenních za přímého tahu: na podzim (VII-X, žlutě) a v zimě (XI-II, modře). Zobrazeny jsou pouze nálezy nad 100 km.

**Map 2:** Recovery locations (within the same season) in autumn (VII-X, yellow) and winter (XI-II, blue) of Wood Sandpipers present in CS during migration (only movements over 100 km are given).

**Mapa 4:** Místa kroužkování protahujících vodoušů bahenních na podzim (VII-X, žlutě) a na jaře (III-V, zeleně).

**Map 4:** Ringing locations in autumn (VII-X, yellow) and spring (III-V, green) of foreign-ringed Wood Sandpipers later recovered in CS.



# Pisík obecný

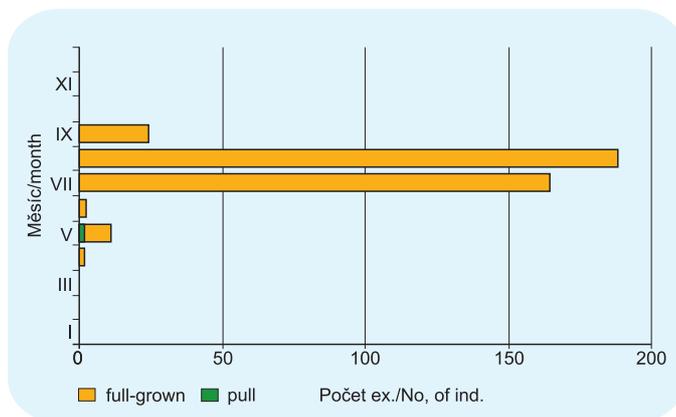
## *Actitis hypoleucos*

Kalužiak riečny

Common Sandpiper

Pisík obecný je monotypickým druhem. Obývá převážnou část Euroasie od Britských ostrovů až po Kamčatku a Japonsko. Na našem území pravidelně hnízdí, a to zejména v jeho východní části. Hnízdním biotopem jsou řeky, potoky s kamenitými břehy a šterkovými náplavy a ostrůvky od nížin až po horské oblasti. Řidčeji hnízdí i u údolních nádrží nebo na březích stojatých vod. Na našem území je to i běžně protahující druh, a tak většinu okroužkovaných ptáků tvoří právě jedinci zastížení na tahu. O tahu u nás hnízdících ptáků tak prakticky skoro nic nevíme. V tomto období se vyskytuje hlavně soliterně a nalezneme ho téměř u každé vodní plochy. V době tahu lze pisíky lehce zaznamenat v noci, kdy je prozradí charakteristické volání. Svému samotářskému způsobu života je pisík věrný i na zimovištích, kde se vyskytuje soliterně, obhajující stejné místo po delší dobu (*BWP*). Menší počty ptáků přežívají již ve Středomoří, ale hlavní zimoviště se nacházejí v Africe, dále na východ v jižní Asii až po Austrálii a Melanésii. Ptáci pocházející z hnízdišť v severozápadní Evropě zimují převážně v západní oblasti subsaharské Afriky, východoevropští ptáci zimují více na východ, a tak je možno nalézt je jak ve východní a střední, tak i v jižní Africe. Jako jeden z mála bahňáků je výrazně vázaný na sladkovodní biotopy, a tak na tahu je jedním z našich nejčastěji okroužkovaných bahňáků (tab. 1). Tradičně nejvíce ptáků bylo okroužkováno na podzimním tahu, a to na Břeclavsku, méně u Heřmanic na Ostravsku, u Kozčína na Klatovsku, České Skalici na Náchodsku a na rybnících v okolí Českých Budějovic. Na Slovensku byli pisíci okroužkováni hlavně u Piešťan (mapa 1). Značná část

zpětných hlášení (80%) připadá na kontrolní odchyty. Pouze 9% hlášení připadá na zabítí člověkem. Ve srovnání s jinými zeměmi to je velmi nízké procento. Např. ve Velké Británii bylo až 54% a v Polsku 23% hlášení právě v této kategorii (*BA, MEISSNER 1997*). Podzimní tah, který je mnohem intenzivnější, začíná v půli července s přiletem dospělých jedinců a vrcholí v srpnu, kdy převažují tohoroční ptáci (graf 1). Poslední protahující ptáci se objevují ještě v listopadu a zřídka se mohou někteří jedinci vyskytnout i v zimních měsících (viz *Fauna, DANKO ET AL. 2002*). Směr podzimního tahu je vesměs jihozápadní. Jen ojediněle někteří ptáci směřují více jižněji nebo západněji. Pevná většina podzimních nálezů je z Itálie a méně z Francie (mapa 2). Zimoviště přes naše území protahujících ptáků se nacházejí od západního Středozeří (1 nález z Francie) směrem k severní Africe (1 nález z Alžírka) a zasahují až na pobřeží Guinejského zálivu (mapa 2). Zimní nálezy z Ghany se týkají jak českých, tak i slovenských kroužkovanců. Mimo ně jsou to ještě jednotlivé nálezy z Pobřeží Slonoviny (březen), Sierra Le-



Graf 1: Měsíc kroužkování později nalezených ptáků.

Fig. 1: Month of ringing of birds later recovered.

one (říjen) a Gabonu (duben). Pro zimoviště ležící jihovýchodně nemáme žádný nález ze zimního období, ale nálezy z podzimního tahu v Maďarsku a Bulharsku a z jarního tahu v Řecku mohou jejich existenci naznačovat (mapa 3). Navíc listopadové nálezy z Itálie se mohou týkat již ptáků na zimovišti. Z našich okroužkovaných mlád'at a adultů nemáme žádné zpětné hlášení ze zimovišť. Nutno však dodat, že počty kroužkovaných mlád'at nebo adultů na hnízdištích jsou velmi nízké (např. v letech 1981 - 2001 bylo mezi 9106 okroužkovanými pisíky pouze 107 mlád'at).

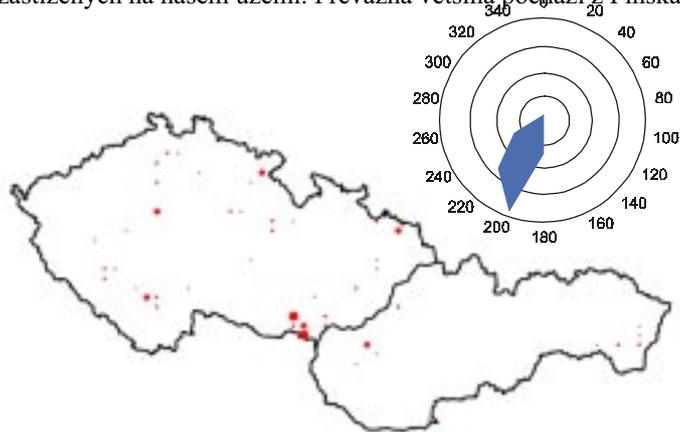
Návrat ze zimovišť je SSV směrem. Jarní tah probíhá od dubna

	<1960	60-69	70-79	80-89	90-02	Celkem Total
<b>Kroužkováno</b> Ringed (%)	5	10	26	34	24	16629
<b>Nalezeno</b> Recovered						
Naši ptáci (%) CZP-rings	4	11	19	29	37	392
Cizí ptáci (%) Foreign-rings	5	16	10	26	42	19

Tab.1: Počty okroužkovaných a nalezených ptáků.

Table 1: Number of birds ringed and recovered.

do května. Ptáci protahující naším územím pocházejí převážně ze Skandinávie (Finsko 14, Švédsko 2, Litva 1) a západního Ruska (4). To potvrzují i kontrolní odchyt zahraničních kroužkovanců zastižených na našem území. Převážná většina pochází z Finska



**Graf 2:** Směr tahu protahujících ptáků (n=30).

**Fig. 2:** Direction of migration.

**Mapa 1:** Místa kroužkování později nalezených ptáků.

**Map 1:** Ringing places of birds later recovered.

(6) a polského pobřeží Baltiku (6) - mapa 4. Přímou polohu hnízdiště dokládá podzimní kontrolní odchyt mláděte z jižního Finska. Několik jarních nálezů je již z července, a naznačují tak možná hnízdiště v severozápadním Rusku, Švédsku a Finsku. Z jarního tahu nemáme ani jeden přímý nález našeho ptáka. Při návratu ze zimovišť byli ptáci hlášeni nejvíce z Finska (11), Itálie (4) a Švédska (2). Jeden jarní nález našeho kroužkovance v Holandsku a podzimní nepřímé nálezy z Belgie (2) a Německa (3) mohou znamenat tah oklikou, nebo se jedná o ptáky, kteří táhnou více rovnoběžkově. Z vysokého počtu kontrolních odchytů se lze domnívat, že pisík je mimořádně věrný jak svým tahovým cestám, tak i odpočinkovým místům. Ze 253 místních kontrol jich 21% bylo v té samé tahové sezóně, přičemž průměrná délka zastávky na téže lokalitě byla 11,8 dne (medián=11 dní, n=53). Staří ptáci se zdržovali průměrně o jeden den déle než mladí a rozdíl ve směru tahu mezi starými a mladými ptáky nebyl statisticky průkazný. Uvedená data kontrastují s nálezy z polského pobřeží Baltiku, kde počet opakovaných kontrol byl naprosto zanedbatelný a drtivá většina ptáků se zastavila na dobu pouze 1 až 2 dní (MEISSNER 1996). Věrnost tahovým ces-

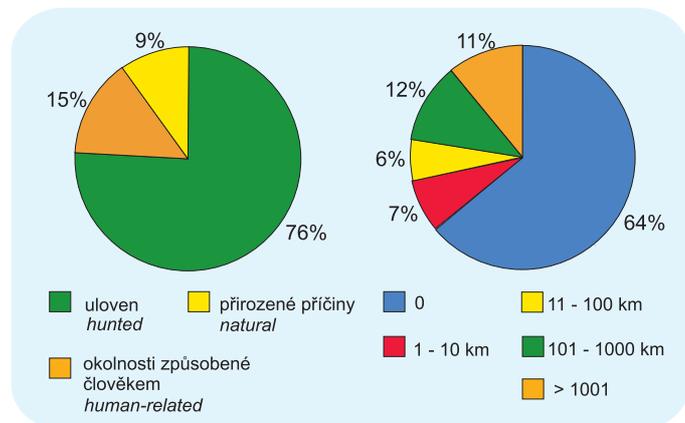
tám a odpočinkovým místům dokládá zbylých 79% kontrolních odchytů v některém z následujících let. Mezi nimi je celá řada hlášení po více jak 5 letech. Podobná věrnost je popsána i pro zimoviště pisíka (*BA*, *BWP*). I když se ptáci mohou zdržet na odpočinkových místech delší dobu, rychlost tahu na zimoviště patří mezi bahňáky k těm vyšším (průměrně 58 km/den, n=28). Nejrychlejším ptákem byl náš kroužkovanec střelený v Itálii na podzimním tahu (R76168), který uletěl 993 km za 3 dny. Vůbec nejstarším dokumentovaným pisíkem byl švédský jedinec, který se dožil 14 let a 6 měsíců (STAAV 1998).

Peter Adamík

<b>Nejstarší pták</b> Oldest bird	<b>12 let, 11 měsíců, 17 dnů</b>	
Z 598432 1y	21.08.1979	Senné (MI)
	07.08.1992	Senné (MI)
<b>Nejvzdálenější nález</b> Longest recovery	<b>5408 km</b>	
Z 606020 1y	17.08.1980	Sedlec (BV)
	15.04.1981	Libreville, Gabon
<b>Hnízdní období</b> Breeding season	<b>V- 1/2 VI</b>	
<b>Početnost CZ / SK</b> Population estimate	<b>200-400 / 700-1300</b>	

## Summary

The Common Sandpiper is a regularly breeding species in CS. The majority of ringed sandpipers are birds on autumn passage. The autumn migration starts in mid July with the arrival of adults. The peak passage occurs in August with the wave of newly arriving first-year birds and then the numbers decline until the end of November. The local literature reports occasional occurrence during winter. A considerable part of recoveries comprises recaptured birds (80 %), while only 9 % have been shot or caught by man. Out of the 253 local recoveries, 21 % were within the same migration period with an average stopover length of 11.8 days (median=11 days, n=53). Adults stopped on average one day longer than juveniles. The high level of stopover site fidelity is confirmed by the remaining 200 local recaptures. The average migration speed on the autumn passage was 58 km/day (n=28). These birds were recaptured after more than a year from the ringing date and there are numerous cases when the bird was recaptured at the same site after more than 5 years. The migration continues in a southwestern direction to Italy and less frequently to France. Indirect southeastern recoveries on autumn and spring passage from Hungary, Bulgaria and Greece possibly indicate a southeastern flyway. The winter recoveries spread from the Mediterranean coast of France (1) to northern Africa (Algeria 1) and further south to Ghana (5). There are three other recoveries from the Ivory Coast (March), Sierra Leone (October) and Gabon (April). However, none of these winter recoveries is related to CS born birds. The spring arrival starts in April and the northeastern passage continues until May. The birds have been later recovered in Finland, northwestern Russia, Lithuania and Sweden. Similarly, foreign-ringed birds recaptured in CS come mainly from the northeast. One recovery of a Finnish bird ringed as nestling documents the northern breeding grounds. A spring recovery from the Netherlands and indirect autumn recoveries from Belgium (2) and Germany (3) possibly indicate a loop migration or more likely these birds followed a more western migration route.



**Graf 3:** Známé příčiny úhynu (n=53)..

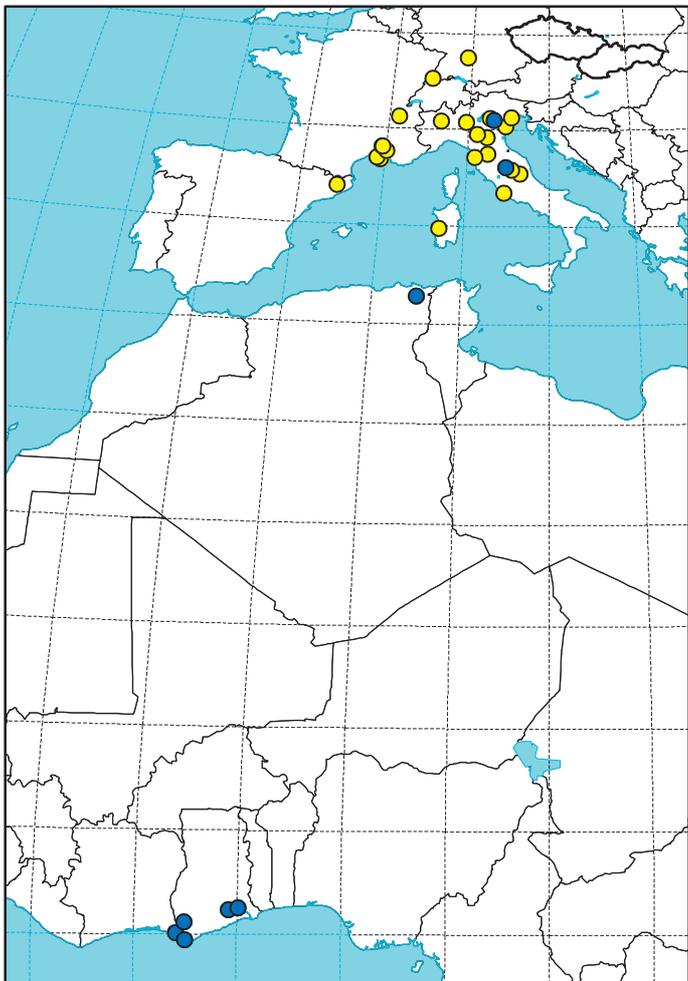
Ostatní okolnosti nálezů: kontrolován 318, neznámé příčiny úhynu 22

**Fig. 3:** Known finding circumstances.

Another recovery details: controlled by ringer 318, unknown causes of

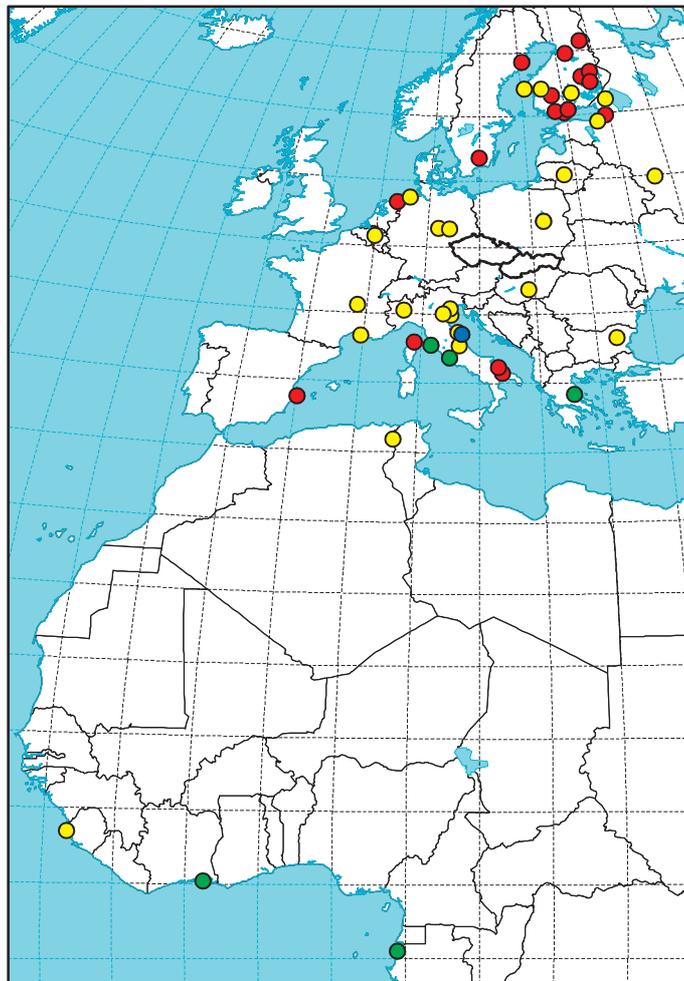
**Graf 4:** Rozložení nálezů podle vzdálenosti od místa kroužkování.

**Fig. 4:** Distribution of recoveries according to distance between ringing and recovery place.



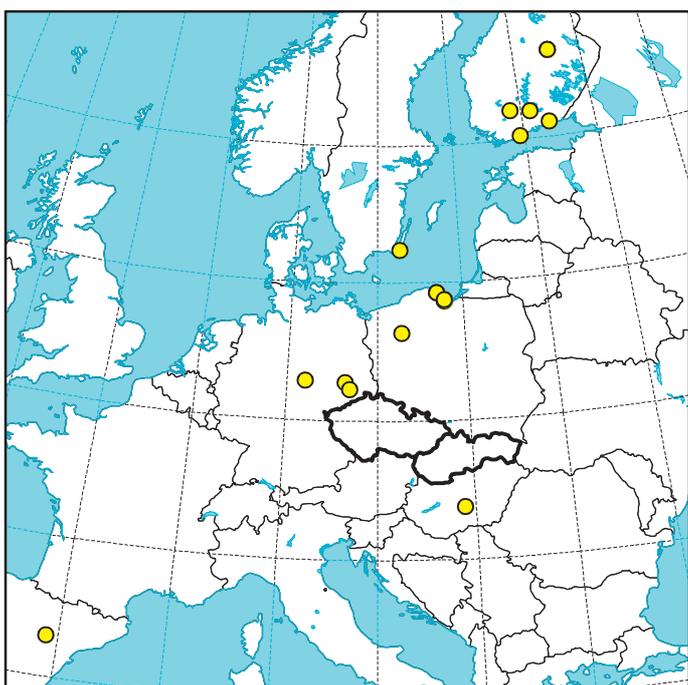
**Mapa 2:** Nálezů protahujících písíků obecných za přímého tahu: na podzim (VII-X, žlutě) a v zimě (XI-II, modře). Zobrazeny jsou pouze nálezů nad 100 km.

*Map 2:* Recovery locations (within same season) in autumn (VII-X, yellow) and winter (XI-II, blue) of Common Sandpipers present in CS during migration (only movements over 100 km are given).



**Mapa 3:** Nálezů protahujících písíků obecných v následujících letech po okroužkování: na podzim (VII-X, žlutě), v zimě (XI-II, modře), na jaře (III-IV, zeleně) a v hnízdní době (V-VI, červeně). Zobrazeny jsou pouze nálezů nad 100 km.

*Map 3:* Recovery locations in subsequent years in autumn (VII-X, yellow), winter (XI-II, blue), spring (III-IV, green) and breeding season (V-VI, red) of Common Sandpipers present in CS during migration (only movements over 100 km are given).



**Mapa 4:** Zahraniční místa kroužkování protahujících písíků obecných na podzim (VII-X, žlutě).

*Map 4:* Ringing locations in autumn (VII-X, yellow) of foreign-ringed Common Sandpipers later recovered in CS during migration.

## Studie 10

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: 619–626.

# 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 non-breeding 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

## Zusammenfassung

### Jahreszyklus und Zugstrategien des Brachpiepers als Habitatspezialisten mit Hilfe von Geolokatoren offengelegt

Habitatspezialisten weisen enge ökologische Nischen auf und nutzen während des gesamten Jahres weitestgehend ähnliche Habitate. Solch ein enger Anspruch an einen Habitattyp könnte die betreffende Art, insbesondere kleine, lokale Populationen, angreifbar für Umweltveränderung machen. Ein fundiertes Wissen zur Ökologie solcher Arten ist demnach ausschlaggebend für gezielte Schutzmassnahmen. In der vorliegenden Studie verwendeten wir Geolokatoren, um die Zugrouten und Aufenthaltsgebiete außerhalb der Brutzeit des an Trockenhabitate gebundenen Brachpiepers *Anthus campestris* zu identifizieren, die aus einer rückläufigen mitteleuropäischen Brutpopulation stammten. Die Mehrzahl der Vögel nutzte auf dem Herbst- und Frühlingszug eine Flugroute nordwestlich der Alpen

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über die Iberische Halbinsel mit Rastplätzen in Nordafrika. Jedoch flog in jeder Zugsaison ein jeweils anderes Individuum einen Umweg um die Alpen östlich zu umgehen. Die Sahara als grosse ökologische Barriere wurde im Herbst von drei der sechs Vögel entlang der Atlantik-Küste überquert, während im Frühling alle Vögel diesen Weg nahmen. Alle untersuchten Pieper überwinterten in der westlichen Sahelzone. Fünf der sechs Vögel nutzten dabei zwei getrennte Überwinterungsplätze, wobei der zweite Aufenthaltsort jeweils westlich vom ersten lag. Die untersuchten Pieper verbrachten 48 % des Jahres in ihrem Überwinterungsquartier, 27 % auf dem Zug und 25 % der Zeit am Brutplatz. Unsere Ergebnisse belegen für den Brachpieper eine starke Zugkonnektivität, die Konsequenzen für zukünftige Schutzmaßnahmen haben könnte.

## 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 (McPeck 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 (Št'astný 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, man-made 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  $0.66 \pm 0.03$  (SD) g, which is less than 5 % of the lean body mass of the birds (mean  $\pm$  SD, males  $25.52 \pm 1.74$  g, females  $23.65 \pm 2.02$  g). All tagged birds were additionally fitted with aluminum 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 re-

capture 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  $\pm 25$ th/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 non-breeding 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 (Online Resource Fig. S1).

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  $52 \pm 11.5$  days (Table 1).

The median departure date from the non-breeding sites was 23 March (Table 1). Four of five birds had their first

**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 in 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

stopover of  $13.5 \pm 4.4$  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 Desert (Online Resource Fig. S1), and all birds, including the remaining individual (CZ-2) 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; Online Resource Fig. S1).

For the three birds in which we obtained full annual tracks, the mean duration of spring migration was  $45.7 \pm 4.0$  days, including the first stopover site in sub-Saharan Africa (Table 1). If this stopover site was excluded, the mean duration of spring migration was only  $30.7 \pm 9.1$  days.

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

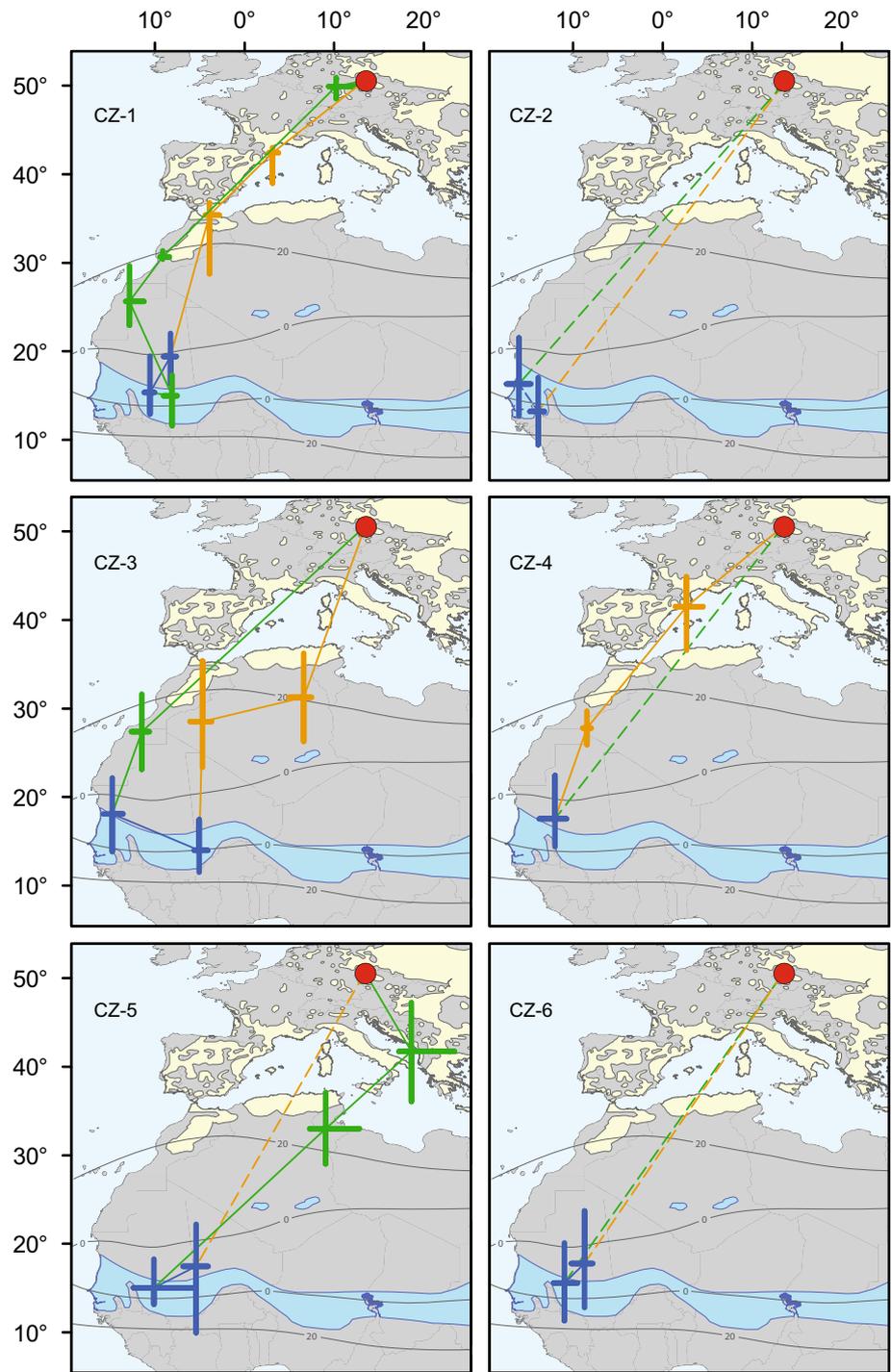
### Non-breeding residency period

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  $592 \pm 314$  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  $334 \pm 129$ , and it was  $149 \pm 102$  km for the second non-breeding residence. Average monthly precipitation from November through the end of February at the non-breeding 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  $\pm$  interquartile range: first site,  $17^{\circ}28' \pm 3^{\circ}48'N$   $8^{\circ}16' \pm 3^{\circ}22'W$ ; second site,  $15^{\circ}37' \pm 0^{\circ}56'N$   $10^{\circ}56' \pm 4^{\circ}11'W$ ). On average, the birds spent more time at the second non-breeding area ( $100.8 \pm 11.5$  days) than the first ( $69.6 \pm 35.9$ ). The total duration at the non-breeding residency areas for the five birds with complete records was  $175 \pm 25.2$  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 Online Resource Fig. S2).

**Fig. 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  $\pm$  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) (colour figure online)



**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 fueling 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-Palaearctic 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; Trerweiler 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 non-breeding 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.

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## Studie 11

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# Timing of migration and African non-breeding grounds of geolocator-tracked European Pied Flycatchers: a multi-population assessment

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## Abstract

Using light-level geolocators, eight European Pied Flycatchers (*Ficedula hypoleuca*) from two breeding sites in Czechia were tracked. We also gathered all available geolocator tracks on 76 individuals from four European populations and compared the timing of annual cycle events and the African non-breeding sites among all populations. Individuals from both Czech breeding sites had overlapping migration events and non-breeding locations. Four individuals resided in the southwestern edge of Mali, two in Burkina Faso, one in Guinea, and the easternmost one in the Ivory Coast. On average, the birds left the Czech breeding grounds on 8 August and took between one to three stopovers during autumn migration. Birds crossed the Sahara on its western edge on average on 13 September. The mean arrival to the African non-breeding grounds was 47.5 days after departure on 2 October (range 10 September to 10 October). One bird showed intra-tropical movement within West Africa when after a 60-day residency it moved approximately 3° westwards. Estimated locations at the African non-breeding grounds overlapped among tracked birds from five European breeding sites. However, statistically, we could detect longitudinal segregation in two clusters. Birds from the British and Finnish breeding populations shared non-breeding grounds and were located in Africa west of the second cluster of the birds from the Czech and Dutch breeding populations. We show considerable population-specific differences in the timing of annual cycle events. Birds from Dutch breeding sites were the first in all three phases—departure from breeding sites, Sahara crossing and arrival to African non-breeding grounds, followed by the British, Czech, and Finnish birds, respectively. All tracked flycatchers so far fill only the western part of the African non-breeding range. For a complete understanding of the migration pattern in the species, we highlight the need for tracking studies from the eastern part of the range.

**Keywords** Annual cycle · Long-distance migration · European Pied Flycatcher · Light-level geolocator · Geolocation by light · *Ficedula hypoleuca*

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## Zusammenfassung

### Zugablauf und afrikanische Überwinterungsgebiete von mit Geolokatoren georteten Trauerschnäppern: ein Vergleich mehrerer Populationen.

Der Langstreckenzug von acht Trauerschnäppern (*Ficedula hypoleuca*) aus zwei Brutgebieten der Tschechischen Republik wurde mit Hilfe von Geolokatoren verfolgt. Zusätzlich verglichen wir den zeitlichen Ablauf des Jahreszyklus und die Überwinterungsorte aller derzeit verfügbaren getrackten Schnäpper ( $n = 76$ ) aus vier verschiedenen europäischen Brutpopulationen. Der zeitliche Zugablauf als auch die Überwinterungsorte der Vögel der beiden tschechischen Brutgebiete überschneiden sich. Vier Individuen hielten sich während der Nichtbrutzeit am südwestlichen Rand von Mali, zwei in Burkina Faso, eines in Guinea und der östlichste Vogel in der Elfenbeinküste auf. Die Vögel verließen ihre tschechischen Brutgebiete im Mittel am 8. August und legten während des Herbstzuges einen bis drei Zwischenstopps ein. Die Sahara wurde im Durchschnitt am 13. September an ihren westlichen Rand überquert. Die Vögel erreichten die afrikanischen Nichtbrutgebiete durchschnittlich nach 47,5 Tagen am 2. Oktober (Spanne: 10. September bis 10. Oktober). Ein Vogel verlagerte nach 60 Tagen seinen Überwinterungsort innerhalb Westafrikas um  $3^\circ$  westwärts (innertropische Bewegung). Die Aufenthaltsorte der Vögel aus fünf verschiedenen europäischen Brutgebieten überschneiden sich im afrikanischen Überwinterungsgebiet weitgehend, wiesen jedoch eine statistisch abgesicherte Clusterformation entlang des Längengrades auf. Vögel der britischen und finnischen Brutpopulationen teilten sich das westlichere Nichtbrutgebiets-Cluster, das zweite östlichere Cluster wurde von Vögeln aus den tschechischen und niederländischen Brutpopulationen gebildet. Wir fanden erhebliche populationspezifische Unterschiede im Zeitablauf des Jahreszyklus. Vögel aus den niederländischen Brutgebieten waren für alle drei Ereignisse – dem Abflug aus den Brutgebieten, der Überquerung der Sahara und die Ankunft in den afrikanischen Nichtbrutgebieten – die ersten, gefolgt von den britischen, tschechischen und den finnischen Vögeln. Die bisher getrackten Trauerschnäpper überwintern im westlichen Teil des afrikanischen Nichtbrutgebiets der Art. Für ein umfangreiches Verständnis der Zugmuster des Trauerschnäppers sind ergänzende Studien aus dem östlichen Teil des Verbreitungsgebiets dringend erforderlich.

## Introduction

Since the beginning of the twenty-first century, advances in bird-tracking devices have unprecedentedly improved our knowledge of the migration ecology of individual small-bodied songbirds. Retrieval of devices from tracked individuals is often labour-intensive, costly and challenging, which results in many studies restricting the fieldwork to single sites and small tracking sample sizes. Spatial replication is, however, critical for a meaningful understanding of the migration ecology of any species. The best approach is to have multi-population studies across a species' range. In recent years an accumulation in the number of studies has shown the power of multi-population assessments in Great Reed Warblers *Acrocephalus arundinaceus* (Koleček et al. 2016), Red-backed Shrikes *Lanius collurio* (Pedersen et al. 2020), Common Rosefinches *Carpodacus erythrinus* (Lisovski et al. 2021), Northern Wheat-eaters *Oenanthe oenanthe* (Meier et al. 2022), and non-Passerines (e.g. Finch et al. 2015; Åkesson et al. 2020; Hahn et al. 2020). Such assessments allow for a deeper understanding of migratory corridors and spatiotemporal organization of distant populations across the year.

To add to this list of multi-population assessments, we tracked the European Pied Flycatcher with light-level geolocators at two breeding sites in Czechia. We aim to provide detailed data on the migration patterns of birds from these Czech sites. In addition, we take the

opportunity to summarize the current knowledge of the species' migration patterns based on published tracking results from four other populations available to date (Ouwehand et al. 2016; Ouwehand and Both 2017; Bell et al. 2022). For all birds sampled across European sites we aim to provide an overview of population-specific non-breeding grounds and timings of annual cycle events. We intend to assess whether there is a role of breeding locations in Europe for the clustering of individuals at African residency areas and whether the timing of annual cycle events is linked to the breeding origin of populations, i.e. northern breeding populations migrate later than the southern ones at all stages of the annual cycle (Briedis et al. 2016; Gow et al. 2019).

## Methods

### Study sites and geolocators in Czechia

We studied the migration of European Pied Flycatchers at two breeding sites in Czechia. The first study site was in Northern Bohemia (50.62 N, 15.83 E); the second site was in North-eastern Moravia (49.95 N, 17.25E). The great circle distance (the shortest distance measured along the surface of a sphere) between the two sites is 170 km. The first site shows stable numbers of breeding birds in a nest box population. At the second site, there is a steady decline of

breeding birds and in some plots with nest boxes, the population underwent local extinction during recent decades.

We deployed light-level geolocators (model GDL2 with 7 mm light stalk, Swiss Ornithological Institute) on adult breeding birds across three different field seasons: 2012, 2014, and 2015. In each season, we deployed 20, 36, and 38 geolocators, respectively (Online Supplement 1, Table S2). All birds (42 males and 52 females) were trapped while they were feeding nestlings (at the age of 6–11 days) in nest boxes. We attached the geolocators on the birds' backs using leg-loop harnesses made of 1 mm thick silicone. Each device, including the harness, weighed approximately 0.6 g (< 5% of the bird's body mass). In the years following the deployment, we recovered one, three, and five geolocators, respectively. Due to technical difficulties, one logger failed recording, and seven geolocators from 2014 and 2015 contained data only for autumn migration and parts of the wintering period. However, we could identify the African non-breeding residency sites of all seven birds. The remaining geocator from 2012 stopped recording on 4 May 2013 shortly after the bird had returned to the breeding area. The overall return rate of logger-tagged birds was 11.5% (6/52) for females and 7.1% (3/42) for males. At both sites, regular control of nest box occupancy by flycatchers and overall nest success was performed but due to a lack of manpower and funding no regular recaptures of nesting birds were done. The second site in Moravia had a small population size which also contributed to the lack of a control group. Thus, we lack a formal control group of ringed-only birds for the two sites. The only relevant data on returns of control birds are from a nearby (13 km to the site in Moravia) long-term study site in Dlouhá Loučka (49.83 N 17.21E). At that site, the return rate during 2005–2019 was 12% for females (3/25) and 13.6% for males (3/22; P. Adamík unpubl. data). There was no significant difference between the overall recapture rates of logger-tagged (9/94) and the above-mentioned untagged birds (6/47;  $\chi^2$  test,  $\chi^2 = 0.27$ ,  $P = 0.604$ ).

### Geocator data analyses

We used the threshold method (Lisovski and Hahn 2012) to determine the sunrise and sunset times of the recorded light data using 'GeoLocator' software (Swiss Ornithological Institute) and setting the light level threshold to 1 unit on an arbitrary scale (i.e., minimum detectable ambient light by the given light sensor). All further analyses were conducted using the R-package 'GeoLight' v 2.0.0 following the standard procedures (Lisovski and Hahn 2012; Lisovski et al. 2020). Using the 'loessFilter' function, in each dataset we first filtered for outlying twilight events that exceed two interquartile ranges ( $k = 2$ ) of the residuals from a local polynomial regression. We determined the stationary periods with the 'changeLight' function by setting the minimal

stationary period to 2.5 days and the probability of change to  $q = 0.9$ .

When calculating geographic positions for the stationary periods, we excluded 7 days on either side of the equinox times and later filtered all positions north from 80°N and south from 20°S (more than 30° latitude from breeding and median African non-breeding site latitudes). We estimated the geographic positions of the stationary periods using sun-elevation angles derived from Hill–Ekstrom calibration, but when it was not possible, we used in-habitat calibration from the pre-migratory period (Lisovski et al. 2020, Online Supplement 1, Table S3). However, neither of the two methods worked for three of our datasets. For these three datasets, we developed and used a new calibration method—'equinox calibration'. This calibration method calculates the appropriate sun-elevation angle for the specified number of days around the equinox time when the day and night length at any given geographic location is just about 12 h long. Thus, any deviation from the 12-h day/night length in the geolocators' recordings reflect the measurement error due to the sensitivity limits of the light sensor or shading by vegetation, weather, etc. The calibration method finds the appropriate sun-elevation angle that would give the desired 12-h day/night length. R-script for this calibration method is provided in Zenodo (Adamík et al. 2023). Due to technical differences in the sensitivity of the geolocators' light sensors between devices used in different study years, the estimated sun-elevation angles ranged widely between  $-2.15$  for the newer generation devices, and  $+11.39$  for the one from the oldest generation device with lower sensitivity light sensor used in 2012. Raw geocator files from the eight Czech birds are freely available in the Zenodo data repository (Adamík et al. 2023).

We also determined the timing of Sahara crossings for all individuals by manually inspecting the daily light patterns recorded by the geolocators. In short, when crossing large ecological barriers like seas and deserts typical nocturnal migrants, including the European Pied Flycatcher, regularly prolong their flights into the day or may fly non-stop (Adamík et al. 2016; Jiguet et al. 2019). Such behaviour is reflected in the geocator's light recordings as lengthy periods of uninterrupted maximal light intensities when the light sensor is exposed to the sun as the bird flies (full light pattern, hereafter FLP or Sahara crossing). Due to difficulties in reliable estimates of stopover locations close to equinox periods, data on stopovers are presented only as timings and median longitudinal estimates.

We estimated migration speed as migration distance divided by duration (including stopovers). Distances between the breeding and African non-breeding sites were estimated as a great circle distance. Migration duration is the time (in days) between departure from the breeding site and arrival to the African non-breeding site (duration.migration).

## Multipopulation assessment

We collated published data on individually tracked European Pied Flycatchers from European breeding sites. To date, there are available data on geolocator-tracked birds from the UK, the Netherlands, Finland, and Norway (Ouwehand et al. 2016; Ouwehand and Both 2017; Bell et al. 2022). From these studies, we extracted data on departure from breeding sites (variable names in parentheses: autumn.departure), timing of Sahara crossing (inferred from light anomalies, FLP), arrivals to African non-breeding grounds (winter.arrival), median nonbreeding location estimates (wint.longitude, wint.latitude) and egg-laying dates (laying.date). We took the dates of the Sahara crossing for the four Finnish birds from Adamík et al. (2016). The full-collated dataset for 76 individuals is available as an Online Supplement 2, Table S1. All variables related to dates are expressed as days of the year.

To assess whether the five European populations differ in African non-breeding site locations or duration of migration, we ran three linear models (LM) with a country as an explanatory variable (five countries) and non-breeding site longitudinal (winter.longitude) or latitudinal location (winter.latitude) and duration of migration (in days) as response variables. In further three LMs, which always had a single predictor, we explored whether non-breeding longitudes (response variable) can be explained by egg-laying dates, departures from breeding sites, and arrivals to Africa.

In further analyses, we used linear mixed-effects models (LMM) to assess whether latitudinal or longitudinal location estimates in Africa (response variables winter.longitude or winter.latitude) are associated with breeding site longitudes or latitudes (fixed predictors: breeding.longitude, breeding.latitude) while accounting for the fact that multiple individuals originate from the same study site. For this reason, we entered the breeding population (country) as a random effect. For evaluating the strength of relationships between the four consecutive phases of the annual cycle (egg-laying date, departure from breeding site, Sahara crossing, arrival to African non-breeding sites) we fitted LMMs which had always a single fixed predictor and country as a random effect. For clarity, the model syntax is provided with the test statistics in the results. For model fitting we used the R package *lme4* (Bates et al. 2015). For model diagnostics, we used the R package *performance* (Lüdtke et al. 2021). The models were run for the full dataset of 76 individuals, however, the sample size was 66 for Sahara crossing, 74 for arrival to non-breeding grounds, 47 for location estimates of nonbreeding grounds and 41 for egg-laying dates.

## Results

### Migration of birds from Czech breeding grounds

On average, Czech flycatchers departed from their breeding grounds on 8 August (range 24 July to 22 August, Table 1). All flycatchers headed SW towards the Iberian Peninsula (Fig. 1 and Online Supplement 1, Fig. S1). We detected between one to three stopover sites per bird. Stopovers before the Sahara crossing lasted on average 9.7 days ( $n=13$ ; range 3–24.5 days) and were located around 4.7°W (range 2.3°E to 9.5°W). Stopovers after the Sahara crossing were slightly shorter, on average 6.8 days ( $n=6$ ; range 3.5–11.5 days; Online Supplement 1, Table S4) and were further west at around 12.2°W (range 9.6–14.1° W). On average, birds crossed the Sahara on its western edge on 13 September (range 30 August–30 September). Mean arrival to the African non-breeding grounds was on 2 October (range 10 September to 10 October). One bird showed intra-tropical movement when it arrived at its first African non-breeding site on 11 September where it stayed for 60 days, after which it moved about 3° westwards to its final residency site. Autumn migration lasted on average 47.5 days (range 34–62 days) including stopovers. The African non-breeding residency sites overlapped for the two tracked Czech populations and for both sexes (t-test on longitudes:  $t=-0.09$ ,  $P=0.928$ ,  $df=6$ ; t-test on latitudes:  $t=0.53$ ,  $P=0.612$ ,  $df=6$ ; Fig. 1). Most birds were clustered around the south-western edge of Mali (four individuals), two in Burkina Faso, one in Guinea, and the easternmost one in the Ivory Coast. As birds from both Czech breeding sites showed considerable overlap in both non-breeding locations and their migration phenology, we pooled the data on them for the pan-European comparison of populations.

For the one bird with data available up until spring, the departure from the non-breeding site was after 204 days of residency on 20 April. The bird initiated a crossing of the Sahara on 23 April and made a 12-day stopover around 6.7° E after the desert crossing.

### Multipopulation assessment of African non-breeding grounds

Birds from all five European breeding populations overlapped at their West African non-breeding grounds (Fig. 2). However, there is a statistically significant effect of the breeding origin of the population on longitudinal estimates of non-breeding locations (LM: winter.longitude ~ country,  $F_{4,69}=28.4$ ,  $P<0.001$ ,  $R^2=0.62$ ). The single Norwegian bird stayed in the most westward location. The four remaining populations created two clusters. Mean location estimates of UK and Finnish birds overlapped around

**Table 1** Data on migration schedules of eight geolocator-tracked European Pied Flycatchers from Czech breeding sites

	5NV	13NP	15HG	15IE	13KR	13NJ	15HW	17LW
Sex	F	M	F	F	F	F	M	M
Year	2012	2014	2015	2015	2014	2014	2015	2015
Site	Moravia	Moravia	Moravia	Moravia	Bohemia	Bohemia	Bohemia	Bohemia
Autumn migration								
Departure	18-Aug	24-Jul	2-Aug	7-Aug	7-Aug	22-Aug	7-Aug	11-Aug
Sahara crossing	16-Sep	30-Aug	7-Sep	10-Sep	28-Sep	30-Sep	2-Sep	19-Sep
Arrival to Africa	28-Sep	12-Nov <sup>a</sup>	19-Sep	26-Sep	8-Oct	10-Oct	10-Sep	27-Sep
Number of stopovers	3	2 <sup>a</sup>	3	1	3	2	2	2
Duration (days)	41	49	48	50	62	49	34	47
Distance (km)	5187	4934	4694	4861	4714	4884	4829	4766
Speed (km/day)	127	101	98	97	76	100	142	101
Median location Africa	7.07 N 4.34 W	11.69 N 10.10 W	13.56 N 8.95 W	10.47 N 5.45 W	12.77 N 8.36 W	11.15 N 8.44 W	11.47 N 6.23 W	10.53 N 5.25 W
Spring migration								
Departure	20-Apr							
Sahara crossing	23-Apr							

<sup>a</sup>Intra-tropical movement, first non-breeding site (9.31° N, 7.46° W) arrival on 11 September

10.5 and 10.7° W, respectively, and were west of the Czech and Dutch populations. The Czech and Dutch populations overlapped at estimated mean longitudes of 7.14 and 7.32° W. Latitudinally the non-breeding locations largely overlapped across all populations (LM: winter.latitude ~ country,  $F_{4,42} = 0.66$ ,  $P = 0.622$ ,  $R^2 = 0.05$ ). Non-breeding longitude tended to be associated with breeding latitude (LMM: winter.longitude ~ breeding.latitude + (1 | country),  $b = -0.37 \pm 0.18$ ,  $t = -2.0$ ,  $P = 0.084$ , marginal  $R^2 = 0.15$ , conditional  $R^2 = 0.64$ ,  $n = 74$ , Online Supplement 1, Fig. S2) but no relationship was found with breeding longitude (LMM: winter.longitude ~ breeding.longitude + (1 | country),  $b = 0.00 \pm 0.11$ ,  $t = 0.0$ ,  $P = 0.977$ , marginal  $R^2 = 0.00$ , conditional  $R^2 = 0.73$ ,  $n = 74$ , Online Supplement 1, Fig. S2).

### Migration timing of European breeding populations

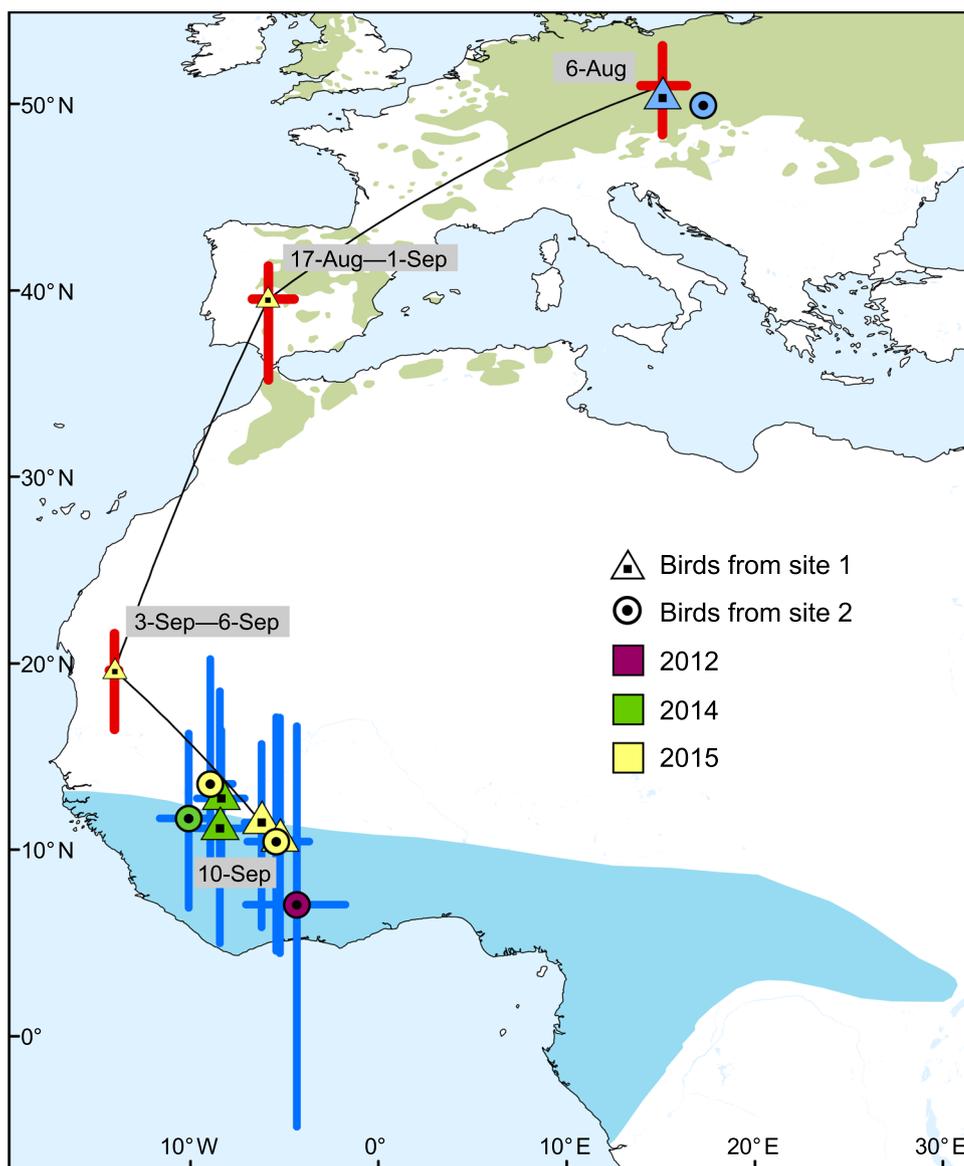
Most birds (54 out of 76) left the breeding sites by the end of the first week of August (range July 15–August 28, Fig. 3). Birds from the Dutch and UK breeding populations were similar in departure timing, with mean departure dates of 1 August and 4 August, respectively. The Czech birds left around 8 August and the Finnish birds departed on average 16 days later. The single Norwegian bird left the breeding site on 16 August. A similar order was found for the Sahara crossing timing, but here the populations differed in the interval between departure from the breeding sites and the Sahara crossing. The shortest interval was in Dutch birds (18 days) and the longest was in the Finnish and Czech birds (36–37 days). Population-specific arrivals to African

non-breeding grounds were again in the same order as breeding site departures. Interestingly, the Finish birds had a very short interval (8 days) between Sahara crossing and arrival to non-breeding locations (mean intervals in other populations were in a range of 17–21 days). The Norwegian bird arrived late to the African non-breeding grounds (14 October vs mean for all birds 16 September).

Autumn migration ranged from 17 to 85 days, and on average, it took 41.3 days to reach the African non-breeding sites. There was a significant effect of breeding population on the duration of migration (LM: duration.migration ~ country,  $F_{4,69} = 4.71$ ,  $P = 0.002$ ,  $R^2 = 0.21$ ) but this was likely due to the unusually short migration time of the Dutch birds (mean 35.3 days) while birds from other populations had similar durations (except for the one Norwegian bird with migration of 59 days). Birds that left their breeding sites late tended to have shorter migration durations (LMM: duration.migration ~ autumn.departure + (1 | country),  $b = -3.31 \pm 0.15$ ,  $t = -2.2$ ,  $P = 0.033$ , marginal  $R^2 = 0.05$ , conditional  $R^2 = 0.36$ ,  $n = 74$ ).

Consecutive phases of the annual cycle were strongly correlated, even when controlling for substantial variation within the breeding populations (Fig. 4). The strongest relationship was found between phases that were closer together (i.e. timing of the Sahara crossing and arrival to African non-breeding grounds (LMM: winter.arrival ~ FLP + (1 | country),  $b = 0.79 \pm 0.12$ ,  $t = 6.5$ ,  $P < 0.001$ , marginal  $R^2 = 0.52$ , conditional  $R^2 = 0.48$ ,  $n = 64$ )). Similarly, a strong relationship was observed between the departure from the breeding sites and the Sahara crossing (LMM: FLP ~ autumn.

**Fig. 1** Locations of African non-breeding grounds (blue crosses) for eight geolocator-tracked European Pied Flycatchers from two breeding sites in Czechia. Years of tracking are depicted in different colours. The map also shows stopover timing and location (in red) estimates for one individual, 15 HW. Location estimates are median values  $\pm$  interquartile range. Background map shows breeding (green) and non-breeding (blue) distributions of the species (BirdLife International and NatureServe 2013)



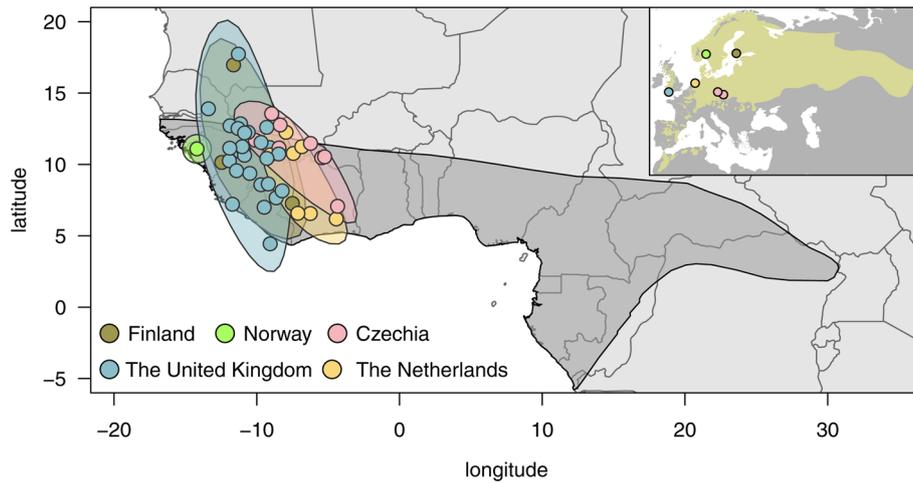
departure + (1 | country),  $b = 0.59 \pm 0.09$ ,  $t = 6.9$ ,  $P < 0.001$ , marginal  $R^2 = 0.21$ , conditional  $R^2 = 0.78$ ,  $n = 66$ ). A weaker relationship was found between breeding site departure and arrival to African non-breeding grounds (LMM: winter.arrival ~ autumn.departure + (1 | country),  $b = 0.51 \pm 0.17$ ,  $t = 3.1$ ,  $P = 0.003$ , marginal  $R^2 = 0.10$ , conditional  $R^2 = 0.40$ ,  $n = 74$ ). There was no relationship between egg-laying dates and departures (LMM: autumn.departure ~ laying.date + (1 | country),  $b = 0.18 \pm 0.17$ ,  $t = 1.0$ ,  $P = 0.303$ , marginal  $R^2 = 0.02$ , conditional  $R^2 = 0.53$ ,  $n = 41$ , Online Supplement 1, Fig. S3).

There was a weak tendency for birds residing at more westerly non-breeding grounds to breed later (LM: winter.longitude ~ laying.date,  $b = -0.07 \pm 0.04$ ,  $F_{1,39} = 3.82$ ,  $P = 0.058$ ,  $R^2 = 0.09$ ; Fig. 5). Longitudinal location in Africa was not associated with individual departure from

breeding sites (LM: winter.longitude ~ autumn.departure,  $b = -0.03 \pm 0.03$ ,  $F_{1,72} = 1.09$ ,  $P = 0.300$ ,  $R^2 = 0.01$ ) but it had an effect on arrival, with birds residing further east arriving earlier (LM: winter.longitude ~ winter.arrival,  $b = -0.04 \pm 0.01$ ,  $F_{1,72} = 8.81$ ,  $P = 0.004$ ,  $R^2 = 0.11$ ; Fig. 5).

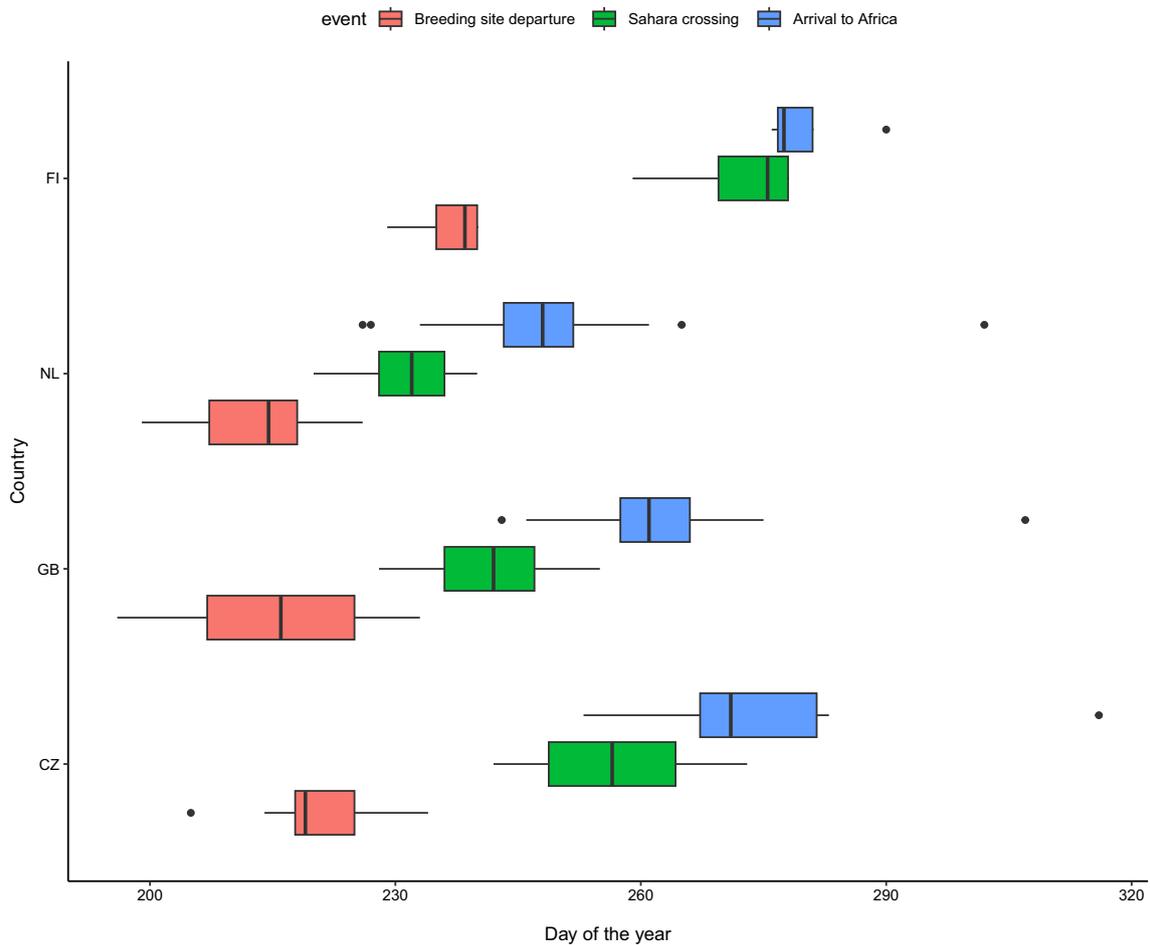
## Discussion

In this study, we brought new European Pied Flycatcher autumn migration data from two subpopulations in a central European region. We did not find any substantial differences in migration schedules and locations at the African non-breeding grounds for these birds. But we should be cautious as the sample size was small and we did not have access to full-year tracking data. Interestingly, from atlas mapping we



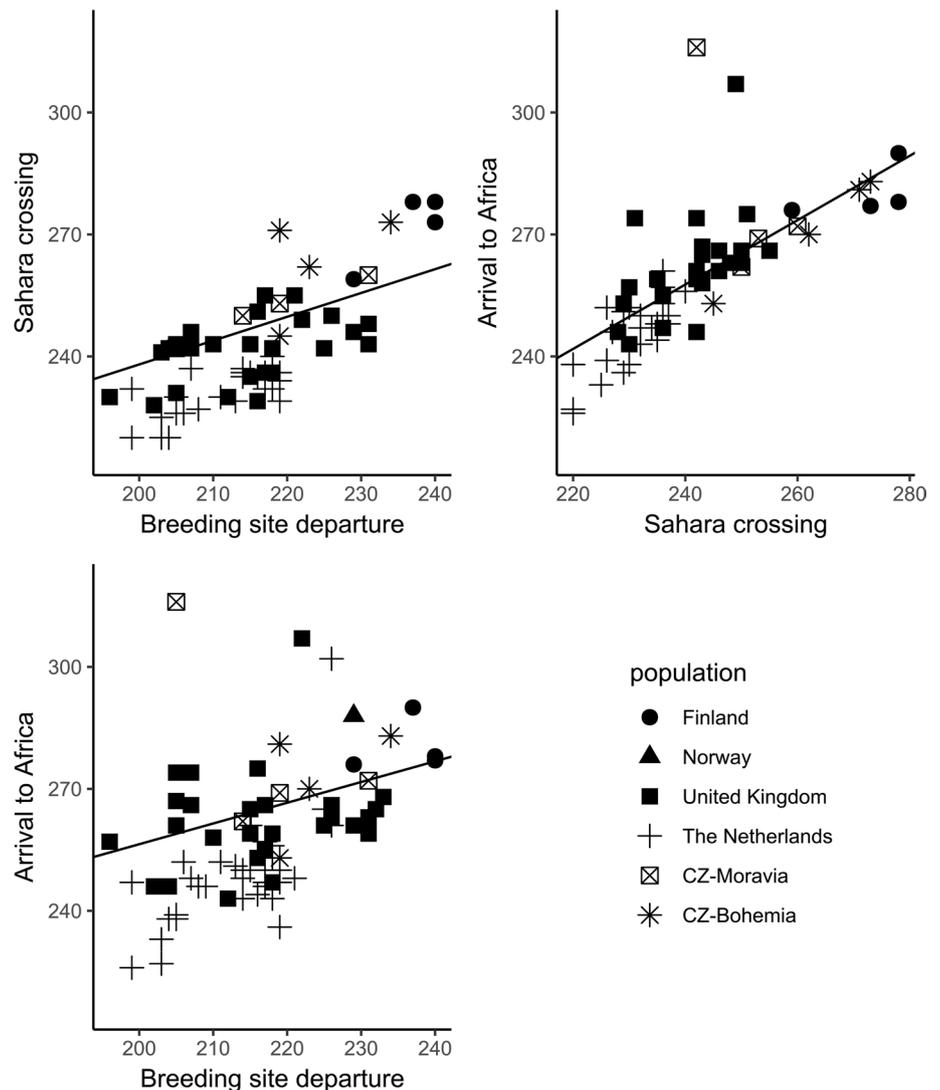
**Fig. 2** Location estimates (medians) of African non-breeding grounds for 47 European Pied Flycatcher individuals tracked with geolocators across five European breeding sites. For better visualization, coloured polygons represent spline-smoothed non-breeding regions of each population based on geolocator records. A convex hull of individual non-breeding sites is smoothed (per population) according to their

distance from the population mean non-breeding coordinates giving 30% margin of the difference between individual points on the convex hull and population mean non-breeding coordinates. For the single Norwegian bird, a circle with a 1° radius around the median location is drawn. The dots in the inset show locations where the birds were tagged at the breeding sites



**Fig. 3** Boxplots of timing of three annual cycle events across four European Pied Flycatcher breeding populations. Populations are ordered by breeding latitude. Data for the single bird from Norway are not visualized. X axis shows day of the year (e.g. 200=July 19)

**Fig. 4** Relationships between annual cycle events in the European Pied Flycatcher. The timing of events is expressed as days of the year

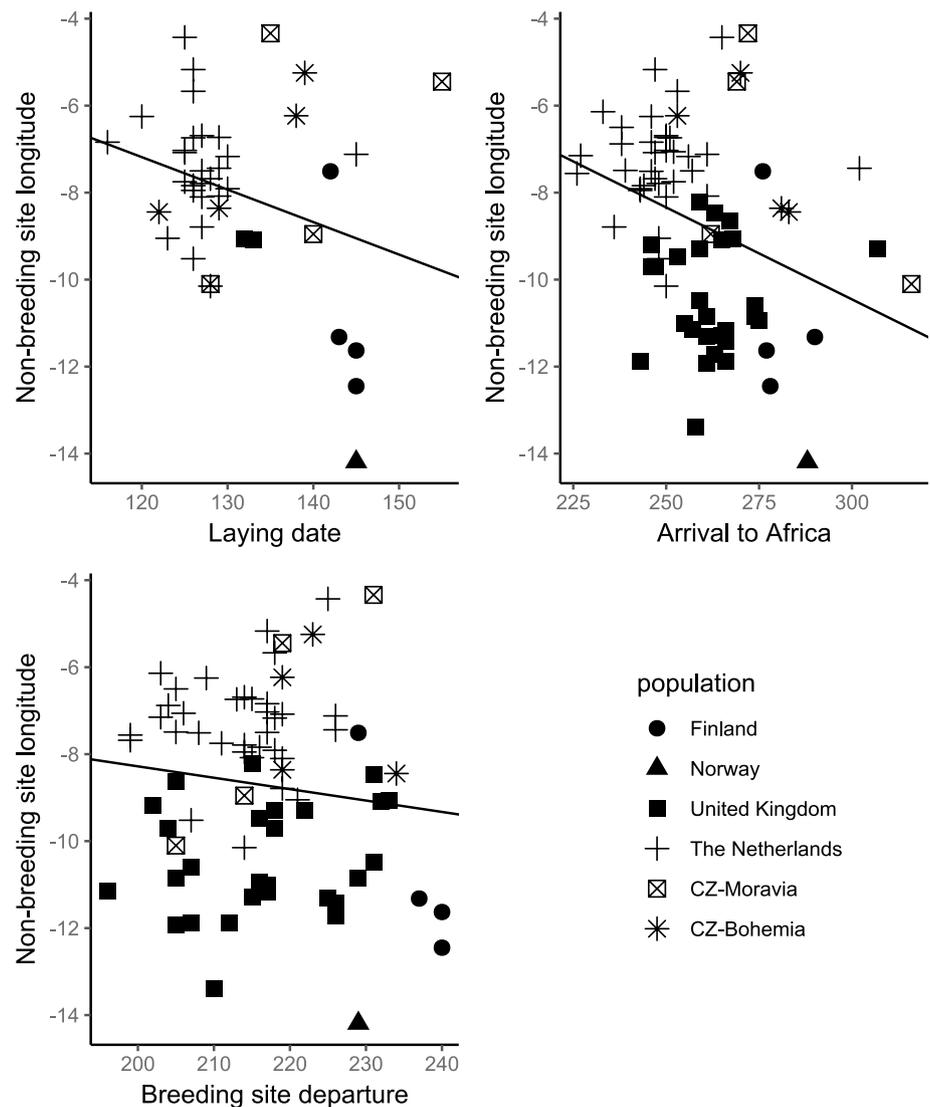


see that the two subpopulations show regionally contrasting population trajectories, the one in Bohemia being stable and the second in Moravia declining (Šťastný et al. 2021). It would be valuable to know where and at which time of year the main drivers of population dynamics act in these two regional populations. For Dutch birds, there is evidence for mechanisms at breeding sites (Both et al. 2006), while across the UK the trends in populations are driven by changes in survival and immigration which probably act outside the breeding season (Nater et al. 2023). The fact that we found overlaps in non-breeding locations of our sample of birds does not necessarily mean that they cannot differ in habitat use at a finer scale, which is below the resolution of geolocation by light.

We were able to detect between one to three stopovers during the autumn migration, usually one or two stops before the Sahara crossing and one after it. Stops before the Sahara crossing were slightly longer, nearly 10 days, while

those after it lasted on average almost 7 days. Pied Flycatchers tracked from the southwest UK usually have two stops during the autumn migration, one before and one after the Sahara crossing (Bell et al. 2022). Interestingly, for the UK-tracked birds' stopover durations were slightly longer after the barrier crossing. Longitudinal estimates of stopovers after the Sahara crossing were in a similar range between the two populations (CZ: 9.6–14.1° W vs UK: 9.8–16.2° W), albeit birds from the Czech breeding population stopped on average 1.1° further east of the UK birds. The increased number of stopovers detected in our sample of birds are likely a consequence of the longer migration distances faced by the Central European birds. This fits with the findings of Fourcade et al. (2022) who estimated stopover durations at a fuelling site in south-western France near the Atlantic coast. At their site the body masses were lower than those from study sites located further South on the Iberian Peninsula (Bibby and Green 1980; Goffin et al. 2020), indicating

**Fig. 5** Relationships between non-breeding site longitudinal estimates and laying dates, arrivals to non-breeding grounds and departures from breeding sites



that one additional stopover was needed for fuelling before the barrier crossing. Only a few individuals at the French stopover site had sufficient fuel loads to be able to cross the Sahara without additional refuelling (Fourcade et al. 2022).

### Multi-population assessment

By collating available geolocator tracks from 76 individuals from five populations in Europe, we provide a comprehensive overview of the locations of African non-breeding residency sites and the timing of autumn migration for individual European Pied Flycatchers. Except for the single Norwegian individual, birds from the other four European breeding populations showed considerable overlap in location estimates at the African non-breeding grounds. Statistically, we could detect longitudinal segregation in two clusters: birds from the UK and Finnish populations overlapped and were west of the second cluster of birds from the

Czech and Dutch populations. There was no evidence of any latitudinal segregation of the populations. However, one has to be careful with the interpretation of latitudinal estimates inferred from light-level geolocators. By default, they have considerable uncertainty, while there are also issues with different calibration approaches, and whether birds from different populations use similar habitats (Lisovski et al. 2012; Lisovski et al. 2018). We failed to find clear support for the role of European breeding locations in the clustering of subsequent African residency areas. Only breeding latitude was very weakly associated with non-breeding site longitude estimates. However, the effect was weaker than in the first study on European Pied Flycatcher tracking by Ouweland et al. (2016). This could be purely a consequence of the sampling effect. Finch et al. (2017) found strong support for a positive link between breeding and non-breeding longitudes but no link between latitudes in several populations of European Rollers (*Coracias garrulus*). In Common Swifts (*Apus*

*apus*) tracked across several European populations, breeding latitudes were positively correlated with non-breeding latitudes, clear evidence for a chain migration pattern (Åkesson et al. 2020). The fact that we failed to find strong support for links in the European Pied Flycatcher might simply reflect the scale of the contemporary study. This is a critical issue in any study on migratory connectivity. In an ideal situation, birds would have to be sampled across the entire species' breeding range.

Migration timing was considerably different among populations. Dutch birds were first in all three phases—departure from breeding sites, Sahara crossing and arrival to African non-breeding grounds—followed by the UK, Czech and Finnish birds, respectively. Interestingly, of all populations, the Finnish birds had the shortest interval of only eight days between the Sahara crossing and arrival to non-breeding grounds. This could indicate that they undertook considerable refuelling prior to the barrier crossing, performing a long endurance flight with arrival close to the African residency sites. The birds could skip refuelling after desert crossing or their stops were very short, below the resolution set for stationary periods in the GeoLight package (given the data quality for detecting short stopovers). Autumn migration ranged from 17 to 85 days and it was similar for Czech, UK and Finnish birds. In contrast, the Dutch birds had the shortest migration of only about 35 days. We also found a negative relationship between breeding site departures and duration of migration, i.e. the later a bird departed the shorter time it was *en route*. This is a similar pattern to Collared Flycatcher (*Ficedula albicollis*) in which later departing individuals migrated at faster speeds towards African residency sites (Briedis et al. 2018a). Very likely, late individuals are trying to catch up with the early ones. Whether such behaviour is innate or the birds adjust it according to seasonal changes in available food resources is unknown. Another interesting finding was that birds residing further west in Africa arrived there later. The effect was much stronger than in the previous study by Ouwehand et al. (2016). In contrast to Ouwehand et al. (2016) we did not confirm the relationship between breeding site departures and non-breeding longitudes. The difference between these two studies is likely attributable to the sampling effect.

Interestingly, we did not find a significant effect of the timing of breeding on the subsequent phases of the annual cycle, even though the phases were positively correlated with each other, a pattern regularly found in other songbirds (e.g. Mitchell et al. 2012; van Wijk et al. 2017; Gow et al. 2019). As we clearly see large differences in the timings of events in the studied populations, we would expect a strong effect of seasonality. However, egg-laying dates were available for only 41 of the 76 tracked individuals. A similar lack of effect on the timing of breeding for subsequent annual cycle events was found in the Collared Flycatcher (Briedis

et al. 2018b). Thus, there must be other factors than just egg-laying that explain the timing of subsequent events. No doubt, there must be a significant role of the photoperiod at the breeding sites that sets the pace for the timing of the circannual rhythms (Gwinner 1996). Briedis et al. (2020) found a strong effect of seasonality shaping the timing of avian annual cycles. Thus, further exploration with a larger number of study sites or experimental translocations would be desirable to explore the role of, for example, site-specific phenology and photoperiod in explaining the variability in the timing of annual cycle events among populations.

In our study, the overall return rate of tagged birds was 9.6%, with males having slightly lower return rates. Unfortunately, for various reasons, we did not have control groups of ringed-only birds at both sites. Our only available data are from a nearby study site with an overall return rate of 12.8%. We know that the true return rate on logger-tagged birds must have been higher, but our study coincided with two seasons of cold and rainy weather at the time of nestlings. In addition, we experienced very high nest mortality due to dormice and marten predation (Adamík and Král 2008). As a result, we often could not catch the adult breeders and control them for geolocators. No matter of this, we have to admit that for these two particular sites we cannot be sure about the tagging effect on return rates. The available published studies report no general tagging effect on return rates (Brlík et al. 2020), and Bell et al. (2017) report no negative effects in British flycatchers. In the Dutch flycatcher population, there was no overall tagging effect, but the type of harness did affect return rates (Ouwehand and Both 2017). Return rates of logger-tracked birds in other populations used in our comparative study were in the range of 4–42% and of the control group in a range of 10–56% (Ouwehand et al. 2016). We think that in our case the loggers did not affect between-population differences in migratory behaviour and the differences found across populations are not related to tags per se. However, this is beyond the scope of our study, and we still know very little for how tagging impacts on behaviour of migratory birds across the years.

With our multi-population assessment, we try to fill a gap by comparing the timing of migration of Western European populations of European Pied Flycatcher. In addition, we show that there is considerable mixing at the African non-breeding grounds of birds from various breeding origins in the western Palaearctic. Across species, various breeding populations seem to frequently mix at African non-breeding sites (Finch et al. 2017). This might have interesting consequences for population dynamics at the breeding grounds as depending on the scale of factors operating at the non-breeding sites they might have (de)synchronising effects. However, with the available tracking studies we could cover only a small part of the populations from the extensive breeding range of the species. This comparative

study only covered western and central Europe and part of Fennoscandia. The species' breeding range extends far into the East (up to 90°E) and there is no tracking study from the European part of Russia and further east to western Siberia. The few ringing recoveries available from the eastern part of the range suggest the general heading during migration is towards the Iberian Peninsula (Spina et al. 2022). Thus, in autumn even birds from the Asian breeding populations pass via Iberia and the western fringe of the Sahara (Chernetsov et al. 2008). From a conservation perspective, this means that the entire population passes through a particular region. Any changes in such bottleneck, that could affect stopover behaviour, for example via fuelling rates, might represent a critical point for different populations (Runge et al. 2014). While the African non-breeding range stretches all the way east to the Central African Republic and the northeastern part of DR Congo, there is not a single recovery connecting these areas to the breeding grounds (Spina et al. 2022). Similarly, all tracked flycatchers so far fill only the western part of the African non-breeding range. We suggest that non-breeding populations further east in central Africa originate from breeding sites at the eastern part of the breeding range. As such, further studies from the eastern part of the breeding range are needed, not only for European Pied Flycatchers but also for a wide range of other species. Furthermore, to get a thorough picture of the patterns of migratory connectivity, we need tracking studies from the African non-breeding sites to find the breeding origins of wintering birds (cf. Blackburn et al. 2017). This may be particularly valuable for the European Pied Flycatcher—a model species for climate change research.

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**Author contributions** The study was conceptualized by PA with input from SH, MB and SB. SB provided resources and with GO did the field work. PA performed statistical analyses, while MB analyzed geolocator data. PA wrote the original draft of the manuscript, and MB wrote part of the methods on geolocation. SH and MB critically edited and revised the manuscript. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data availability** The dataset used in the current study is available in supplementary online materials. Raw geolocator data from the eight Czech birds are available at Zenodo: <https://doi.org/10.5281/zenodo.7434786>.

## Declarations

**Conflict of interest** None.

**Ethics approval** Deployment of geolocators was granted by a ringing licence of the National Museum issued to S. Bureš.

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## Studie 12

Briedis, M., Beran, V., Adamík, P. & Hahn, S. 2020: Integrating light-level geolocation with activity tracking reveals unexpected nocturnal migration patterns of the tawny pipit. *Journal of Avian Biology* 51: e02546.

# JOURNAL OF AVIAN BIOLOGY

## Letter

### Integrating light-level geolocation with activity tracking reveals unexpected nocturnal migration patterns of the tawny pipit

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Migratory birds complete their seasonal journeys between breeding and non-breeding sites with a series of migratory flights that are separated by prolonged stopovers. While songbirds are the most common taxa among migratory birds, empirical data on flight and stopover behaviour along their entire migratory journeys are still rare. Here, we integrate activity and barometric pressure tracking with classical light-level geolocation to describe migration behaviour of tawny pipits *Anthus campestris* breeding in central Europe. Surprisingly, tracked pipits used, on average, as many as 10 stopover sites during their six week, > 5000 km long autumn migration. This conforms to a typical hop-type pattern of migration. In contrast to common knowledge which considers the tawny pipit as a typical diurnal migrant, our data revealed that more than two thirds of all migratory movements were carried out at night. Nocturnal departure times were highly variable within individuals and spread across the entire night while landing most often took place within the first few hours after sunrise. Consequently, there was a negative relationship between departure timing relative to sunset and flight duration. Short flights of up to 2 h were most common and median flight duration was 4.5 h. There was a hyperbolic relationship between flight duration and maximum flight altitude and flight altitudes during night were two times higher compared to daytime. The overall ratio of flight versus stopover duration during migration was on average 1:6.5. This closely matches predictions from theoretical models. We show that multi-sensor tracking has the potential to provide unprecedented details on migratory behaviour of individual birds along their entire migratory journeys, and it also improves the precision of geographical locations derived from light-level geolocators.

Keywords: accelerometer, annual cycle, bird migration, departure, flight performance, nocturnal migrant

#### Introduction

Migratory journeys of birds comprise flight phases when distance is covered through energy consumption, and stopover phases when energy reserves are usually replenished. Piersma (1987) outlined three general travel schemes that are shaped by the



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relationships between fuel loads, stopovers and flight bouts: 1) jump migration that relies on high fuel loads, few long endurance flights and few lengthy stopovers, 2) skip migration with intermediate fuel loads, and several stopovers and flights of intermediate duration and 3) hop migration that is characterized by low fuel loads, frequent and short flight phases and multiple short stopovers. The overall duration of the movement phase of migration (between the first departure and arrival at the final destination) is directly dependent on the travel scheme employed as fuel load upon the initial departure will determine how far the bird can fly on its first flight phase (Lindström et al. 2019). In small and medium sized passerines, theoretical models predict that the total duration of migration is divided between flight and stopover phases at a ratio of 1:7, with disproportionately more time spent on stopovers, which include the initial fuelling before first migratory flight (Hedenström and Ålerstam 1997). Despite passerines being by far the most numerous taxon among migratory birds (Hahn et al. 2009), empirical data to support these theoretical predictions still remain limited.

Because most time of migration is spent on stopovers for refuelling, fuel deposition rate largely underpins the total migration duration (Lindström et al. 2019). Most passerines, however, do not feed at night, hence using nighttime for migratory flights do not interfere with fuelling and can potentially reduce the total migration duration. As the current knowledge on Afro-Paleartic migrants suggest, 63% of species are assumed to migrate during the night (nocturnal migrants), while only a handful of species – 16%, mainly aerial foragers, are assumed to migrate during daytime (diurnal migrants; Dorka 1966, Adamík et al. 2016). The remaining pool of species are thought to exercise a mixed strategy. However, it is to be pointed out that the distinction between nocturnal and diurnal migrants is not always unequivocal and many species that predominantly migrate at, e.g. daytime, have also been recorded to migrate during the night or vice versa (Hansen 1954, Adamík et al. 2016). Under what exact circumstances this happens, remains largely unknown.

The majority of nocturnal migrants are known to depart within the first few hours after the sunset (Liechti et al. 1997, Bulyuk and Tsvey 2006, Schmaljohann et al. 2011). This allows for compass calibration at twilight for orientation (Moore 1987, Muheim et al. 2006) and for longer nocturnal flights when larger distances can be covered. Landing typically occurs around sunrise (Bruderer and Liechti 1999) giving a maximum nocturnal flight duration of ca 12 h during autumn migration in the Northern hemisphere in September and ca 10 h during spring migration in April (Bauchinger and Klaassen 2005). There is, however, a considerable spectrum in both departure and landing times relative to sunset/sunrise among individuals (Bolshakov et al. 2007, Schmaljohann et al. 2013) which can vary seasonally (Bolshakov et al. 2007). Much of our current understanding about nocturnal departure and landing times of migrants comes from studies conducted at a single location along the migration route (Bolshakov and Rezvyi 1998, Bolshakov et al. 2003) or at ecological barriers where long flight duration

with early nocturnal onset may be the prevailing pattern (Adamík et al. 2016, Ouweland and Both 2016, Jiguet et al. 2019). Similarly, many of these studies have been conducted using radar observations (Schmaljohann et al. 2007), which does not allow for distinguishing species-specific behaviours, as species identification in radar signals remains a challenging issue (Bauer et al. 2019). As a result, studies done so far provide only snapshots at specific points in time and space, and we are still missing information on departure and landing behaviour of individual birds along their full migration cycles.

State-of-the-art multi-sensor tracking devices that integrate measurements of ambient light, activity and barometric pressure have the potential to bridge this gap in our knowledge and to provide novel insights into species- and individual-specific migratory behaviour along their entire migratory journeys (Bäckman et al. 2017a, b, Dhanjal-Adams et al. 2018, Liechti et al. 2018, Sjöberg et al. 2018). Here we use multi-sensor individual tracking to describe migratory patterns and flight behaviour over the entire journey of tawny pipits *Anthus campestris* breeding in Central Europe. The tawny pipit is among the few Afro-Paleartic migratory species that are characterized as a ‘typical diurnal migrant’ (Dorka 1966, Ålerstam 1990, Schmaljohann 2019), however, conclusive evidence is still missing. We employ novel analytical tools to test this long-standing assumption with a particular focus on describing flight and stopover behaviour and take-off and landing times of pipits in relation to sunset/sunrise throughout the migration journey. Furthermore, we integrate classical light-level geolocation with activity and barometric pressure measurements allowing for more detailed and precise estimates of migration timing and geographic positions of stationary sites and migration routes.

## Methods

### Field work

We studied tawny pipits breeding in open lignite mines in western Czech Republic (50.5°N, 13.83°E). During the breeding season in 2018, we captured 13 adult birds using mist-nets and perch traps and equipped them with multi-sensor geolocators (GDL3-PAM, Swiss Ornithological Inst.; Liechti et al. 2018) that were mounted on the birds’ backs using flexible silicone harness. The loggers accommodated sensors for measuring ambient light intensity, atmospheric pressure and acceleration. The light sensor was equipped with a 7 mm long light guide and light intensity was measured every minute storing maximum values in 5 min intervals. Acceleration was measured along the Z-axis for 3.2 s at 10 Hz frequency every 5 min storing the sum of the absolute differences between consecutive measures (31 values). Atmospheric pressure recordings were set to 30 min intervals.

In 2019, we successfully recaptured and retrieved geolocators from 5 of the 13 previously tagged individuals. One more bird was seen in the study area, but we failed to recapture it,

amounting the total return rate to 46%. One of the retrieved geolocators contained data encompassing the full annual cycle. Two devices stopped recording during spring migration before the birds had returned to the breeding area and two more devices stopped recording while the birds were still in their non-breeding residency sites in sub-Saharan Africa.

## Data analyses

Geocator data analyses were carried out using the R-packages ‘TwGeos’ (Lisovski et al. 2015), ‘SGAT’ (Wotherspoon et al. 2013) and ‘PAMLR’ (Dhanjal-Adams et al. 2020). Location data were analysed using a threshold approach following general guidelines described in Lisovski et al. (2020) and integrating activity and atmospheric pressure recordings for more precise designation of migration timing, i.e. movement and stationary phases (flight, migratory stopovers and long residency periods).

For distinguishing between movement and stationary phases during the annual cycle, we used accelerometer and atmospheric pressure recordings. Because tawny pipits use flapping flight for migration, we used the flapping flight classification from the R-package ‘PAMLR’ and set the threshold to 1 h (equals to 12 consecutive readings of flapping activity at 5 min recording intervals) to classify migratory flights. Thus, activity measures that were classified as flapping and lasted for at least 1 h were regarded as migration episodes. A visual inspection of the atmospheric pressure readings revealed that some migratory flights when individuals clearly changed their location were, however, missed. Therefore, we performed a second classification based on atmospheric pressure recordings and cross-validated the two approaches. Atmospheric pressure is not expected to change rapidly when the bird is stationary (weather related changes) but can vary considerably as the bird takes altitude or covers substantial distance in flight (Liechti et al. 2018, Sjöberg et al. 2018). Because background variation in air pressure linked to weather rarely exceeded  $1 \text{ hPa } 30 \text{ min}^{-1}$ , we used a threshold of atmospheric pressure change  $> 1.5 \text{ hPa } 30 \text{ min}^{-1}$  for identifying flight phases within the dataset. This approach allowed for identification of start times of migratory flights and their length with an accuracy of 30 min. If the bird was stationary for at least 24 h, we considered this a stopover. To derive geographic positions, we first log-transformed the recorded light values and derived sunrise and sunset times in the R-package ‘TwGeos’ using a light intensity threshold of 1 unit on the log-transformed scale. Recorded twilight times were then calibrated against the actual sunrise and sunset times at the breeding sites of the birds prior to the start of the autumn migration (i.e. in-habitat calibration; Lisovski and Hahn 2012). Further, we used the R-package ‘SGAT’ to model the most likely migration path, stopover and residency locations along with their confidence intervals. For this, we used a grouped Estelle model where location estimates coming from the same site (based on acceleration and pressure classification) were grouped together. This procedure increases the overall accuracy of the stationary positions (Lisovski et al.

2020). We applied a spatial mask that confined stationary sites to terrestrial habitats only while movement was allowed to cross over oceans and seas. The twilight error distribution was assumed to follow Gamma distribution as based on the parameters inferred from the in-habitat calibration. The final model also included a movement model – birds were allowed to move only when preceding activity and pressure analyses had detected migratory flights and movement duration was restricted to the duration of migratory flight hours at the specific day (dt parameter in the ‘groupedThresholdModel’ function). Speed distribution for the movement model followed a Gaussian distribution (shape=30, scale=0.6) with the highest probability of ground speeds between 40 and 60  $\text{km h}^{-1}$  during the movement phase. The start of all tracks and the end of the single complete track were fixed to the known tagging/breeding location. To initiate the model, we first ran a ‘modifiedGamma’ model with relaxed assumptions for 1000 iterations. Then the resulting model was tuned five times (300 iterations each) with all assumptions/priors (‘Gamma’ model) before initiating the final run with 2000 iterations to ensure convergence. We present the most likely migration tracks and stationary locations as inferred from median location estimates along with 95% probability distributions of location estimates.

We calculated the ratio between the duration of flight and stopover phases as the total number of flight hours versus the total number of stationary hours between the initial departure flight and final arrival flight. Thus, our estimates do not include the initial fuelling before departure (Hedenström and Ålerstam 1997). Departure (i.e. take-off) and landing times were compared to sunset and sunrise times as derived from the data recorded by the geolocators light-sensor. In-habitat calibration revealed that sensitivity of the light-sensors was on average higher than Sun’s azimuth of  $0^\circ$  relative to the horizon (actual sunrise/sunset) at  $-4.8^\circ \pm 0.5$  (mean  $\pm$  SD). Thus, the migratory flight timing here is expressed relative to the approximate start of civil twilight (centre of the Sun  $6^\circ$  below the horizon) rather than sunrise/sunset when the centre of the Sun is at  $0^\circ$  relative to the horizon.

Maximum flight altitude (measured in m above sea level, m asl) during each flight was calculated applying the hypsometric equation to the atmospheric pressure measurements assuming standard atmospheric conditions (Stull 2016, Liechti et al. 2018). We compared flight altitudes during diurnal and nocturnal migratory phases using linear mixed effects model accounting for random effects of individual identity in R-package lme4 (Bates et al. 2014). The precision of altitude estimates of the used loggers is described in Liechti et al. (2018); rarely under extraordinary atmospheric conditions it can exceed 200 m (approx. 25 hPa).

## Results

Throughout the year, the start and end of the daily activity patterns coincided with sunrise and sunset times as recorded

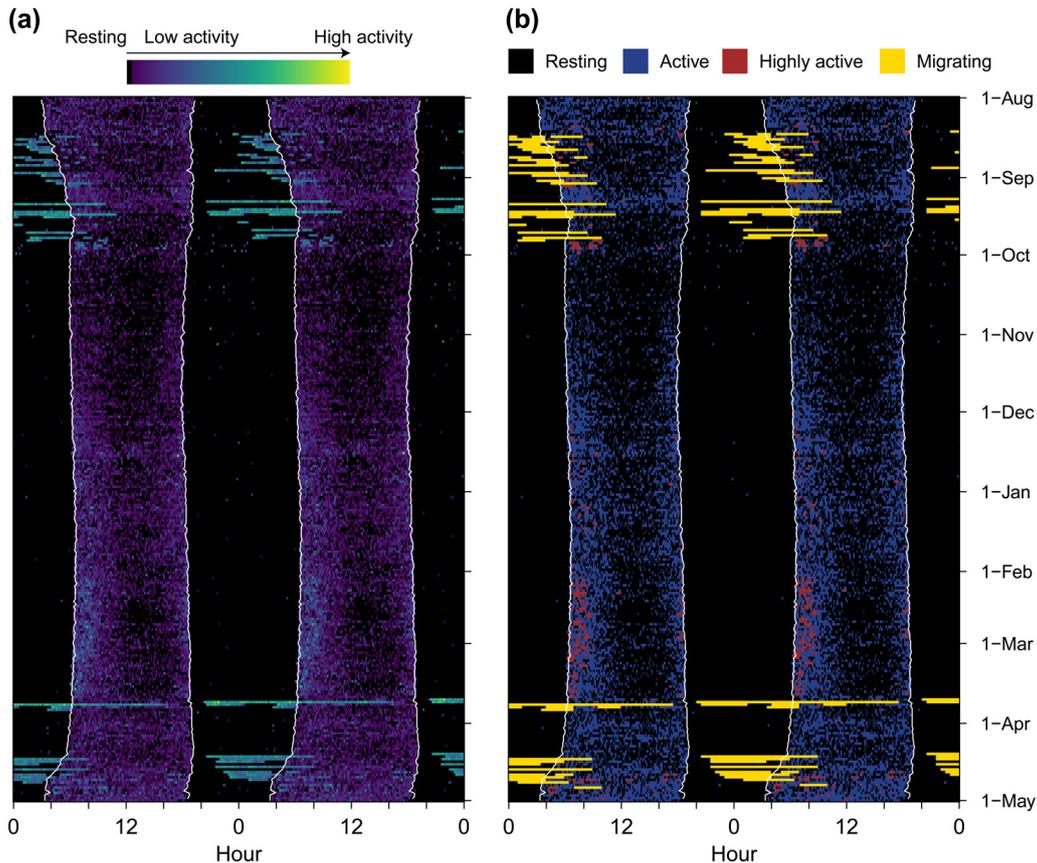


Figure 1. Actograms showing the annual activity pattern of a tawny pipit (bird ID: 22BK) from 1 Aug 2018 until 1 May 2019. (a) Raw accelerometer measures, (b) activity data classified into 4 categories – resting, active, highly active and migrating. In both panels, each horizontal line represents the activity data of two consecutive days, where the second day is repeated as the first day on the next line. White lines in the actograms represents sunrise and sunset times as recorded by the geolocator’s light sensor.

by the geolocators light sensor in such a manner that the tracked birds were immobile (resting or sleeping) during the dark hours of the night. The only exception to this was migratory flights, most of which took place at night. Actogram summarizing annual activity patterns of the individual 22BK, the single individual with a full annual track, is shown in Fig. 1, actograms of the remaining four individuals are given in the Supplementary information. Pipits were often most active during the early morning hours after sunrise and in the evening a few hours before sunset (Fig. 1, Supplementary information). The time period in the middle of the day was often spent resting/sleeping.

### Migration timing, distance, stopovers

In autumn, all birds migrated along the western flyway to their non-breeding sites in West Africa (Fig. 2; see Supplementary information for comparison of location estimates, their CIs, and migration timing estimates when using classical light-level geolocation where data analyses are performed using only the light data). Migration started in the second half of August and birds arrived in sub-Saharan Africa

about six weeks later (average migration duration = 43 d) in late September–early October. A summary of autumn migration parameters for each individual is given in Table 1. Two birds (20NT and 22BN) spent long periods (> 40 d in total) at multiple intermediate stopover/non-breeding sites in sub-Saharan Africa before they arrived at their final non-breeding residency site in the second half of November – these movements were not considered as part of the autumn migration. Overall, during the autumn migration, tracked pipits used on average 10 different stopover sites where birds stopped for at least 24 h. Longer stopovers of more than 3 d, however, were scarce, averaging at 3.2 per individual. Interestingly, the ratio of flight to stationary days during the movement phase of autumn migration (from departure until arrival) was on average 1:1 (21.4 flight days versus 21 stationary days; Table 1). From the total migration duration (measured in hours), the proportion of time spent in migratory flight was 13.3% while the remaining 86.7% of time was spent on stopovers, which includes all stops of any length. Thus, the ratio of flight versus stopover duration was on average 1:6.5. Pipits on average migrated more than 5000 km reaching an average travel speed of 125 km day<sup>-1</sup>.

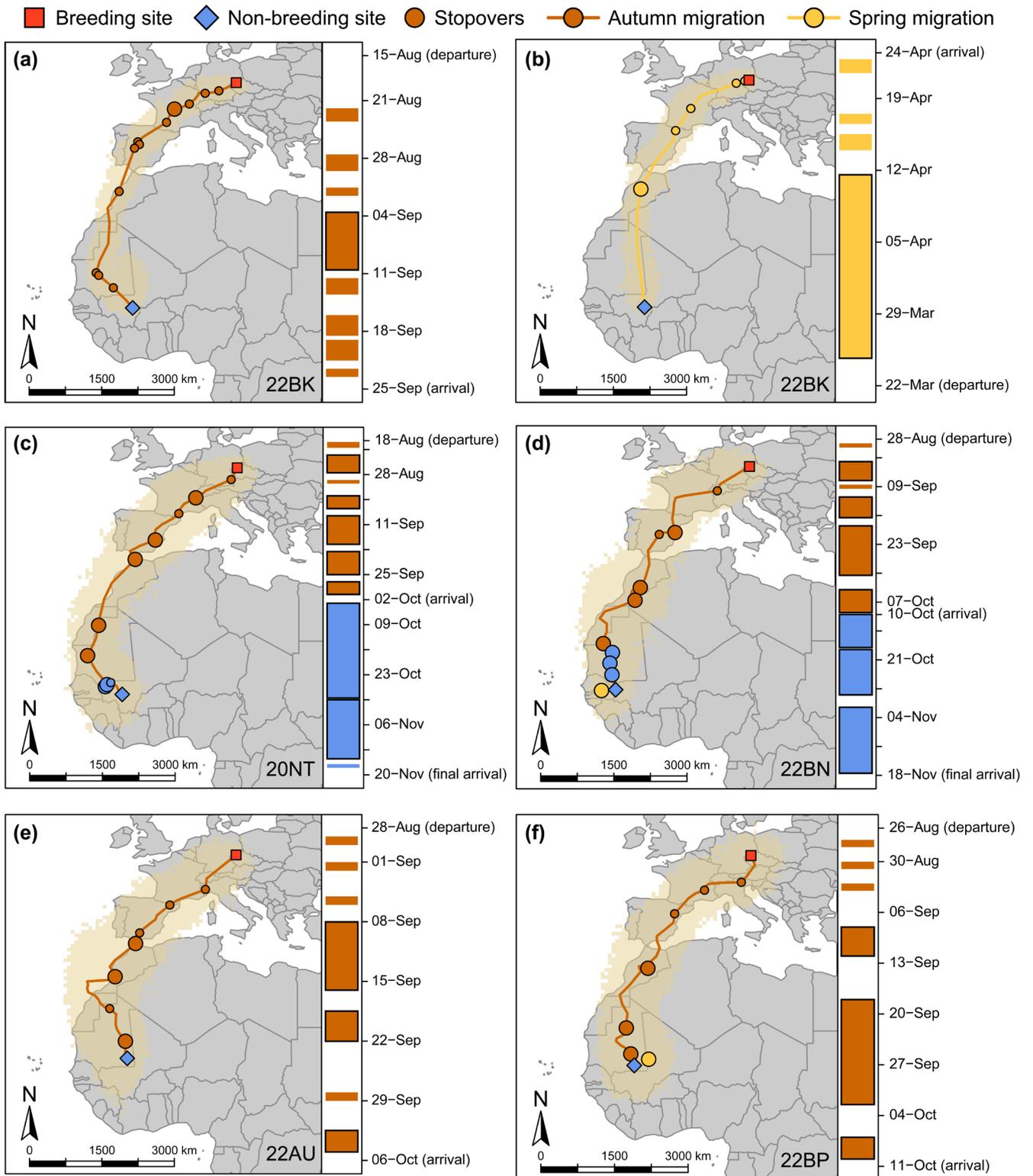


Figure 2. Migration routes, stopovers and non-breeding sites of five geolocator-tracked tawny pipits. Shaded areas show 95% probability distributions of location estimates. For each bird, timing and duration of migration is shown alongside the map where coloured bars indicate stopovers longer than 24 h (stopovers longer than 3 days are marked with black borders) and white spaces between them indicate movement periods between the stopovers. Please note that bars indicating migration timing have variable scales. Panels a and b represent autumn and spring migration of the same individual. Intermediate non-breeding sites are marked in blue for the two birds that showed non-breeding site itinerancy (panels c and d).

Table 1. Summary data for each bird. Note that departure date is always given as the date of the evening of the night when the first migratory flight occurred. Arrival is given as the date of the morning when the last migratory movement occurred. Total duration, however, is given as the number of days (rounded to full days) between the precise time of departure and arrival, thus in some instances creating a discrepancy in the numbers given in the table and the absolute difference in days between departure date and arrival date.

	Autumn					Average	Spring
	22BK	20NT	22AU	22BN	22BP		22BK
<b>Migration characteristics</b>							
Departure	15-Aug	18-Aug	28-Aug	28-Aug	26-Aug	23-Aug	22-Mar
Arrival	25-Sep	2-Oct	6-Oct	10-Oct	11-Oct	5-Oct	24-Apr
Total duration (days)	40	45	39	42	46	43	33
Migratory track distance (km)	5440	5290	5340	4890	5370	5266	4810
Great circle distance (km)	4480	4740	4390	4410	4450	4494	4480
Travel speed (km day <sup>-1</sup> )	136	118	137	116	117	125	146
Travel speed great circle distance (km day <sup>-1</sup> )	112	105	113	105	97	106	136
No. flight days	26	19	22	17	23	21	13
No. stopover days	14	26	17	25	23	21	20
No. stopovers	12	10	11	7	9	10	5
No. stopovers (>3 days)	1	5	3	4	3	3.2	1
Proportion in flight	13.1%	12.3%	15.8%	11.9%	13.3%	13.3%	12.2%
Proportion stationary	86.9%	87.7%	84.2%	88.1%	86.7%	86.7%	87.8%
<b>Flight characteristics</b>							
No. flights	27	25	25	19	23	23.8	15
Median flight duration (hh:mm)	3:30	3:00	5:30	6:00	4:30	4:30	5:00
Cumulative flight hours (hh:mm)	126:30	132	146	121	144:30	134	95:30
Longest flight (hh:mm)	14:30	20:00	16:00	11:30	20:30	16:30	21:00
Proportion of migratory flight at night	75.4%	64.2%	73.7%	75.7%	54.2%	68.6%	70.4%
Flight speed along migratory track (km h <sup>-1</sup> )	43	40.1	36.6	40.4	37.2	39.5	51.6
Maximum flight altitude (m asl)	3159	2611	2978	3182	2912	2968	3662

## Flight performance

Tracked pipits completed their autumn migration with an average of 23.8 individual flights. The total number of flight hours ranged between 121 and 146 h for the five individuals (Fig. 3). During barrier crossing, flights were prolonged into the day lasting on average  $14 \pm 3.8$  h (SD;  $n=11$  from a total of 132 tracked flights) and up to 20 h for two of the five tracked individuals (Table 1). Average ground speed along the most likely migration track (orange lines in Fig. 2) was estimated at  $39.5$  km h<sup>-1</sup> (Table 1).

Pipits predominantly travelled during the night (on average 68.6% of all migratory movements; Table 1). Time of nocturnal departures were spread across the entire night with an average departure time  $4:25 \pm 5:17$  h (SD,  $n=132$ ) after the sunset (Fig. 4a). Longer flights (including Sahara crossing flights) typically started shortly before or after sunset and there was a general decline in flight duration with increasingly later nocturnal departure times (Fig. 4c).

Landing most often occurred around sunrise (average landing time relative to sunrise:  $0:45 \pm 3:41$  h (SD),  $n=132$ , Fig. 4b). Median migratory flight duration across all five birds

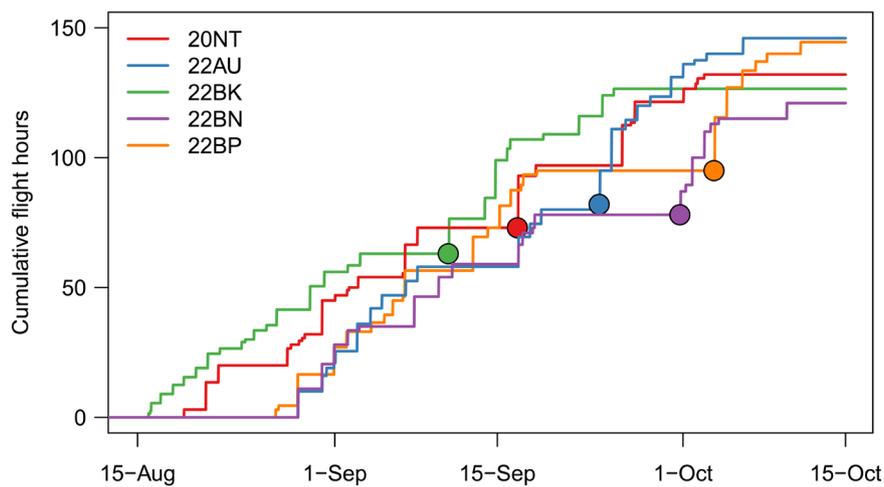


Figure 3. Cumulative flight hours of five tawny pipits during the autumn migration between 15 Aug and 15 Oct 2018. Start of Sahara crossing for each bird is indicated with a dot.

was 4:30 h (Table 1) and short flights of up to 2 hours were the most common accounting for 30% of all recorded flights (40/132; Fig. 4d). Maximum flight altitudes ranged between 2600 and 3200 m a.s.l. for different individuals and there was a positive hyperbolic relationship between individual flight duration and the maximum altitude reached (Table 1, Fig. 5). Flight altitudes during night were higher compared to daytime (night:  $1090 \pm 728$  m a.s.l. (SD); daytime:  $498 \pm 428$  m a.s.l.;  $\beta = 590 \pm 38$ ,  $t = 15.7$ , random effects variance: bird identity 2417 (49.2 SD)).

### Spring migration

The departure date for spring migration could only be estimated for three birds which showed a variation of more than one month: 22BP=18 Feb, 22BN=12 Mar, 22BK=22 Mar. Loggers 22BP and 22BN stopped recording shortly

after the birds departed while 22BK recorded until the bird arrived at the breeding site on 24 Apr. Spring migration of this individual started with a 21 h long non-stop flight across the Sahara and compared to autumn migration spring migration was overall shorter (both in distance – 11.6%, and duration – 17.5%), the migration speed was higher (7.4%), the total number of flight hours was lower (24.5%), while the maximum flight altitude reached was 500 m higher (3662 m a.s.l.) (see Table 1 for all migration parameters).

### Discussion

Our results of activity and barometric pressure tracking revealed that tawny pipits predominantly migrate at night contradicting the earlier notion of the species as a typical diurnal migrant (Dorka 1966, Alerstam 1990, Schmaljohann

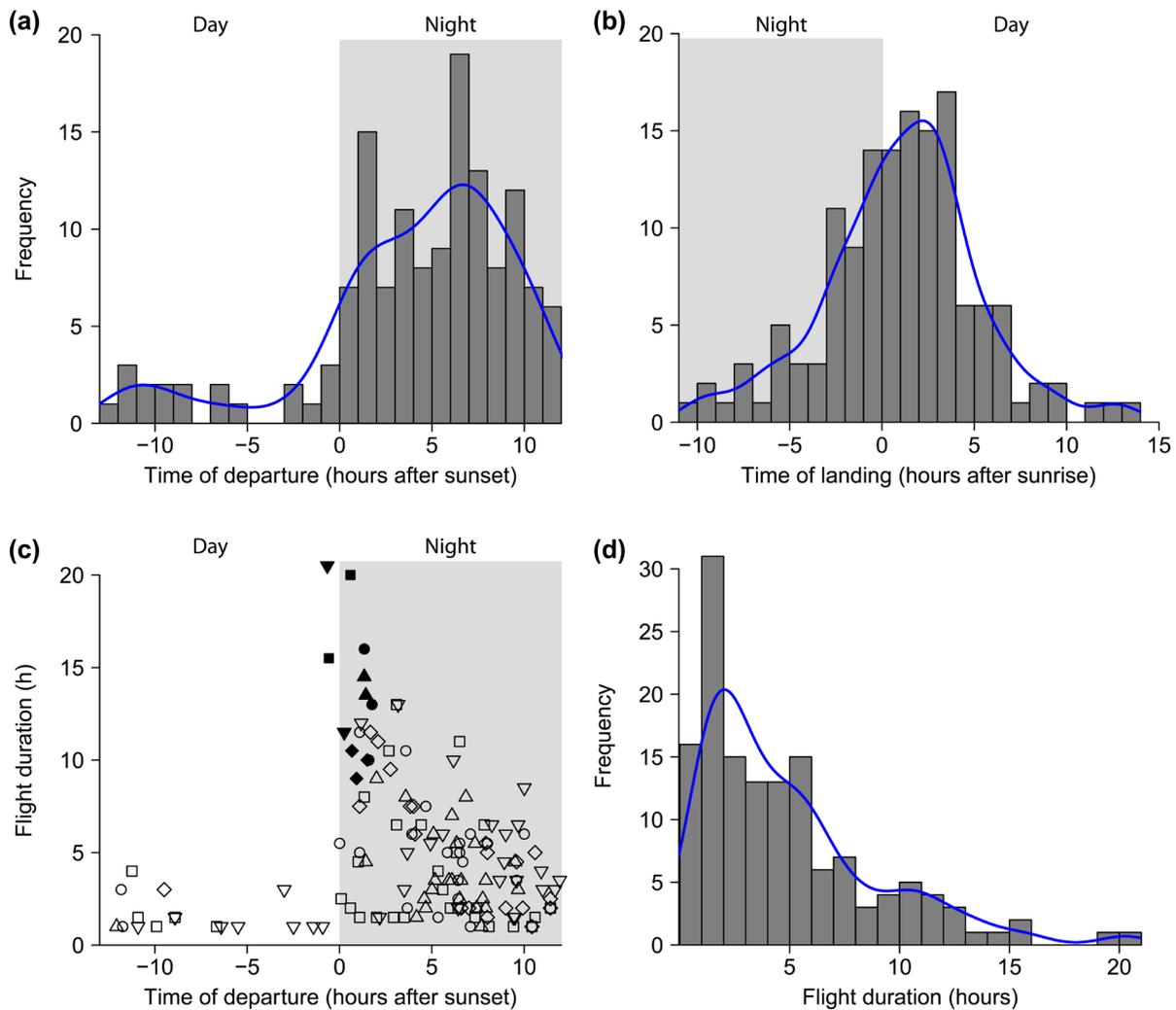


Figure 4. Characteristics of migratory flights of tawny pipits. (a) Frequency distribution of departure time relative to sunset, (b) landing time relative to sunrise, (c) relationship between flight duration and departure time relative to sunset (different symbols denote different individuals (legend as in Fig. 5), filled symbols denote barrier crossing flights), (d) frequency distribution of flight duration. Blue lines in panels a, b and d are estimated frequency density curves. Note that sunrise and sunset times here are derived from geolocators' light recordings and approximately correspond to a sun's azimuth of  $-4.8^\circ$  (see Methods).

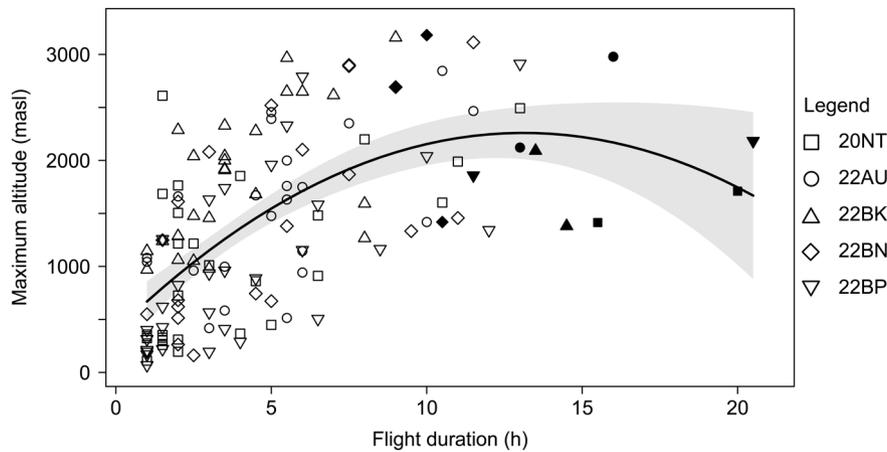


Figure 5. Relationship between flight duration and the maximum altitude during autumn migration. Different symbols denote different individuals, filled symbol indicate Sahara crossing flights. Quadratic model fit is depicted by a solid line with 95% CI (shaded area).

2019). We found that landing most often occurred within the first four hours after sunrise, which could explain the earlier observation-based assumption of diurnal migration by tawny pipits. Similarly, barrier crossing flights over the Sahara often stretched into the daytime as shown in other long-distance migrants (Schmaljohann et al. 2007, Adamík et al. 2016, Ouweland and Both 2016, Jiguet et al. 2019). Departure times of migratory flights were spread across the night, contrasting the commonly shown pattern of departures being clustered shortly after sunset (Kerlinger and Moore 1989, Liechti et al. 1997, Bruderer and Liechti 1999, Bolshakov et al. 2003). Departure times relative to sunset were highly variable within and across individuals during the migration season. Thus, it is likely that environmental settings and individual body condition, rather than an inherent circadian clock, are the main drivers of departure time (cf. Bulyuk and Tsvey 2006, Müller et al. 2016).

During migration, tawny pipits employed a hop migration pattern with numerous short flights and stopovers (Piersma 1987). Our conclusion of the pipits conforming to a hop migration is clearly dependent on the high temporal resolution of our data making it possible to identify 24–72 h long stopovers. The number of longer stopovers (> 3 d) varied from 1 to 5 between different individuals and in many cases prolonged stopovers were associated with Sahara crossing which was completed with long endurance flights (Fig. 2, 3). Such co-occurrence is likely attributed to prolonged fuelling to build energy stores necessary for crossing ecological barriers (Schaub and Jenni 2000, Fransson et al. 2006). The ratio between the duration of flight and stopover phases was on average 1:6.5 which is slightly lower than the predicted ratio of 1:7 based on theoretical models (Hedenström and Ålerstam 1997). However, our estimates of the total stopover duration did not include the fuelling period before the initial departure for migration (Lindström et al. 2019). It is likely that with this period included, the ratio of flight versus stopovers would match the theoretical predictions (Hedenström and Ålerstam 1997).

Overall, exercising a hop migration pattern may have energetic benefits for individuals. Birds can save energy on reduced transport costs if they migrate in short flight steps and low fuel levels (Ålerstam 2001). Consequently, birds need to spend less time on stopovers refuelling and reduction in total energy requirements will also enable to reduce the total duration of migration. Such migration strategy is, however, possible only if resources along the migration routes are widespread and settling costs at new stopover sites are small. The observed difference in flight altitudes between night and day may suggest that birds employ a fly-and-search migration when prolonging the flight into the day. Flight of short duration and diurnal flights were most commonly carried out at altitudes below 500 m asl which may allow the birds to search for favourable landing sites where food for refuelling may be found. This may also explain why pipits prefer late night/early morning flights where new stopover sites may be visually located after sunrise. Thus, hop migration may be inevitably linked with fly-and-search migration strategy and hence, late night departure times and landing times after sunrise.

Our estimates of the average ground speed of  $39.5 \text{ km h}^{-1}$  along the most likely migration track is slightly lower than the ground speed measurements of ca  $50 \text{ km h}^{-1}$  for passerines obtained using tracking-radar (Bruderer and Boldt 2001). Such discrepancy is not surprising, because geolocators provide positions only twice per day and the migration path between them is smoothed. Therefore, with a positional frequency averaging at 12 h intervals, we cannot account for small in-flight detours of the birds when estimating ground speed. Consequently, both ground speed and travel speed (average of  $125 \text{ km day}^{-1}$ ) are likely underestimated.

Tawny pipits' migration routes via the Iberian Peninsula and non-breeding sites in the Sahel zone in West Africa were largely similar to an earlier tracking study of this population (Briedis et al. 2016). Integration of activity and barometric pressure tracking into the classical light-level geolocation, however, opens a new avenue in the details we can reveal

about migration patterns. This includes a detailed description of the seasonal flight and stopover behaviour as well as their interrelationship which can then be tested against theoretical predictions for different migratory strategies. Developing algorithms that can translate activity recordings into daily, seasonal and year-round energy budgets have the potential to further our understanding on the linkages between particular evolutionary and behavioural strategies we observe in the wild and their energetics.

## Transparent Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/jav.02546>

## Data availability statement

The bird tracking dataset is available from Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.fbg79cnsd>> (Briedis et al. 2020) and available upon request from the Movebank online database (<https://www.movebank.org/>, project ID: 1210376764).

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*Authors' contributions* – MB, PA and SH conceived the idea and study design; VB carried out fieldwork; MB performed data analyses and drafted the manuscript with inputs from all other authors.

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Supplementary information (available online as Appendix jav-02546 at <[www.avianbiology.org/appendix/jav-02546](http://www.avianbiology.org/appendix/jav-02546)>).

## Studie 13

Adamík, P., Wong, J. B., Hahn, S. & Krištín, A. 2024: Non-breeding sites, loop migration and flight activity patterns over the annual cycle in the Lesser Grey Shrike *Lanius minor* from a north-western edge of its range. *Journal of Ornithology* 165: 247–256.



# Non-breeding sites, loop migration and flight activity patterns over the annual cycle in the Lesser Grey Shrike *Lanius minor* from a north-western edge of its range

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## Abstract

The Lesser Grey Shrike is a typical Palaearctic songbird for which we have limited knowledge of its migration ecology. All that is known about its non-breeding movements is inferred from observational data of birds on passage. The few available ring recovery data do not link breeding and African non-breeding grounds. By deploying two types of loggers, light-level geolocators and multi-sensor loggers, on birds from a declining Slovak breeding population, we present the first direct evidence for non-breeding grounds, loop migration, stopover sites and the timing of annual cycle events. With barometric data, we provide details on flight altitudes during migration. The two tracked birds migrated in a clear anti-clockwise loop to S Africa. Autumn migration tracks went through the Balkan Peninsula, Mediterranean Sea towards Libya with unusually long stays around N Chad and Niger. The next stopovers were in Angola, and the main non-breeding sites were in Botswana. Spring migration commenced on March 29 and April 7 and the birds took routes along East African countries, with stopovers later in Somalia and Saudi Arabia, before crossing the eastern Mediterranean Sea. Nocturnal migration dominated, but for three days in August, while crossing the Sahara Desert, the bird extended flights into the day with a sudden increase in flight altitudes at dawn. Flight altitudes were higher during barrier crossing and during the last phase of spring migration compared to the remaining periods, with the most extreme event recorded at 4530 m asl.

**Keywords** Passerines · Non-breeding grounds · Flight altitude · Long-distance migration · Behaviour

## Zusammenfassung

**Nichtbrutgebiete, Schleifenzug und Aktivitätsmuster im Jahreszyklus bei Schwarzstirnwürgern *Lanius minor* vom nordwestlichen Rand seines Verbreitungsgebietes**

Der Schwarzstirnwürger ist eine der paläarktischer Singvogelarten, für die nur begrenzte Kenntnisse der Zugökologie vorliegen. Alle Informationen zu Bewegungen außerhalb der Brutzeit stammen von Beobachtungsdaten durchziehender Vögel. Die wenigen verfügbaren Ringwiederfunde erlauben keine Verbindungen zwischen Brut- und Überwinterungsplätzen. Wir präsentieren hier den ersten direkten Nachweis des Schleifenzuges, die zeitliche Abfolge der Ereignisse im Jahreszyklus, sowie die Rast- und Überwinterungsgebiete von Schwarzstirnwürgern einer abnehmenden, slowakischen Brutpopulation basierend auf Licht- und Multisensor-Loggerdaten. Barometrische Daten liefern zudem detaillierte Angaben zu individuellen

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Flughöhen während des Zuges. Die beiden getrackten Vögel zogen in einer klaren Schleife gegen den Uhrzeigersinn nach Südafrika. Der Herbstzug führte über die Balkanhalbinsel und das Mittelmeer nach Libyen, gefolgt von unerwartet langen Zwischenstopps im nördlichen Tschad und Niger. Die nächsten Rastgebiete lagen in Angola, die Überwinterungsgebiete in Botswana. Der Frühlingszug begann am 29. März und 7. April. Die Vögel flogen über Ostafrika mit Zwischenstopps in Somalia und in Saudi-Arabien, ehe sie das östliche Mittelmeer überquerten. Nächtliche Flüge dominierten während des Zuges. Bei der Durchquerung der Sahara im August waren jedoch drei der Nachtflüge um mehrere Stunden in den Tag hinein verlängert und wiesen einen plötzlichen Anstieg der Flughöhen während der Morgendämmerung auf. Die Flughöhen während der Barrieren-Überquerung und während der letzten Phase im Frühjahrszug waren zudem höher als in der restlichen Zugzeit, wobei eine maximale Flughöhe mit 4530 m ü. M. erreicht wurde.

## Introduction

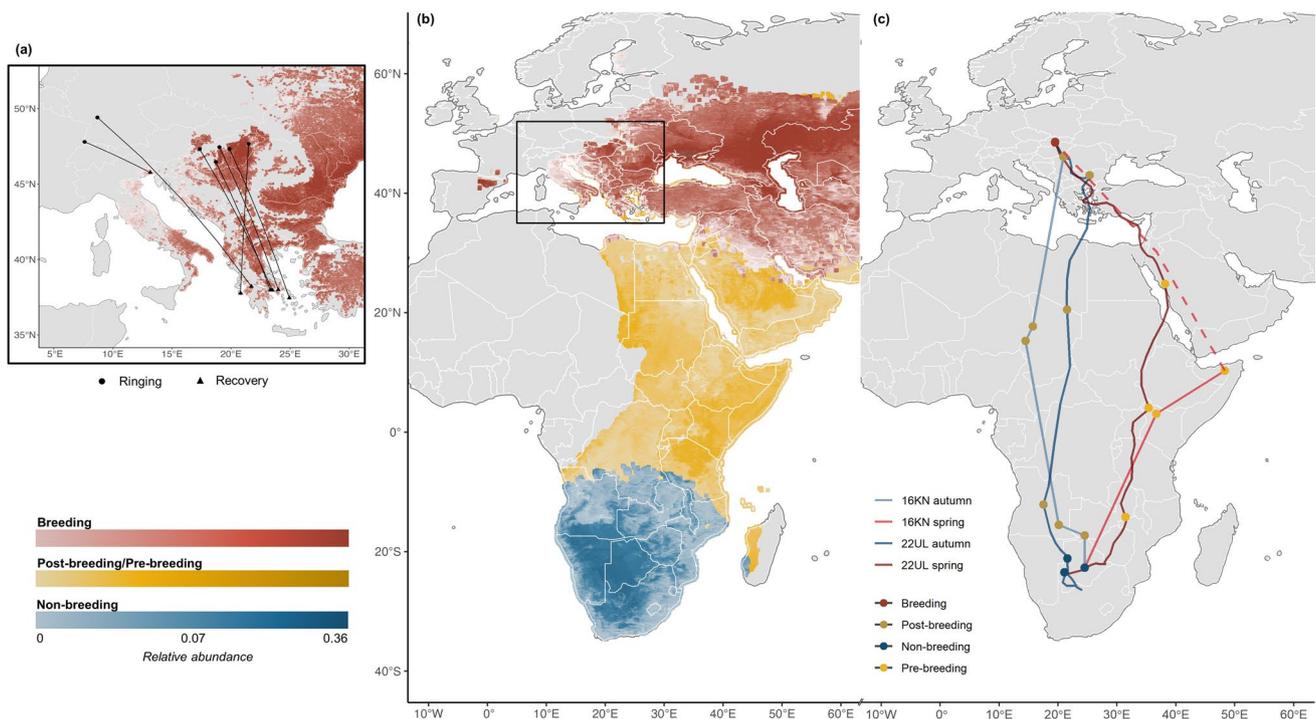
The Lesser Grey Shrike has a considerable breeding range spanning from NE Spain in the West, the Pannonian basin and the eastern Europe to Altai in the East, but unusually, its non-breeding range funnels in Southern Africa to a relatively small area (Lefranc and Worfolk 1997). Its populations at the western edge of its distributional range underwent substantial declines and area shrinkages, and decreasing numbers are also reported at the African non-breeding grounds (Herremans 1998; Bronskov and Keller 2020; PECMBS 2022). At the same time, we have very limited knowledge on the migration and overwintering ecology of the species. All available information on migration is inferred from bird observations. Earlier authors proposed an anticlockwise loop migration pattern, where in spring most birds use the Arabian Peninsula and Anatolia when heading towards the breeding sites (Stresemann 1943; Moreau 1961; Dowsett 1971; Lefranc and Worfolk 1997). This migration pattern is clearly visible in seasonal observation maps generated by bird observations submitted to the eBird database (Fink et al. 2022; Fig. 1b). To date, there is only a single observation linking breeding and non-breeding grounds (Krištín 2008). To fill parts of this gap, we analysed available ring recovery data and deployed two types of loggers (light-level geolocators and multi-sensor loggers) on shrikes in a breeding population at the North-western edge of its distributional range. We aimed at identifying for the first time individual-based migration tracks, locations of stopover sites and non-breeding sites of Lesser Grey Shrikes.

## Material and methods

We studied Lesser Grey Shrikes at the foothills of Poľana Mts., Central Slovakia (48.5909N, 19.5161E as a centre of study area, 460–750 m asl). Here, this declining and endangered species breeds in a traditionally cultivated rural landscape; c.f. Krištín et al. (2000, 2007), still with a local population size of 30–35 nests/20 km<sup>2</sup> in 2017–2022 (own unpublished data). Adult shrikes were trapped within their breeding territories with clap nets (baited with crickets or larvae of *Zophobas*) during the spring of 2017 and 2019.

All trapped birds were marked with aluminium rings and an individual combination of two colour rings. In 2017, we equipped 10 birds (8 males and 2 females) with GDL3-PAM multi-sensor loggers (Swiss Ornithological Institute, Sempach). In 2019, we equipped another 10 birds (6 males and 4 females) with uTags (Swiss Ornithological Institute, Sempach). Loggers were attached using a leg-loop backpack harness (1 mm thick braided nylon string). The mean weight of the GDL3-PAM logger was 1.35 g and for the uTags 1.90 g. The mean male body mass was  $44.6 \pm 2.4$  g (range 39.6–48.6 g), and the female body mass was  $49.0 \pm 5.74$  (44.1–52.6 g). In the following years, we detected four birds (males only) with loggers. We retrieved three loggers and one bird we failed to catch. Return rates of logger-tracked birds were 28.6% (4/14) for males and 0% (0/6) for females. As the population is very small and declining, we did not have return rates on ringed-only birds during the period of this study. However, return rates were 40% for males and 25.2% for females during 1996–2000 (Krištín et al. 2007). The two loggers contained data for the full year, while the third logger stopped working after two months. We do not present data on this bird. Raw data on all three birds are available at the Zenodo data repository (Adamík et al. 2023).

To supplement the geolocator data with other available data sources on bird migration, we requested data on ringing recoveries from the EURING and SAFRING. We requested recoveries which fulfilled the condition of > 100 km between the ringing and recovery site. Only EURING had relevant data. This yielded nine encounters but we used only seven as two were of short distance and uninformative about migration (138 and 182 km within France and the UK, respectively, see Online Supplement 1, Table S1). For estimating distances, we used the ‘orthodrom.dist’ function (great circle distance) in the R-package *birdring* (Korner-Nievergelt and Robinson 2014). In addition, we used the eBird relative abundance maps to depict the predicted seasonal distribution of shrikes across the annual cycle (Sullivan et al. 2009; Fink et al. 2022). We used the eBird classification of seasons: breeding Jun 21 –Jul 27, non-breeding Dec 14 –Mar 1, post-breeding Aug 3–Dec 7, pre-breeding Mar 8 –Jun 14. Note that these map layers are modelled data and as such inevitably contain inaccuracies, e.g. they model presence of the species in Madagascar where it does not occur.



**Fig. 1** Comparison of available Lesser Grey Shrike distribution data relative to the data collected in this study. **a** Ringing and recovery sites of Lesser Grey Shrikes connected by great circle distance lines relative to eBird observer data. **b** Modelled relative abundance of Lesser Grey Shrikes per season from eBird (Fink et al. 2022). Abundance is presented as a gradient in red (breeding season), yellow (post-breeding/pre-breeding season) or blue (non-breeding season), and darker colours indicate higher relative abundance and lighter colours indicate lower relative abundance within the season. **c** Estimated migration tracks and stationary sites used by individuals 16KN

(autumn=light blue, spring=light red) and 22UL (autumn=dark blue, spring=dark red) in this study. The track of 16KN was estimated using *GeoPressureR*, and shows the shortest most likely path of the bird. The dashed portion of the track connecting the last pre-breeding stopover site to the breeding site is the great circle distance between the two sites. The track of 22UL was estimated using *SGAT* and shows the median most likely path of the bird. The circles indicate the stationary sites used during each season (red=breeding, dark yellow=post-breeding, blue=non-breeding, light yellow=pre-breeding). Stationary sites were defined as stops  $\geq 48$  h

Light-level data collected from the uTag (bird 22UL) were analyzed using R packages *TwGeos* (Lisovski et al. 2016) and *SGAT* (Wotherspoon et al. 2013) to obtain the most likely geographic positions of the shrike. We followed the approach outlined in Lisovski et al. (2020) and the parameters used in Wong et al. (2022), first annotating twilight events using a light-level threshold of 1 in *TwGeos*. Stationary periods were defined as stops lasting  $\geq 2$  days. Briefly, we derived median reference solar zenith angles based on the recorded light readings at a non-breeding site (i.e., Hill-Ekstrom calibration). We discerned stationary and movement periods based on abrupt changes in sunrise, sunset, midday and midnight times, and used the ‘mergeGroups’ function in *SGAT* to group together similar twilight times to a single site. Using *SGAT*’s Group model, we specified the parameters for the twilight error distribution (gamma), the flight speed distribution (shape: 2.2, rate: 0.08), and a land mask constraining positions to land. A modified gamma model was first run for 1000 iterations to initiate the model, before the model was tuned for five runs with 300 iterations.

The final run of the model for 2000 iterations produced the median migration tracks and associated 95% confidence intervals. Calibration parameters used in *SGAT* are available in Online Supplement 1, Table S2.

The addition of atmospheric pressure information to light-based geolocation has been shown to greatly enhance the accuracy of location estimates (Nussbaumer et al. 2023a). Thus, pressure, activity, and light data recorded from the single GDL3-PAM multi-sensor logger (16KN) were used to predict positions with the R package *GeoPressureR* (Nussbaumer et al. 2023b). We followed the steps detailed in Nussbaumer (2022). Essentially, *GeoPressureR* creates a likelihood map of positions based on matching geolocator-measured ambient air pressure data and global reference weather data, and a second likelihood map based on ambient light intensity data to further refine location estimates (Nussbaumer et al. 2023b). We distinguished between stationary and migratory periods based on simultaneous drops in pressure and sustained high activity. We handled outliers using a visual inspection as suggested in

Nussbaumer (2022) using TRAINSET (<https://www.trainset.geocene.com>). This allowed us to compare pressure and activity data simultaneously, and we removed outlying single pressure points that differed significantly from preceding or following points (within 30 min) and did not match the activity level. We used a two-day threshold for stationary sites (i.e.  $\geq 48$  h), and light data was analyzed based on the threshold method, using breeding-site calibration. The combination of pressure and light likelihood maps is then used to model the trajectory of the bird, based on a gamma-distributed flight speed distribution (min. groundspeed: 20 km/h, average groundspeed:  $< 120$  km/h). The resulting simulated most-likely path is the shortest path between the estimated stationary sites, and a marginal probability of each stationary site regardless of the bird's trajectory is also produced. Parameters used in GeoPressureR are available in Online Supplement 1, Table S3.

To gain insight on the migratory behaviour of the shrikes throughout the annual cycle, we further classified the activity data recorded by the multi-sensor logger using the R package *PAMLR* (Dhanjal-Adams 2022). Following the guidelines in Dhanjal-Adams et al. (2022), we used the 'classify\_flap' function to identify periods of low to high activity (flapping flight) using k-means clustering. Sustained high activity of 60 min or more was considered migration. The function 'classify\_summary\_statistics' was then used to summarize pressure changes and respective flight altitudes per classified flight. All analyses were conducted in R version 4.1.3 (R Core Team 2022). All times are given as UTC.

## Results

### Ring recoveries

All seven recoveries were related to autumn migration, linking breeding and southern passage sites (Fig. 1a), and none linked breeding and African non-breeding sites. Four birds were ringed as nestlings. Six birds were recovered in Greece in late August and early September (range 23 Aug–20 Sept, mean 8 Sept, mean distance 1200 km). One bird ringed as a nestling in Germany was recovered after 478 km and 60 days on 28 Aug in N Italy. Four birds were recovered in Greece within the same season. Two birds ringed at Hungarian breeding sites were recovered in Greece in the following autumn. Details on recoveries are provided in Online Supplement 1, Table S1.

### Geolocation

The first bird (22UL, Fig. 1c) left the breeding site on July 21 (Table 1) and the first stopover was detected for 23 days in Bulgaria (July 25–Aug 18) and a second stay in northern

**Table 1** Migration table for two geolocator and multi-sensor logger tracked Lesser Grey Shrikes

Bird ID	22UL	16KN
<i>Autumn migration</i>		
Departure breeding site	21 July	23 July
Arrival to main NBS	13 Nov	14 Nov
Duration (days)	115	114
Great circle distance (km)	7777*	8167
Site-to-site distance	8038*	8481
# stopovers	3 (2)	5 (4)
Sum stopover days	99 (42)	95 (43)
Migration speed great circle distance (km/day)	68 (106)	72 (115)
Migration speed site-to-site (km/day)	70 (110)	74 (119)
Travel speed (km/day)	486	430
<i>Spring migration</i>		
Departure	29 Mar	7 Apr
Arrival to BS	15 May	17 May
Duration (days)	47	40
Great circle distance (km)	8053**	8167
Site-to-site distance	9041**	9711
# stopovers	3	2
Sum stopover days	16	10.5
Migration speed great circle distance (km/day)	171	204
Migration speed site-to-site (km/day)	192	243
Travel speed (km/day)	260	277

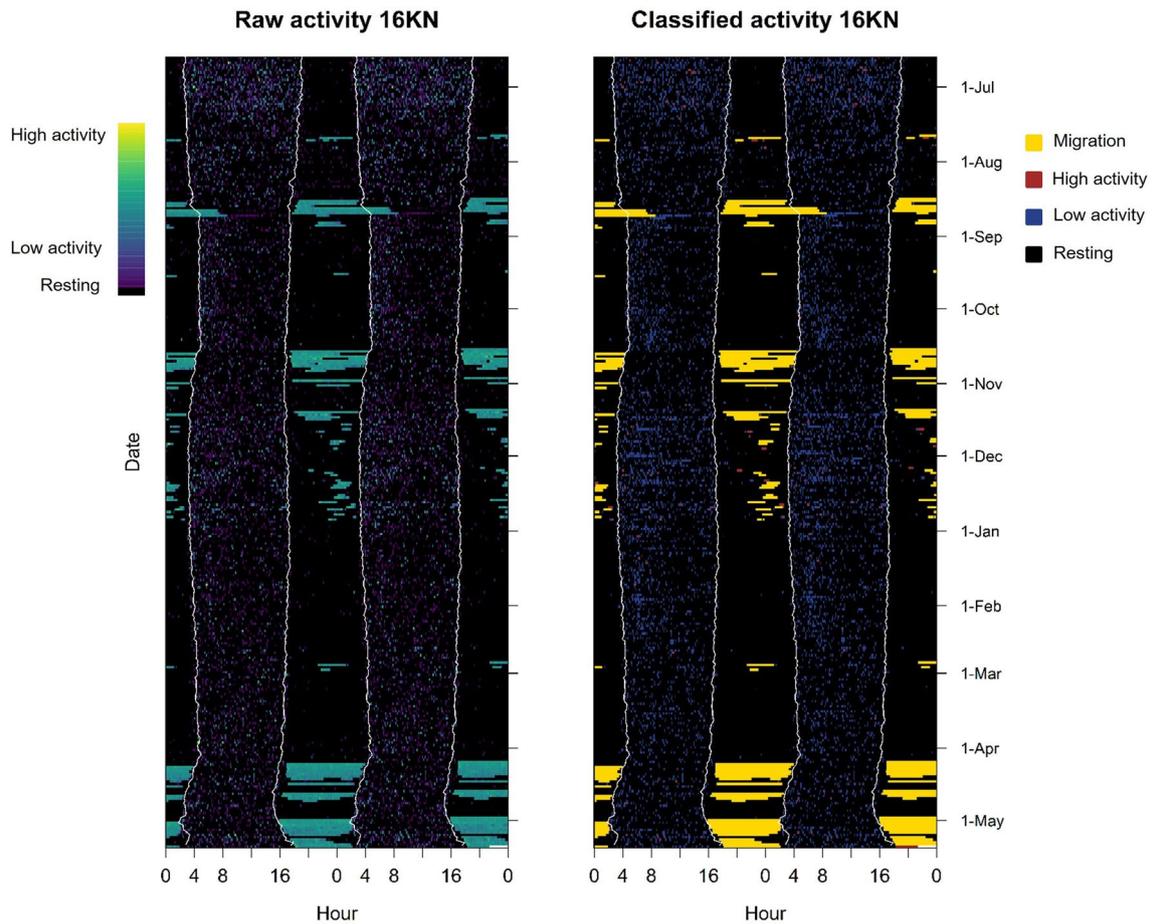
NBS non-breeding site. Migration speed was estimated as the distance between breeding and African NBS divided by the total duration of migration, including stopovers. Great circle distance estimates are between the breeding and African non-breeding sites. Note that only stopovers  $\geq 2$  days are considered here

Numbers in parentheses refer to estimates without the residency/stopover in Chad

\*to first NBS, \*\*from the second NBS

Chad on the border with Libya for 57 days (Aug 24–Oct 20). After that, the bird made a quick 3700 km long movement and on Oct 23 it arrived at Angola where it stayed for 19 days. On Nov 13, the bird arrived at its first main non-breeding site in W Botswana, where it remained until Jan 10 (58 days). After that, it moved about 2° further South within Botswana to spend another 73 days (Jan 15–Mar 29) at the second main non-breeding site. The bird initiated the spring migration on Mar 29 and between Apr 7–9 it took a short stopover in the area of W Mozambique. After that, it took another 10-day stopover from April 15 in NW Kenya, west of Lake Turkana. The last detected stopover was estimated for three days (Apr 29–May 2) in Saudi Arabia. The bird flew towards the breeding site via Cyprus, Anatolia and Balkan with final arrival to the breeding site on May 15 (Fig. 1c).

The second individual (16KN, Table 1; Fig. 1c) departed the breeding site on July 23. It quickly moved to the border



**Fig. 2** Actogram of the Lesser Grey Shrike (16KN) over its annual cycle. The left figure shows unclassified activity, the right one classified into four behavioural states (resting, low activity, high activity

and migration) using *PAMLr*. The two white vertical lines indicate the local sunrise and sunset times as recorder by the logger

region of W Romania and SE Hungary around the Mureş River, where it stayed for 25 days (July 25–Aug 18). On Aug 18, the bird took off for migration. Changes in pressure data show flight for six consecutive nights (Online Supplement 1, Fig. S1). On Aug 24, following the Mediterranean Sea and Sahara crossing, it took a three-day stopover (Aug 24–27) at an estimated location in the border area of Niger and Chad. After that, on Aug 27 it made a short movement further south, where after two nocturnal flights arrived on Aug 29 in the Kanem region, Chad. There, the bird stopped for 52 days (Aug 29–Oct 19), which resembles the pattern in the previously tracked bird (22UL, with departure on Oct 20). On Oct 19, the bird took off and over a series of 9 nights, it moved further south to the next stopover in Angola, where it stayed for 4 days (Oct 27–31). After that, the bird moved southeast, staying 11 days (Nov 3–13) in Western Zambia, in the border region between Angola and Namibia, near the Zambezi River. After this stop, the bird continued further and on Nov 14 it arrived at its final non-breeding site in Central Kalahari Game Reserve, Ghanzi District, Botswana. On

Apr 7, after 144 days of residency, the bird initiated spring migration. For eight nights in a row it migrated, took a break from Apr 14, and continued with flight on the night of Apr 15. After that, it took a stopover around Lake Turkana, Kenya for 3.5 days (Apr 16–19). Over the next four nights, the bird moved northeast and it took another 7-day stopover (Apr 23–30) in Somaliland, Somalia, in the area between Karkaar Mts and the Nugaal Valley (Fig. 1c). On Apr 30, the bird departed from the site. Changes in pressure show that the bird continued to make a series of nocturnal flights until May 15, with only one 1-day short stopover on May 7. However, these stopovers are below the set 2-day threshold, and therefore not shown. For comparison, a track modelled with a 12 h threshold, can be seen in Online Supplement 2.

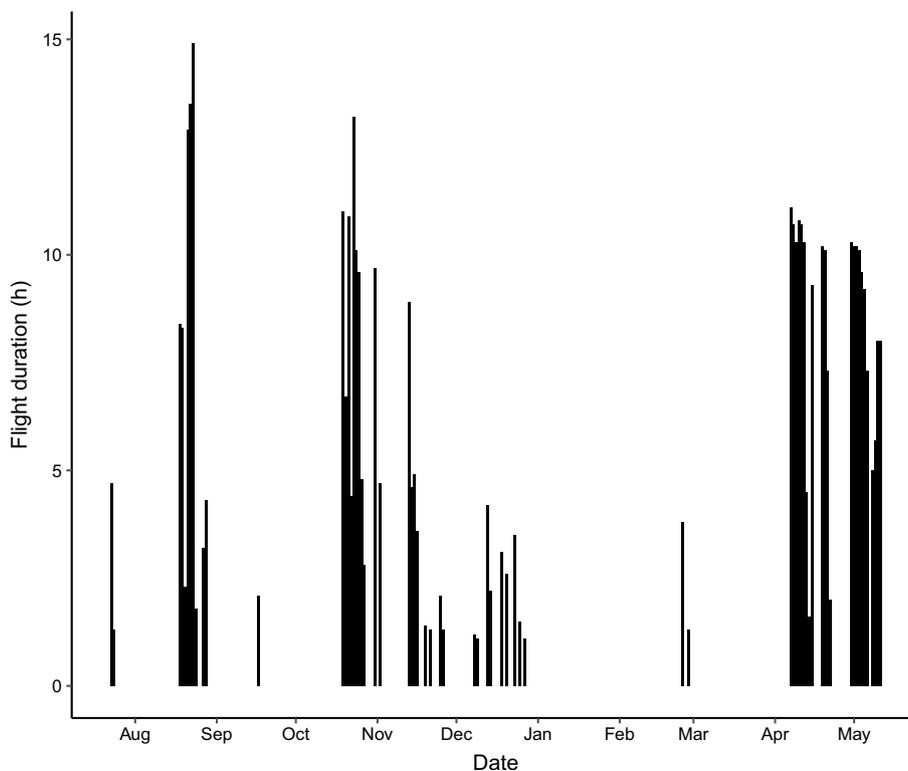
### Flight behaviour on migration

Nocturnal flights were the norm in both autumn and spring (Fig. 2). However, three prolonged flights into the day (22–24 Aug) occurred during the barrier crossing of the

Mediterranean Sea and the Sahara Desert. Cumulatively, autumn migration lasted 176.8 h for this individual (with events classified as flights  $\geq 1$  h). On July 23, the bird initiated the first migration flights (4.7 and 1.3 h) across two consecutive nights to its first stopover site in Romania (Fig. 3). Flight durations while barrier crossing ranged from 12.9 to 14.9 h per night. Between the stopover sites in Romania and Chad, the bird made nine flights in total for 69.5 h, mean 7.7 (range 1.8–14.9). From Chad towards the main non-breeding site in Botswana, the bird flew in several bouts, totalling 101.4 h (mean 6.8, range 2.7–11.0).

Spring migration was initiated with a series of nocturnal flights across eight consecutive nights (cumulatively 69.8 flight hours, mean 8.7). After a one-day break, the bird continued with a 9.3 h flight on April 15. Another set of nocturnal flights was initiated on Apr 19 for four consecutive nights (cumulatively 29.5 flight hours). On Apr 30, the bird initiated another set of nocturnal flights (mean 8.5 h, range 5–10.3) but the logger stopped working while the bird was on the move (May 15). By May 11, the spring part of migration took cumulatively 201.8 flight hours. Interestingly, on several occasions while the bird was residing in the same area, it took short nocturnal flights (Fig. 3). For example, while residing in Chad, on Sept 17 it took 2.1 h climb flight up 1096 m. Similarly, on Dec 18 it took a short flight up 1085 m (Online Supplement 1, Fig. S2).

**Fig. 3** Flight durations (in hours) over the annual cycle in Lesser Grey Shrike (16KN). Only flights longer than 1 h are shown



## Altitudes of migratory flights

Flight altitudes in autumn were the lowest during the first two flights between the breeding site in Slovakia and the first stopover site, when the single bird reached the first night max 1329 m. Altitude range and heights reached were higher during the barrier crossing phase than during the period when on the move between Chad and Botswana (Table 2). Maximum flight altitude during barrier crossing was 3274 m asl, mean  $1198 \pm 949$  SD m asl. Interestingly, we detected an increase in altitudes at dawn, when the bird started its ascent. This happened on all three mornings when the bird extended nocturnal flight into the day (Fig. 4). At the non-breeding residency site in Botswana, the bird stayed at a relatively constant altitude of 1000 m asl (Online Supplement 1, Fig. S2). Climbing height, record flight altitude (4530 m asl) and altitude range were the highest during the last stretch of migration, after Apr 30 (Table 2).

## Discussion

The few available ringing recoveries of the Lesser Grey Shrike show that birds from European breeding sites migrate via Greece in autumn. Funnelling via Greece was likely common for birds from the extinct western European breeding sites (as indicated by the two recoveries of birds from German breeding sites). The only recovery in Africa is a

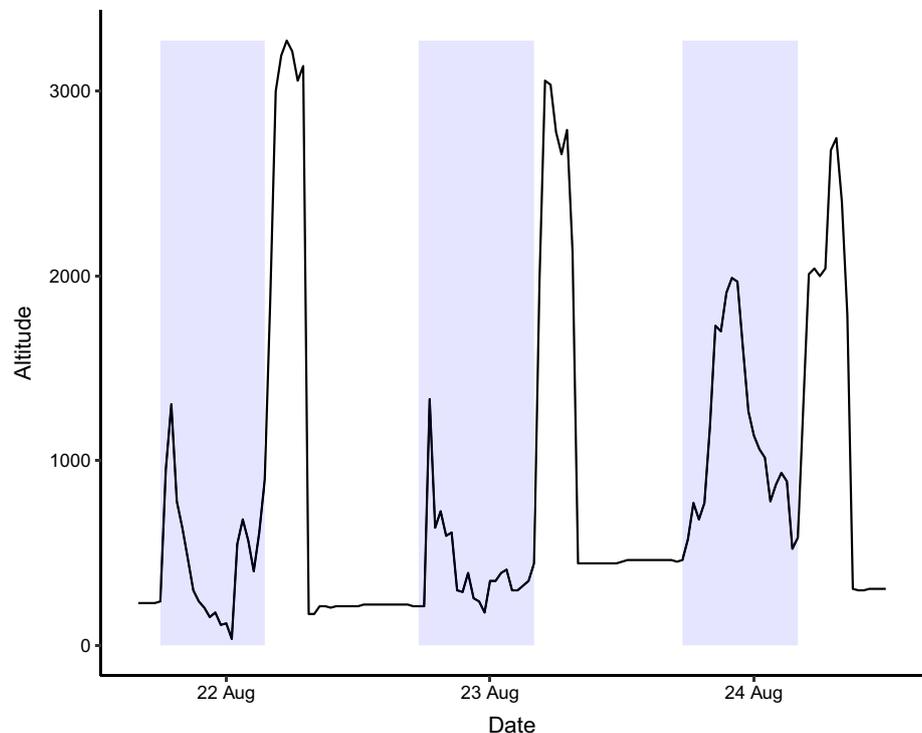
**Table 2** Characteristics of migratory flights of the Lesser Grey Shrike based on data from the multi-sensor logger

Travel period	Dates	Mean altitude (m)	SD (m)	Max. altitude (m)	n	Altitude range (m)	Climb mean	No. flights	Mean flight duration (h)	Flight hours
1	Jul 23–24	898	411	1525	11	1329	752	2	3.0	5.9
2	Aug 18–29	1417	909	3274	139	3238	1944	9	7.7	69.5
3	Oct 19–Nov 14	1589	659	3378	199	2335	1238	15	6.8	101.4
4	Apr 7–16	1859	712	3930	157	2831	1273	9	8.8	79.0
5	Apr 19–22	1261	492	3114	59	2361	1132	4	7.4	29.5
6	Apr 30–May 11	1955	962	4530	167	3551	1946	11	8.5	93.3

Recording interval 30 min; n refers to no. of sampling events. For flight durations, only events over 1 h in duration and classified as migration were considered. Altitude range—the total flight altitude range during that travel period. Climb mean—mean of altitude ranges during that travel period

Travel periods: 1 From the breeding site to first stopover site in Romania, 2 from Romania, via Greece, barrier crossing flights to Chad, 3 from Chad to Angola, 4 spring migration towards the stopover site in Kenya, 5 from Kenya to Somaliland, 6 from Somaliland to breeding site in Slovakia

**Fig. 4** Changes in flight altitudes of the Lesser Grey Shrike (16KN) during the nocturnal and diurnal parts of barrier crossing of the Mediterranean Sea and Sahara Desert. Blue areas indicate nights. Note that these are three flights interrupted with diurnal stops



female colour-ringed at our Slovak breeding site on June 10, 1998 by AK and resighted on April 12, 2000 in the area of Awash, Ethiopia (9.00N, 40.17E; Krištín 2008). Data from our two-tracked individuals confirm the earlier suggestions of Stresemann (1943), and Moreau (1961) of an anticlockwise loop migration pattern in this species. This is comparable to the loop migration pattern in the Red-backed Shrike (Tøttrup et al. 2012). Furthermore, both birds in our study made long stops either in the Sahel zone or in an oasis in the Sahara Desert. There, both birds spent nearly 2 months before moving further south to stopover sites in Angola.

Again, this resembles the behaviour of the Red-backed Shrike for which Tøttrup et al. (2012, 2017) and Pedersen et al. (2020) found that the birds spent 1 to 2 months in S Sudan after Sahara crossing, before moving further south to the final non-breeding sites. Such a long residency indicates that this region might be of critical importance for shrikes after barrier crossing. Tøttrup et al. (2012) suggested that the shrikes likely encounter favourable foraging conditions in this area and store fuel for rapid southward movements.

Both tracked individuals resided during boreal winter in the area of the Kalahari Desert. This is the area where the

entire global population of the species is seen to concentrate at that time of year (Herremans 1998). Earlier observational studies reported the first arriving birds from late October (Zimbabwe) to late November (Cape Province, S Africa) (Dowsett 1971; Lefranc & Worfolk 1997). Our tracked birds arrived at remarkably similar dates in mid-November. For the spring migration, we confirmed that the species migrates along the E African countries towards Ethiopia and Somalia, the Red Sea, the Middle East, Anatolia and the Balkan Peninsula. In line with the expected pattern of faster migration in spring (Nilsson et al. 2013; Briedis et al. 2020a), the migration speeds of shrikes were also much faster in spring than in autumn. However, travel speeds (i.e. speed excluding stopovers) were much faster in autumn. This resembles the pattern in the Great Reed Warbler when the total flight duration used for covering the full-migration distance was on average shorter in autumn than in spring (Emmenegger et al. 2021). However, all of these estimates should be taken with caution as no geolocator study can provide data on the first fuelling period prior to departure. The question of whether to consider the long autumn residency period in Chad as a stopover also arises. It is likely the birds undergo a partial moult there (Lefranc and Worfolk 1997), and if we assume residency in Chad, our migration speed estimates would be underestimated (but note that we also provide migration speed estimates without the Chad residencies). For example, Schmaljohann et al. (2022) do not consider an interruption of endurance flights due to moult as a stopover. Thus, if the shrikes undergo moult in this area, we should consider this residency period as a unique annual cycle event. This raises the question of how to define autumn migration, e.g. whether to view it as two events – prior and after the Chad residencies. Arrivals of the two birds to the breeding site in mid-May correspond with the long-term observations (mean arrival May 6; Krištín et al. 2007 and Krištín unpubl. data).

For the single individual with the multi-sensor logger data, we show that nocturnal migration was the prevailing pattern. This is in line with the typical pattern of prevailing nocturnal migration found for most trans-Saharan avian migrants (Dorka 1966; Schmaljohann et al. 2007b). The bird only extended its flights shortly into the day on three nights in autumn, during its crossing of the Mediterranean Sea and the Sahara Desert. This observation fits into the expected pattern that prolonged flights occur during barrier crossings (Adamík et al. 2016; Jiguet et al. 2019). Similarly, the extensions of nocturnal flights into the day during Sahara crossing were also found for two Red-backed Shrikes tracked with data loggers (Bäckman et al. 2017a, b). Schmaljohann et al. (2007a) showed that under favourable tail winds, the passerine nocturnal migration measured by radar continued into the day. In their study, landing tendency (sink rate) correlated negatively with tail winds. Thus, both radar and geolocation from this study

provide solid evidence for the extension of flights into the day by trans-Saharan migrants. Activity data also significantly improved our understanding of migration behaviour. For example, we could see that migratory flights in spring are more compressed in time than in autumn, with the exception of a series of short nocturnal flights in the autumn. The single individual migrated on average for around 6 h per night in autumn and over 8 h per night in spring. In autumn, the migration was divided into three segments, with similar numbers of flights as was found for the Red-backed Shrike (Sjöberg et al. 2018). Flight altitudes were usually in the range of 1000–3000 m asl, with a record of 4530 m asl., and lowest during the first segment of autumn migration in Europe. These findings are in line with the flight altitudes recorded by the Red-backed Shrike (Tøttrup et al. 2017; Sjöberg et al. 2018). A similar pattern of low flight altitudes over Europe and a sudden increase in altitudes during barrier crossing was also found in European Nightjars (Norevik et al. 2021). Our tracked individual climbed the most metres during the diurnal part of the barrier crossing phase in autumn and in the last stretch of spring migration after leaving Somalia. We found that starting the ascent at dawn occurred over three barrier-crossing events. This was a similar pattern to the Great Reed Warbler described by Sjöberg et al. (2021) or to the sudden daytime ascents in migratory Great Snipes (Lindström et al. 2021). It is likely that the sudden increase in flight altitudes served the bird to find more favourable wind conditions or to reduce water loss (e.g., Schmaljohann et al. 2009). The highest flight altitude of 4530 m asl was recorded during the spring passage (May 2). It was higher than in the Red-backed Shrike or Tawny Pipit (Briedis et al. 2020b), similar to Eurasian Hoopoe, but lower than in the diurnal flights of the Great Reed Warbler (up to 6267 m asl; Sjöberg et al. 2021; Liechti et al. 2018). However, we should interpret this with caution as we had altitudinal data only from a single individual.

Although we provide details on migration behaviour of only two individuals, the gathered data greatly enhance our knowledge of this little-known and endangered long-distance migratory species. Our findings fit well into what was expected (loop migration, prevailing nocturnal migration) or what is already known about nocturnal migrants (extending nocturnal flights into the day, climbs at dawn). Thus we suggest that our findings likely show the general migration pattern in the Lesser Grey Shrike. Collecting data on these few individuals was a challenge in the field. The breeding population continues to decline in our study area and within few years there could be no individuals to track.

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**Author contributions** PA and AK designed the study, collected data, and wrote the manuscript. PA requested and processed the EURING data. JBW analysed the geolocator and multi-sensor logger data, and wrote parts of methods with an input from SH. Maps and actogram: JBW; flight duration and altitude visualization: PA. All authors reviewed and commented on the manuscript.

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**Data availability** Raw datalogger data from the tracked birds are available at Zenodo (Adamík et al. 2023).

## Declarations

**Competing interests** None.

**Ethics statement** The permissions to handle the birds were issued by the Slovak Ministry of Environment, and the Slovak ringing scheme to AK.

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## Studie 14

Wong, J. B., Adamík, P., Bažant, M. & Hahn, S. 2024: Migration and daily flight activity patterns in the barred warbler *Curruca nisoria* over the annual cycle. *Journal of Vertebrate Biology* 73: 23085-1.

# Migration and daily flight activity patterns in the barred warbler *Curruca nisoria* over the annual cycle

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**Abstract.** The barred warbler, *Curruca nisoria*, is an Afro-Palaearctic migrating bird with a wide breeding distribution across eastern Europe to central Asia. Ring recoveries and direct observations have suggested they migrate to non-breeding grounds in East Africa. However, little is known about their migration routes and flight behaviour during migration and on the non-breeding grounds. Using geolocators and multi-sensor loggers, we tracked three barred warblers from a Czech breeding site to document their migration routes, stopover and non-breeding sites, and flight activity patterns across the annual cycle. All three tracked birds took south-eastern autumn migration routes through the Levant, with a shared stopover in Syria before crossing the Arabian Desert, the Red Sea and eastern Sahara Desert and stopping in Sudan for ca. two months. After 109 days (average), birds arrived at their main non-breeding sites of W Kenya or S Ethiopia. A single stopover on the Red Sea coast of Saudi Arabia was used during the spring migration before continuing NW across the Mediterranean. Pressure and acceleration data showed that warblers migrated exclusively at night, with the longest flights crossing the Sahara and travelling from Sudan to non-breeding sites. Daily diurnal activity patterns were uniform across all stationary sites.

**Key words:** geolocation, tracking, nocturnal activity, diurnal activity, Afro-Palaearctic bird migration system

## Introduction

Knowledge of the annual cycle of migrating birds, including where and when they can be found at different times of the year, provides important information about the factors affecting bird movement, breeding and survival. For example, poor conditions (e.g. low rainfall and resulting decreased food availability) at tropical non-breeding sites have

been shown to delay spring migration, resulting in later arrival at breeding grounds and lower reproductive success (Rockwell et al. 2012, Cooper et al. 2015). Similarly, cold weather conditions along migratory routes have also been shown to affect migratory performance in long-distance migrants, carrying over to late arrival and low return rates at breeding sites due to increased mortality *en route* (Briedis et al. 2017). These observations suggest that

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understanding avian migration routes and behaviour is fundamental to understanding the population dynamics of long-distance migratory birds.

The barred warbler, *Curruca nisoria*, is an Afro-Palaeartic long-distance migrant with an estimated world population of 4 to 7.8 million individuals across a breeding range of about 16 million km<sup>2</sup> from eastern Europe to central Asia (BirdLife International 2023). Barred warblers favour richly structured habitats consisting of bushes and shrubs, and as a result, their inconspicuous behaviour has made observations of their behaviour challenging. Ring recoveries have shown that warblers breeding in Europe migrate to East Africa, and the high concentration of recoveries in the Middle East suggests funnelling to Africa likely occurs via the Levant (Aymí et al. 2021, Spina et al. 2022). However, direct observations at non-breeding grounds are restricted to a small region in eastern Africa, namely parts of Kenya and northern Tanzania, and a few in eastern Uganda and Ethiopia from November to March. The only two available ring recoveries from the putative African passage and/or non-breeding range are recorded from the River Nile valley in Sudan (Spina et al. 2022). Still, no tracking study on individual barred warblers has been published to verify the migration routes used, and little is known about the flight behaviour of warblers during migration and the non-breeding period.

Thus, we aimed to unravel the migration tracks, stopover sites, non-breeding sites and daily activity patterns of individual barred warblers to better inform knowledge of their migration ecology during the annual cycle. We focus on spatial-temporal occurrences along the flyway and the presumably restricted non-breeding grounds, as those sites seem important for many populations across the Palaeartic breeding range.

## Material and Methods

### Study site

We studied barred warblers at Načeratický kopec, an abandoned military training area near Znojmo, Czech Republic (48.83 N, 16.10 E). The study area (ca. 130 ha) is a nature sanctuary with dominant open steppe grassland habitats. Thorny shrubs (especially the dog rose *Rosa* spp. and hawthorn *Crataegus* spp.), planted old fruit trees, and smaller wild trees form a minor part of the site.

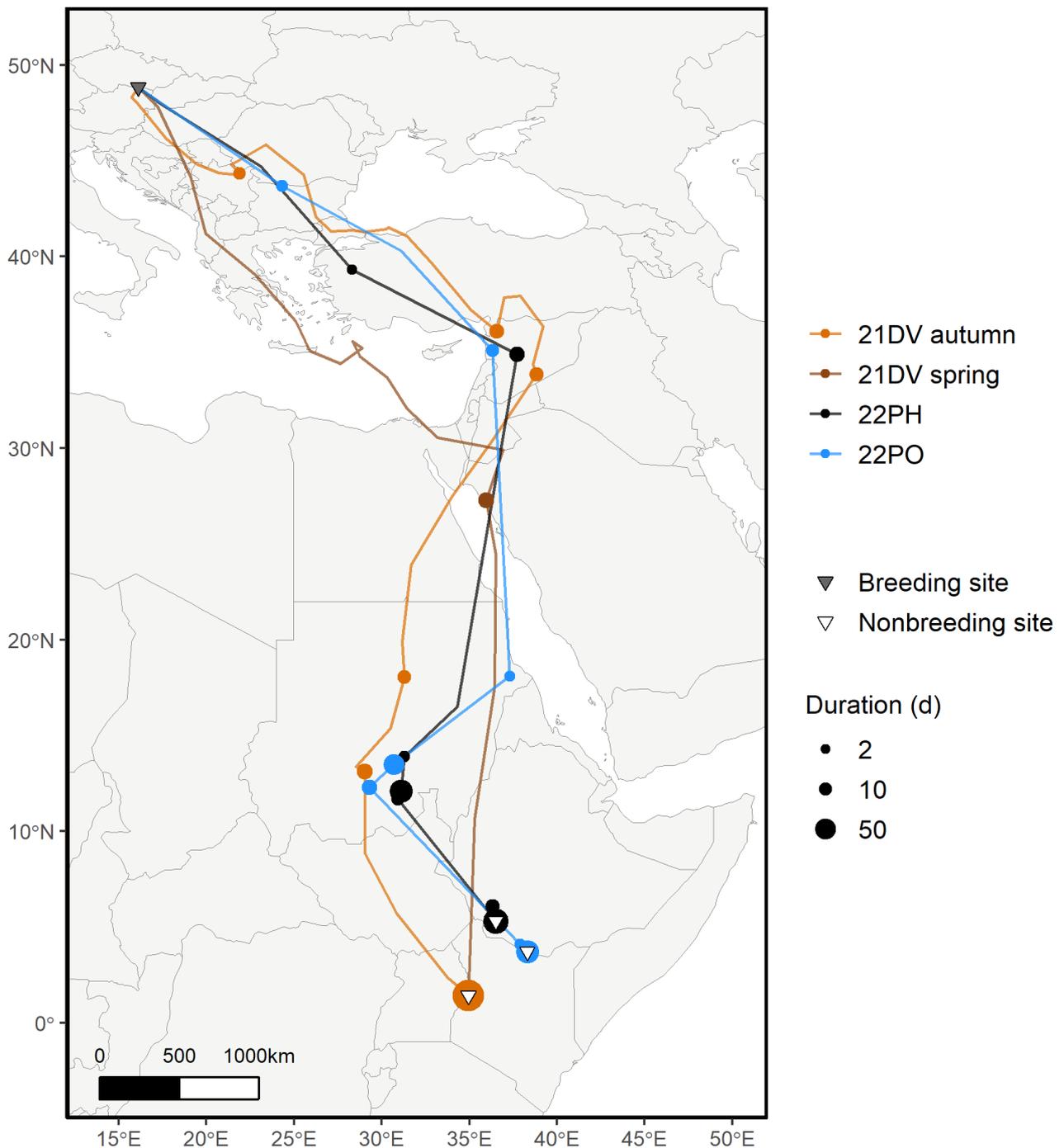
### Fieldwork

In 2017, we deployed 16 light-level geolocators (model SOI-GDL2, Swiss Ornithological Institute) and two multi-sensor loggers (model SOI-GDL3-PAM, Swiss Ornithological Institute) on ten males and eight females. In 2019, we deployed seven geolocators and ten multi-sensor loggers on nine males and eight females. The mean weight of geolocators was 0.68 g and of multi-sensor loggers 1.48 g. The mean body mass of adult males equipped with loggers was 22.7 g  $\pm$  1.3 SD (range 20.8–26.8 g), while the mean female body mass was 25.5 g  $\pm$  1.9 (range 22.3–29.8 g). In May and June, we trapped all adult birds with mist nets within their breeding territories. In the following breeding seasons, we retrieved one geocator and two multi-sensor loggers (all from males; one logger was retrieved after two years). The return rate of logger-tagged birds was 15.8% (3/19) for males and 0% (0/16) for females. The return rate of control birds (ringed only) was 8.8% for males (5/57) and 7.9% for females (3/38) from 2016 to 2021. Thus, the odds ratio of tagged males returning compared to untagged males was 1.8 (95% CI: 0.4–8.3), while the odds ratio of tagged females returning compared to untagged females was 0.3 (0.01–6.8).

### Analysis

Ambient air pressure was recorded every 15 min, while day light intensity and the bird's activity (accelerometer) were recorded every 5 min. Geographical position estimates of the warblers were calculated in one of two ways: from light-only data (logger 21DV; SOI-GDL2 tag) using the R package SGAT (Wotherspoon et al. 2013) or from the combination of pressure, light and activity data (loggers 22PO and 22PH; SOI-GDL3-PAM tags) using the R package GeoPressureR (v.3.1.2) (Nussbaumer & Gravey 2022). The light-only logger provided data on a complete annual cycle from the breeding to the non-breeding grounds and back, while the multi-sensor loggers contained data from the autumn migration and the non-breeding residence sites until 4 February and 13 March when the batteries depleted.

We analysed light-only data in similar steps outlined in Wong et al. (2022), and the light, pressure and activity data following the guidelines of the GeoPressure Manual (<https://raphaelnussbaumer.com/GeoPressureManual/>; Nussbaumer et al. 2023). In short, SGAT uses a Bayesian approach to estimate locations based on the twilight error distribution, the flight speed distribution (gamma distributed;



**Fig. 1.** Modelled autumn and spring migration tracks used by three barred warblers originating from a Czech breeding site. 21DV (orange/brown) was modelled using SGAT and shows the most likely median path, while 22PH (black) and 22PO (blue) were modelled using GeoPressureR and show the path that maximises the overall probability. Each dot represents a stopover site ( $\geq 2$  days stop) used by the individual bird, and the size of the dot is scaled to the minimum duration of days spent at the site. Triangles represent the breeding site (grey) or the main non-breeding site (white). 22PH and 22PO tracks represent only autumn migration until tags stopped recording at the non-breeding site. Uncertainties associated with position estimates are presented per individual in Figs. S1-S3.

shape: 2.2, rate: 0.08), and a land mask to give locations on land a higher prior. Meanwhile, GeoPressureR combines the additional pressure information to create a 1) likelihood map of positions from matching logger-recorded pressure data to global reference weather data and then enhances position estimates by constructing a 2) likelihood map from

light data. From this, the path that maximises the overall probability is modelled between estimated stationary sites while taking into account a gamma-distributed flight speed distribution (shape: 7, scale: 7, low-speed fix: 15). Calibration was performed by deriving the median reference solar zenith angles from the breeding site. As the minimum duration for

**Table 1.** Migration timing, distance, and speed for three geolocators (21DV) and multi-sensor loggers (22PH, 22PO) tracked barred warblers. BS = Breeding site; NBS = Non-breeding site. Further details about individual distances travelled and duration between stationary sites are provided in Table S1.

	21DV	22PH	22PO
<b>Autumn migration</b>			
Departure from BS	1 Aug	30 Jul	12 Aug
Arrival to main NBS	29 Oct	5 Dec	24 Nov
Duration (days)	89	128	109
Travel duration (days)	21	24	20
Great circle distance (km)	5555	5196	5372
Site-to-site distance (km)	6486	6007	6588
# stopovers	5	5	5
Sum of stopover duration (days)	70	115	95
Migration speed great circle distance (km/day)	62	41	49
Migration speed site-to-site (km/day)	73	47	60
Travel speed (km/day)	309	250	329
<b>Spring migration</b>			
Departure from main NBS	1 Apr	-	-
Arrival to BS	1 May	-	-
Duration (days)	30	-	-
Travel duration (days)	10	-	-
Great circle distance (km)	5555	-	-
Site-to-site distance (km)	5804	-	-
# stopovers	1	-	-
Sum of stopover duration (days)	20	-	-
Migration speed great circle distance (km/day)	185	-	-
Migration speed site-to-site (km/day)	193	-	-
Travel speed (km/day)	580	-	-

physiological recovery in migratory songbirds is one day (Eikenaar et al. 2023), we defined stationary sites as stops  $\geq 48$  h (as in Adamík et al. 2024).

To understand the flight and activity patterns of barred warblers throughout the year, we analysed the activity data recorded by the multi-sensor loggers. We classified flapping activity using the function 'classify\_flap' in the R package PAMLR (Dhanjal-Adams et al. 2022). This function determines the threshold between high and low activity using k-means clustering, and classifies continuous high activity (i.e. continuous flapping flight) over our set threshold of 20 min as migratory flight. We used the function 'classify\_summary\_statistics' to calculate the flight altitudes and duration of each migratory flight (Dhanjal-Adams et al. 2022).

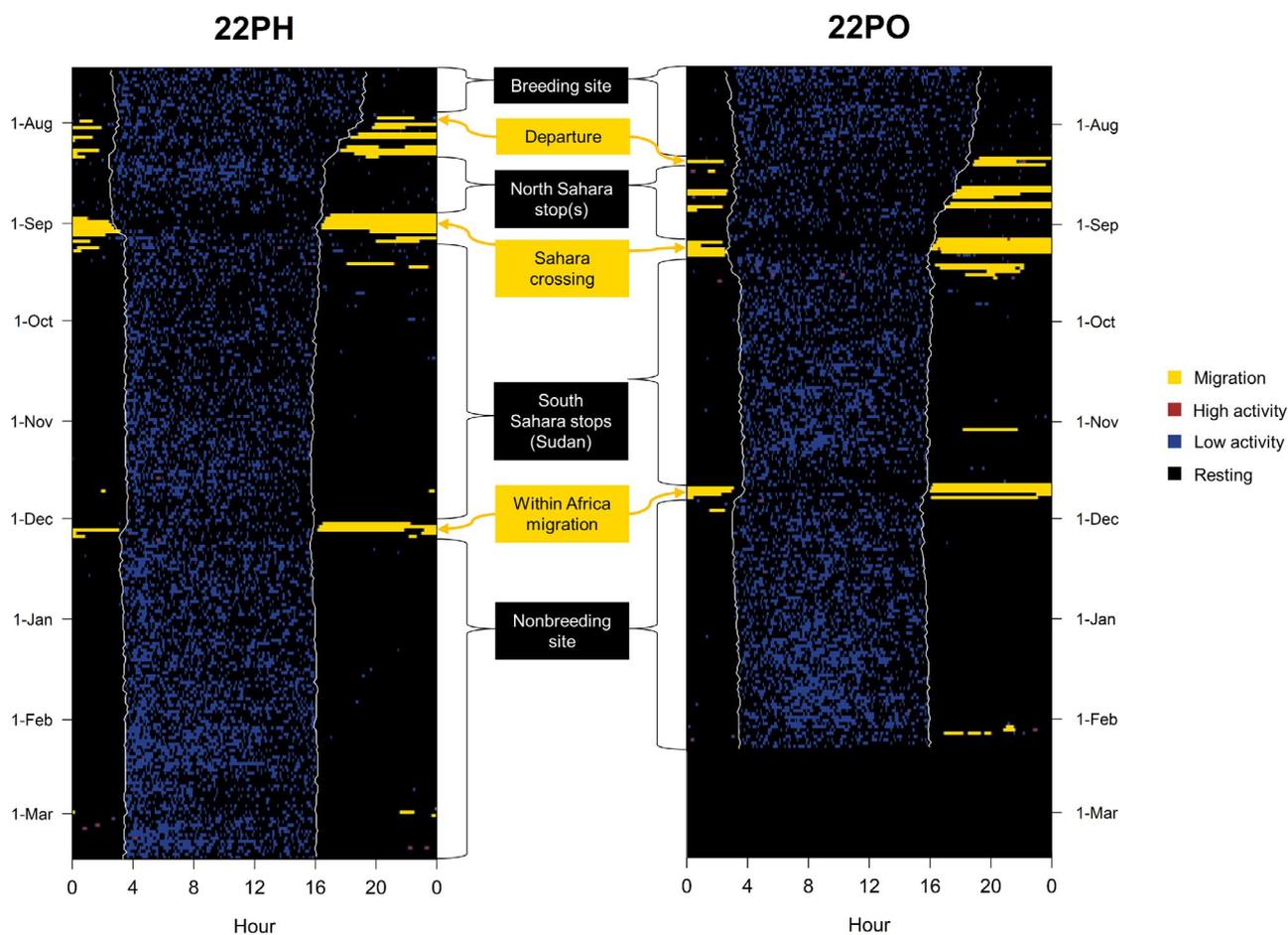
Great circle distances were calculated between stationary sites to evaluate the total flight distance travelled by migrating birds using the

'distVincentyEllipsoid' function in the R package geosphere (Hijmans 2021). The total migration distance per season was calculated by summing the distances between stationary sites.

## Results

### Autumn migration

All three barred warblers departed from their Czech breeding grounds in late July/early August (mean: 4 August; range: 30 July-12 August) in a southeast direction circumventing the Mediterranean Sea (Fig. 1). Before crossing the Sahara, the birds made 2-3 stopovers from August to September in Romania (22PO), Serbia (21DV), Turkey (22PH) or Syria (all birds; mean stopover duration: 11.4 days). After flying over the Red Sea and crossing the Sahara at its eastern part between 31° E to 38° E, warblers stopped at 2-3 sites in Sudan, arriving in mid-September (mean stopover duration per site: 23 days; mean total stopover duration in Sudan: 63 days) and departing



**Fig. 2.** Actograms showing the classified activity of two individuals (22PH and 22PO) from post-breeding (July) until the late non-breeding period (February and March) based on PAMLr classification by flapping activity. Sustained high activity for  $\geq 20$  min was classified as migration. White lines delineate sunrise and sunset times.

on average in mid-November. One individual (22PO) made an additional stopover in Ethiopia at the end of November (duration: 5 days). Warblers arrived at their final non-breeding sites on average around November 20 (range: 29 October–5 December) in W Kenya (21DV) or S Ethiopia (22PH, 22PO) after a total average autumn migration journey of 109 days (range: 89–128 days) (Table 1). After 91 days at its main Ethiopian non-breeding site, individual 22PH moved to a second site in Ethiopia on February 29, where it remained until the logger stopped recording on March 13. The site-to-site migration distance travelled by the birds in autumn averaged 6,360 km (range: 6,007–6,588 km), compared to an average direct great circle distance (not accounting for the route used by the birds) of 5,393 km (range: 5,196–5,555 km) between the breeding site and non-breeding site (Table 1). Overall, the longest travel distances occurred *en route* to Syria, Syria to Sudan, and Sudan to the final non-breeding sites of Kenya or Ethiopia (Table S1).

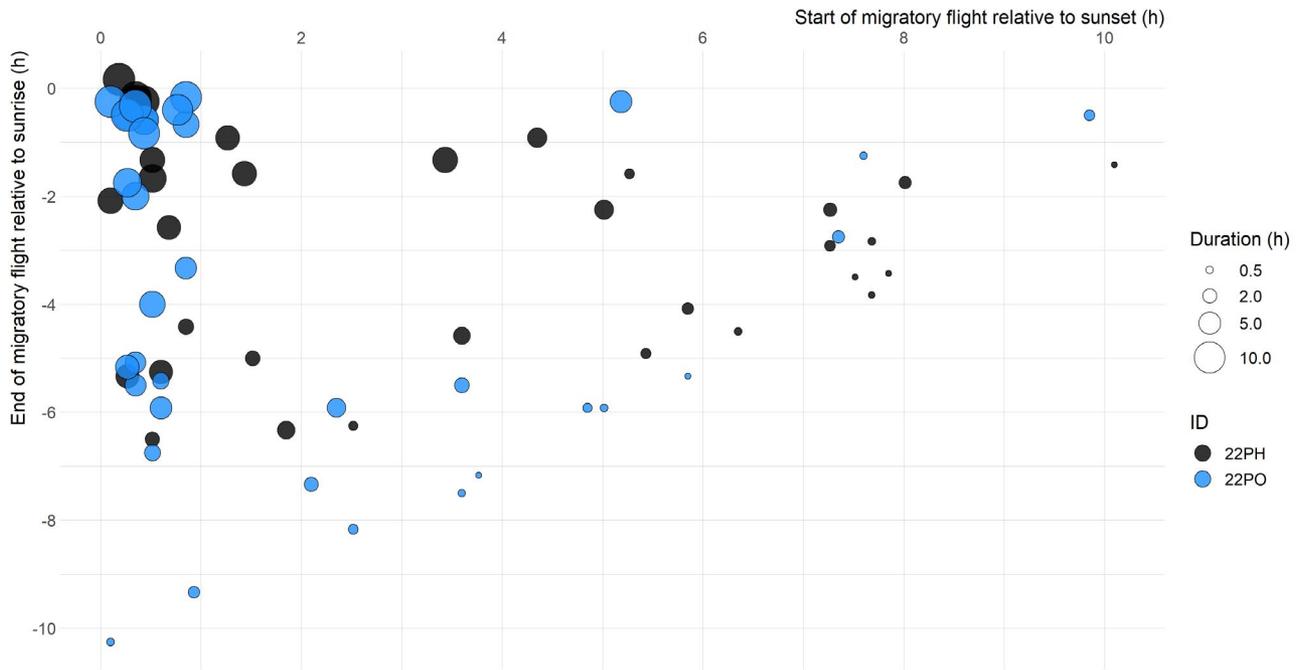
### Spring migration

Spring migration information was only available for one individual (21DV), which departed its non-

breeding site in W Kenya on April 1 and arrived at a stopover site in Saudi Arabia on April 3 (Fig. 1). There, the bird remained for 20 days before departure on April 23 in a NW direction. In contrast to autumn migration, this individual took a Mediterranean path through the Greek islands, returning to Czechia through the Balkans, Hungary and Slovakia, arriving on May 1 back at the breeding site (Fig. 1, Table 1). The total site-to-site distance of spring migration was 5,804 km, with similar distances travelled from Kenya to Saudi Arabia, and Saudi Arabia to Czechia (Table 1, Table S1).

### Individual behaviour during migration and the non-breeding period

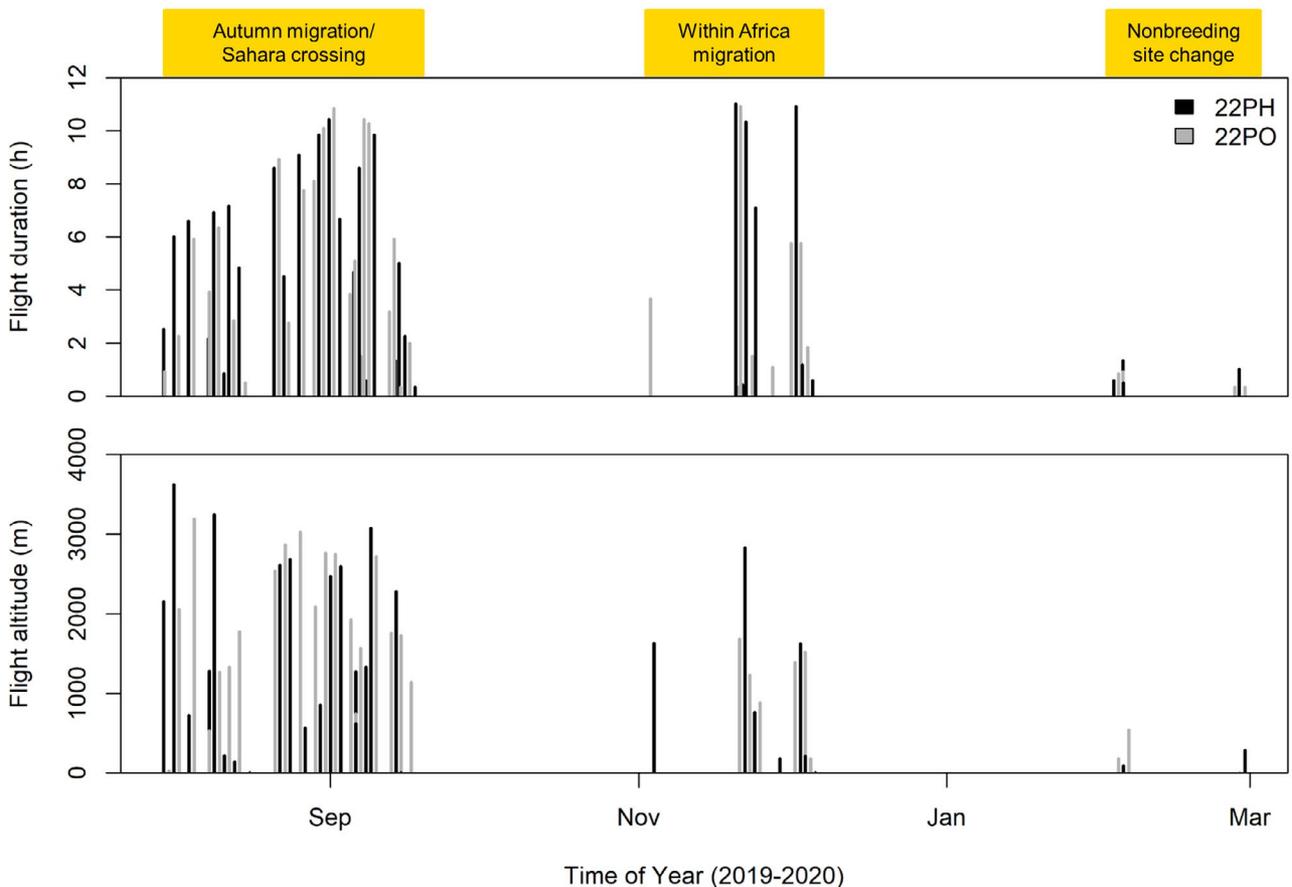
Accelerometry data showed that the two warblers migrated only at night and were less active during the day leading up to a nocturnal migratory flight (Fig. 2). The median time for both birds to start migratory flights was 0.9 h (54 min) after sunset (22PH: 2.2 h; 22PO: 0.8 h), and the median time of landing was 2.8 h before sunrise (22PH: 2.4 h; 22PO: 4 h) (Fig. 3). The start and end of migratory flights was primarily related to the duration of the



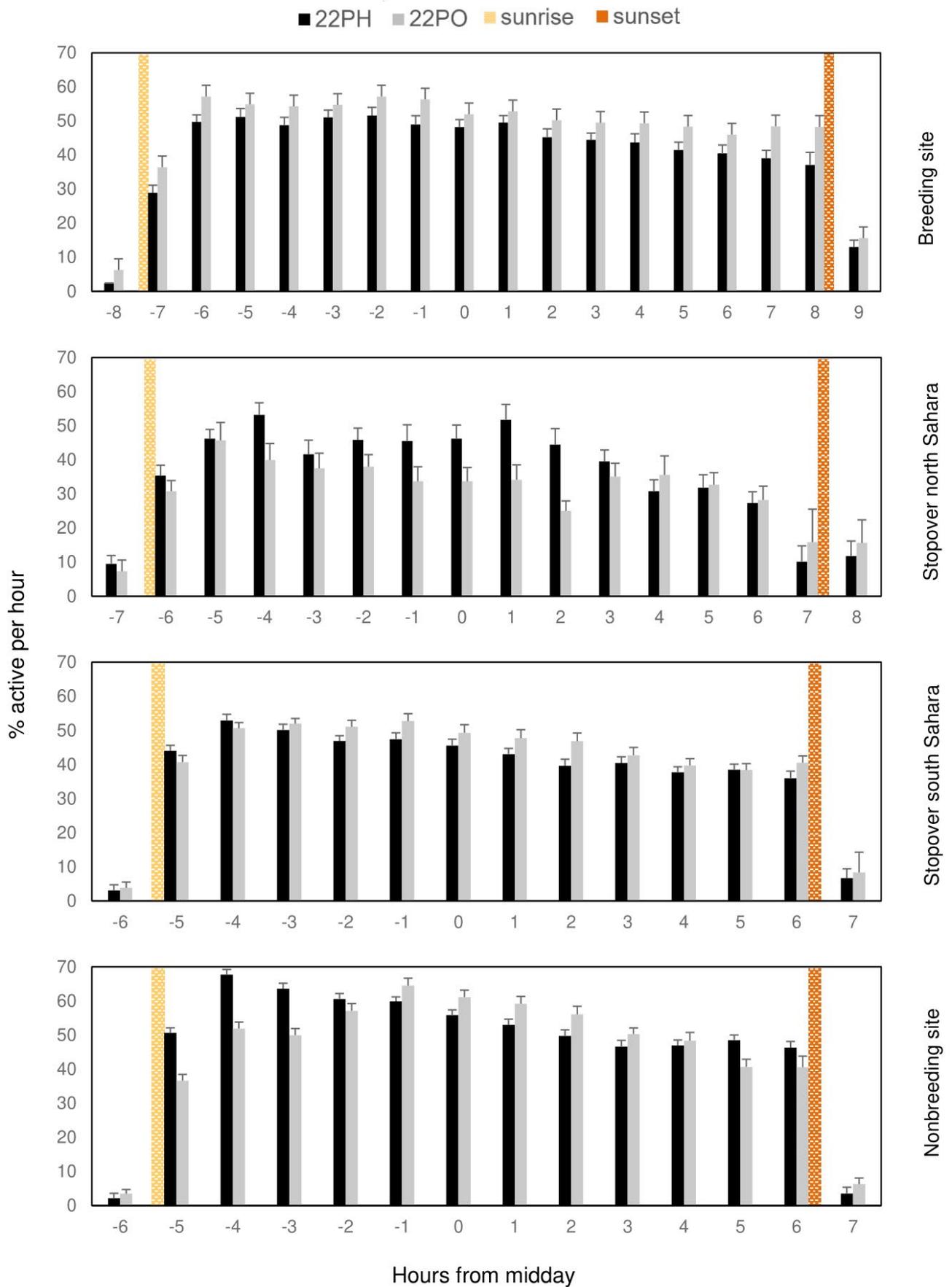
**Fig. 3.** Starts of migratory flights relative to sunset and the ends of migratory flights relative to sunrise, shown per individual (22PH and 22PO) across the annual cycle. Each circle represents a migratory flight, and the size of the circle represents the relative duration of that flight. Migratory flights ranged in duration from 0.3 to 11 hours.

flight, with longer duration flights starting closer to sunset and ending closer to sunrise (Fig. 3). Flight durations were remarkably similar between the two

individuals, with the longest single migratory flights of 10.8 h (22PH: 2-3 September) and 10.4 h (22PO: 8-9 September), occurring during the crossing of the



**Fig. 4.** Migratory flight durations and altitudes (based on PAMLR classification by flapping activity) for two individuals (22PH and 22PO) during autumn migration and when itinerant between non-breeding residence sites in Africa.



**Fig. 5.** Average proportion of activity (> resting, as classified by PAMLR) by individual (22PH and 22PO) per hour relative to sunrise and sunset, across the four main stationary periods. Variation in day length across the periods accounts for differences in sunrise and sunset across different stationary periods, as recorded by the light data.



Sahara (22PH: 29 August-8 September; 22PO: 6-11 September) and 10.9 h (22PH: 3-4 December) and 11 h (22PO: 22-23 November) between the migratory period from Sudan to their final non-breeding sites (22PH: 2-5 December; 22PO: 21-24 November) (Fig. 4). The Sahara crossing flight of 22PH was the only flight to extend into sunrise, by 0.16 h (3 September), but actograms showed that all remaining migratory endurance flights were not extended into the day (Figs. 2, 3). The median flight duration per individual was 3.0 h (22PH; range: 0.3-10.9 h) and 4.7 h (22PO; range: 0.3-11 h) (Fig. 3). The median altitude across migratory flights per individual was 1,273.7 m (22PH; range: 0-3,622.8 m) and 1,303.6 m (22PO; range: 0-3,070.7 m) (Fig. 4). The total cumulative flight hours for each bird to reach their main non-breeding sites were 140.3 h (22PH) and 167.8 h (22PO).

In contrast to migration, warblers were active almost exclusively during the day during annual periods of residency (Figs. 2, 5). Although birds appeared to be less active in the hour after sunrise, analysis of the hourly activity during residency periods showed no distinguishable patterns in daytime activity across sites (breeding sites, stopovers, non-breeding sites) nor daylight hours (Fig. 5).

## Discussion

Our tracking study confirms that barred warblers from the Czech breeding site spend the main non-breeding residency period in W Kenya and S Ethiopia, and in addition, use migration routes through the Levant and Middle East during autumn and pass through the Mediterranean during spring migration. These findings correspond with the presumed autumn migration corridor of barred warblers, in which most known western Palaearctic breeding populations are thought to bypass the Mediterranean on their southward journey (Moreau 1961). The use of and arrival at non-breeding sites in Kenya and S Ethiopia are also within expected regions and timing (Raz et al. 2023), with former records detailing arrivals from late October/early November onwards to Kenya (21DV arrived October 29), and arrivals to inland Ethiopian sites from late-September to mid-December (22PO arrived November 24, 22PH arrived December 5) (Cramp 1985, Urban et al. 1997). We identified several important stopover sites and provide the first data on stopover durations.

Notably, all three birds utilised a ca. 19-day stopover in Syria before crossing the Sahara in autumn. The Levant is well known as a funnel between the Mediterranean

Sea and the Arabian Desert for many long-distance migrants. In barred warblers, 26 out of 29 long-distance ring recoveries during migration were made in this region (Spina et al. 2022). Stopping here appears to be the last option for refuelling before crossing the Sahara, which requires substantial accumulated fuel for nocturnal endurance flights (see Fig. 2).

Following the Sahara crossing, all three birds stopped in Sudan for a long ca. two-month stopover. This halt is similar to long residencies detected in shrikes after crossing this significant barrier (Adamík et al. 2024). There may be several environmental conditions like food and shelter availability and physiological needs that favour the use of such a long stopover. One possibility is the recovery from long-endurance flights and replenishing exhausted body reserves for further migration, which might take several days but not such an extended residency period. Another explanation for the long stopover is post-breeding moult, which occurs when passerine birds renew flight feathers and usually avoid large movements. Interestingly, barred warblers are known to have a seasonally split wing-moult pattern in which, before autumn migration, they interrupt the regular moult of flight feathers after the renewing of primaries and complete the moult of secondaries at African non-breeding sites (Hasselquist et al. 1988, Lindström et al. 1993). Whether the Sudanese stopover sites are used to complete a wing feather moult awaits future investigations. A candidate for resource tracing is the steep gradient in stable sulphur isotopes between Sudanese sites and the warblers' main non-breeding grounds (Brlík et al. 2022), which allows quantification of site-specific contributions.

Optimal habitat conditions are a prerequisite to accomplishing keratin synthesis and feather development within a reasonable time and without interruptions that could substantially weaken feather quality. The elongated Sudanese stopovers used by the barred warblers in our study range between 29° E and 32° E longitude, i.e. the longitudinal range wherein the River Nile flows in this region. The Sudanese portion of the Nile flood plains is associated with several important wetland areas and is also known to harbour a great diversity of plants and insects, which provide suitable conditions for insectivorous migratory species (Paltenea et al. 2008). The rainy season occurs in Sudan from June or July to September when the Intertropical Convergence Zone lies over the northern tropics of the Sahel region, resulting in a resource peak for insectivorous birds (Pearson & Lack 1992). This seasonal pattern of rainfall in the southern part of Sudan coincides



well with the timing of the arrival and departure of warblers in our study.

Favourable environmental conditions likely also dictate the choice of the main non-breeding site. Not only do the non-breeding sites of our tracked birds in north-western Kenya and southern Ethiopia correspond to the currently documented non-breeding distribution in Kenya and Ethiopia from November to March (<https://ebird.org/species/barwar1>), but they also fall within the wider Great Rift Valley area. The wider Great Rift Valley region is known to support a high diversity of birds and other animals (Lemma & Desta 2016), and barred warblers have been known to frequent the Valley in autumn and spring (Cramp 1985, <https://ebird.org/species/barwar1>). Rainfall in the presumed non-breeding regions occurs in southern Ethiopia from October to November and in Kenya from November to December (Pearson & Lack 1992). This finding suggests warblers likely select sites based on precipitation or proximity to a water body, which contributes to high insect availability, and likely depart when resource conditions deteriorate following the end of the rainy season.

Insight into the activity of barred warblers during migration and the non-breeding period was also revealed. Warblers generally took off on migratory flights within an hour after sunset and landed less than four hours before sunrise. In contrast to other songbirds (Adamík et al. 2016), barred warblers generally showed no elongation of flights into the day during barrier crossing, suggesting these birds may instead utilise optimal flight conditions (i.e. tailwinds) or have some flexibility in their choice of stopover sites (i.e. stopping anywhere before sunrise), which allow the avoidance of diurnal flights.

The actograms (Fig. 2) and the hourly proportion of activity (Fig. 5) indicate that warblers forage for diurnally active prey but show slightly lower foraging activity in the first hour after sunrise. Interestingly, the daily activity of barred warblers at the Sudanese sites was similarly high compared to breeding and subsequent non-breeding residence sites, indicating the same diurnal pattern of foraging and rest across stationary sites. This result may suggest that all stationary sites used present equal foraging opportunities.

Spring migration is the final step to complete the annual cycle, for which we provide data for the first time. The departure of 21DV from Kenya on April 1 is within the late March to early April range for which

previously recorded departures of barred warblers (of unknown origin and fate) were recorded (Urban et al. 1997, Aymí et al. 2021). Using a single long, 20-day stopover at a site near the Red Sea coast in northern Saudi Arabia also matches records of barred warblers in high numbers in the southern Levant in April (Cramp 1985). The Red Sea coast of Saudi Arabia is a highly biodiverse region with a high prevalence of vegetation and invertebrates (Price et al. 1998), which suggests migratory warblers likely use this area as a primary refuelling site after a long flight from Africa and in preparation for another long flight across the Mediterranean. However, the spring passage through the Mediterranean and the southern Balkan peninsula has not been previously documented, as ring recoveries suggested warblers also return north using a Middle Eastern, Levantine route. The detailed flight activity and altitudes of this Mediterranean crossing flight remain unexplored as the bird carried a light-only geolocator tag.

Here, we provide a first look at the migration routes, stationary sites and daily flight behaviour of barred warblers. Despite data from just three individuals, our findings fit the expected non-breeding range and provide evidence for the Balkan and Levant migratory path speculated for this species. As species distributions are expected to shift with changes in climate and food availability, documenting the natural history of migratory birds is valuable to increase our understanding of their annual cycle and flight behaviour.

## Acknowledgements

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## Author Contributions

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*J.P. Wong, P. Adamík and S. Hahn designed the study, P. Adamík and M. Bažant conducted fieldwork, J.P. Wong analysed the data, and J.P. Wong and S. Hahn wrote the manuscript. All authors commented and agreed on the manuscript.*

## Data Availability Statement

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*The geographic positions and multisensory logger data supporting this study's findings are archived at Movebank ([www.movebank.org](http://www.movebank.org), ID 3146197948) and Zenodo (<http://doi.org/10.5281/zenodo.10209430>).*



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## Supplementary online material

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**Table S1.** Great circle distances (km) and durations from departure to arrival (days) between stationary sites on the autumn and spring migration, including the total great circle migration distance travelled per individual per season. Values have been rounded to the nearest km.

**Fig. S1.** Modelled track and stationary site position estimates for 21DV with associated uncertainty from analysis of light data using SGAT.

**Fig. S2.** Marginal probability of modelled track and stationary site position estimates for 22PH from analysis of pressure data using GeoPressureR.

**Fig. S3.** Marginal probability of modelled track and stationary site position estimates for 22PO from analysis of pressure data using GeoPressureR.

(<https://www.ivb.cz/wp-content/uploads/JVB-vol.-73-2024-WongJ.B.-et-al.-Table-S1-Fig.-S1-S3.pdf>)

## Studie 15

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

# SCIENTIFIC REPORTS



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

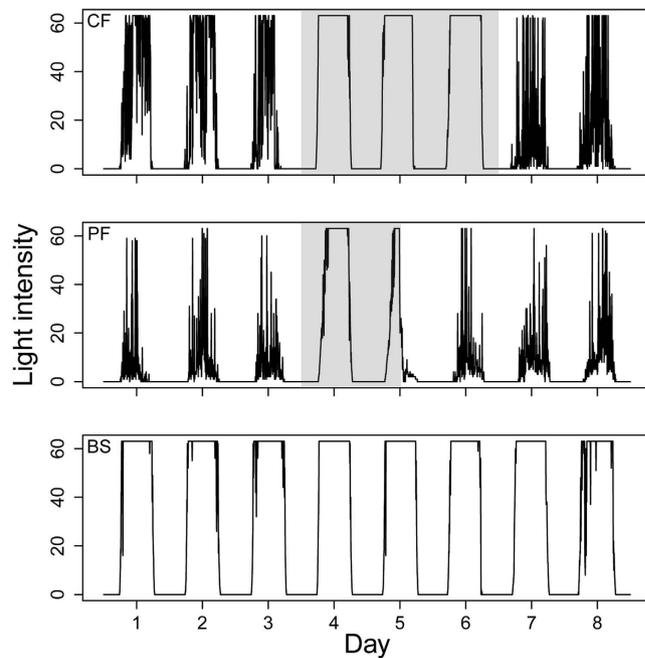
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Over decades it has been unclear how individual migratory songbirds cross large ecological barriers such as seas or deserts. By deploying light-level geolocators on four songbird species weighing only about 12 g, we found that these otherwise mainly 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 non-stop, 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.

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<sup>1</sup>. An estimated 2.1 billion songbirds and near-passerines move from Europe to Africa each autumn<sup>2</sup>. 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<sup>3</sup> 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<sup>3</sup>. However, since the 1980s, an accumulating number of studies brought evidence in favour of the alternative intermittent migratory strategy<sup>4–7</sup>. 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<sup>8–11</sup>. 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

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**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.

from nocturnal to partially diurnal migration. In general, nocturnal migration is the prevailing pattern in small birds within the Palaearctic African migration system<sup>12</sup>. With our own survey we estimate that about 63% of species (44 out of 70 trans-Saharan migrants for which we have collated data; Supplementary 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<sup>13</sup>, 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<sup>14–16</sup>. 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 and temporal occurrence of light anomalies.** 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 Supplementary 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 (Supplementary Table S2). The majority of the stopover sites preceding and following FLPs are located North and

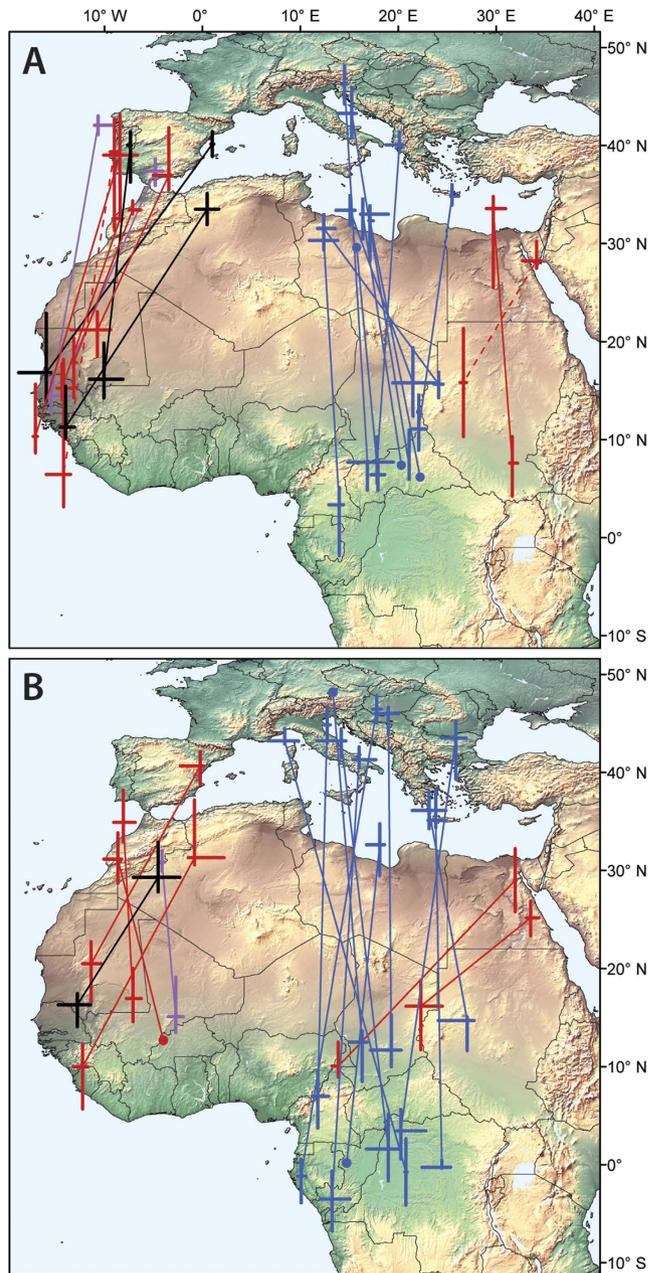
Light pattern		Occurrence in		Description	Interpretation	
		Autumn	Spring			
	No FLP	26.5% (9)	-	Shaded sensor during the day	Bird stays in habitat, no diurnal migration	<b>A</b>
	Perfect FLP	26.5% (9)	34.8% (8)	No sensor shading during the day	Diurnal movement or resting in sun-exposed habitat	<b>B</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	<b>C</b>
	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	<b>D</b>
	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	<b>E</b>
	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	<b>F</b>
	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	<b>G</b>
	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	<b>H</b>

**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).

South of the Sahara (Fig. 3), demonstrating that FLP occurred while the birds were crossing the Sahara and/or the Mediterranean Sea.

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 ( $b = 0.033 \pm 0.009$  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  $\pm$  SE: autumn  $52.1 \pm 7.7$  h, spring  $47.7 \pm 7.6$  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 Supplementary Table S2). Four out of 22 birds tracked during

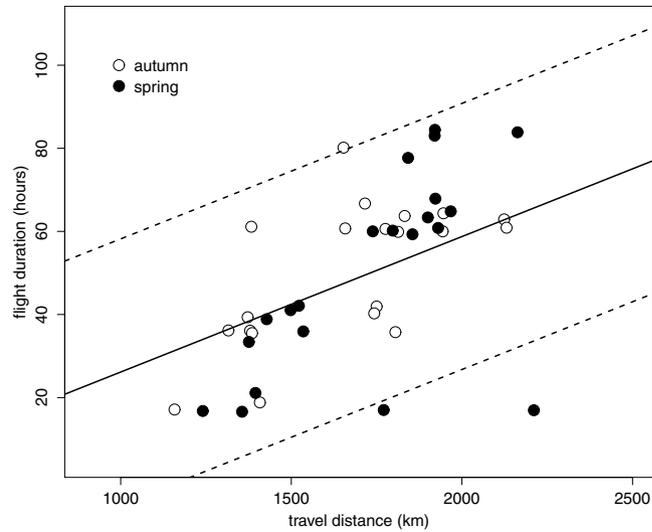


**Figure 3.** Autumn (A) and spring (B) stationary sites of birds (median  $\pm$  25<sup>th</sup> and 75<sup>th</sup> percentiles of location estimates) just prior and after the occurrence of the full light pattern (blue = collared flycatcher, black = pied flycatcher, red = Eurasian reed warbler, purple = 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.

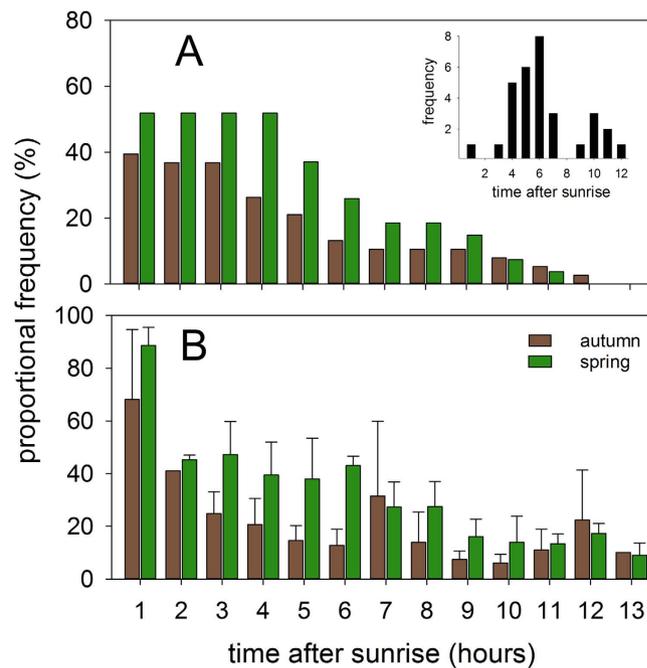
both migratory periods showed the same pattern of barrier crossing (Supplementary Table S3). If we consider categories B and C (Fig. 2) as a variation on the same pattern, then 9 out of 22 birds showed the same pattern.

Consistent with radar measurements (Fig. 5b<sup>6</sup>) 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 day-time) 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  $5.8 \pm 3.0$  (SD) hours ( $n = 15$  cases) after sunrise in autumn and  $6.8 \pm 2.1$  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



**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  $\pm$  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  $\pm$  SD) recalculated from a radar field study in the Mauritanian Sahara<sup>6</sup>.

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 (Supplementary Fig. S3). The simulation shows that for spring migration a slightly higher percentage of daytime flights are necessary for crossing the desert (Supplementary 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 (Supplementary 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.

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<sup>17</sup>. 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 geocator studies showed fast crossing of the Sahara desert<sup>7,18,19</sup>.

Earlier field studies demonstrated that nocturnally migrating birds of unknown provenience prolong their flights into the day<sup>3,11,20,21</sup>. It was generally believed that these prolonged flights had just a very short duration and most birds tended to land shortly after dawn<sup>6,11,22</sup> (but see<sup>10</sup>). 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<sup>6</sup> (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.*<sup>6</sup>. 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<sup>23</sup> 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<sup>24</sup>. Tailwinds are similar in autumn but at lower flight altitudes, in hotter and dry air<sup>24</sup>, 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<sup>11</sup>. 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<sup>4,17</sup>) 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<sup>3,9,10</sup> but were supposing that a small number of birds were doing so and that landing occurred shortly after dawn<sup>6</sup>. 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<sup>13</sup>. 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<sup>25–27</sup>. 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<sup>28</sup>. 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 song-bird 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 (Supplementary 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<sup>29–32</sup>. When inspecting geocator 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 Supplementary 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 Geocator (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<sup>33</sup>) 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 (Supplementary 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<sup>34</sup>. 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 95<sup>th</sup> percentile in barn swallows were 127 min and 91 min, respectively (Supplementary 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  $\pm$  their 25<sup>th</sup>/75<sup>th</sup> 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<sup>35</sup>. 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 Supplementary 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<sup>36–38</sup>. 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<sup>11</sup>. 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<sup>6</sup>. 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<sup>-1</sup> 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<sup>39</sup>.

**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.

## Additional Information

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## Studie 16

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

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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.

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 sub-optimal 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 (Ouweland 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.

## Material 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 aluminum 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 (Supplementary material Appendix 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 geocator including the harness weighed  $0.6 \pm 0.04$  g which represents less than 5% of the body mass of the tagged birds (mean  $\pm$  SD, northern population: males =  $13.2 \pm 0.5$  g,  $n = 59$ ; females =  $13.7 \pm 0.7$  g,  $n = 40$ ; southern population: males =  $12.9 \pm 0.6$  g,  $n = 33$ ; females =  $13.2 \pm 0.6$  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-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 Supplementary material Appendix 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:  $13^{\circ}47'S$ ,  $23^{\circ}56'E$ ; southern population:  $16^{\circ}30'S$ ,  $23^{\circ}38'E$ ). 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  $14^{\circ}$ – $20^{\circ}$  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

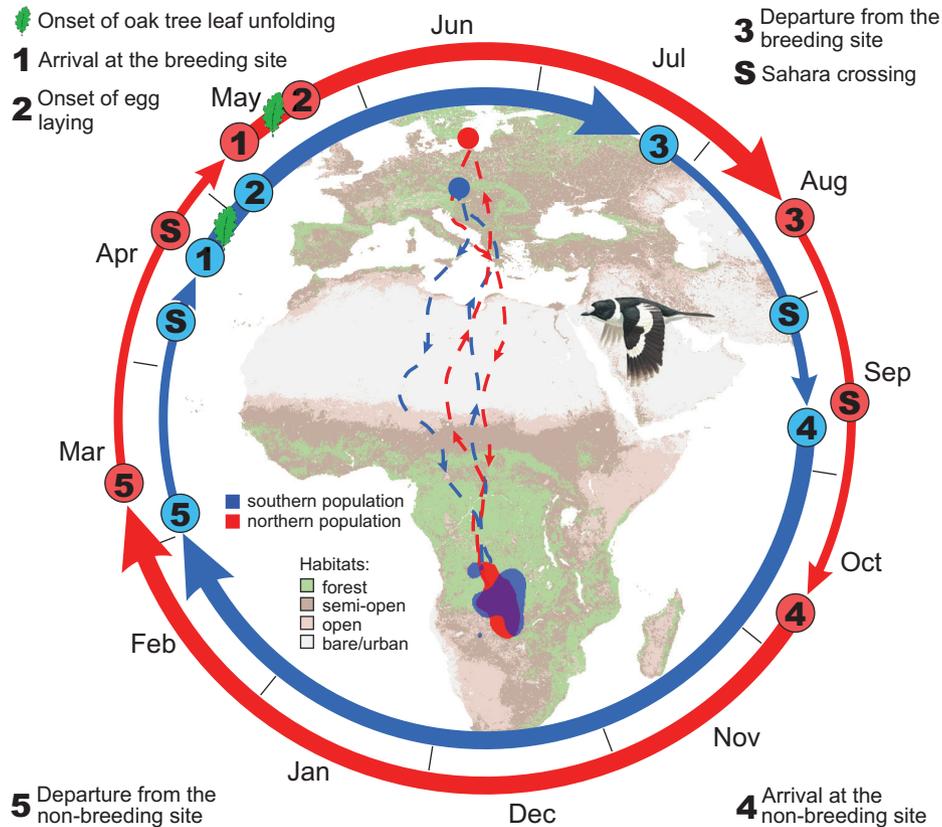


Figure 1. Spatiotemporal organization of the annual cycle of the northern (red) and southern (blue) breeding populations of a trans-Equatorial migrant, the collared flycatcher. Breeding sites (dots), migration routes (population median routes expressed as changes in observed longitude in respect to time elapsed since departure) and non-breeding residency areas (70% kernel density isopleths). North-south 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.

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 non-breeding 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. 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,  $W = 0$ ,  $p < 0.001$ ).

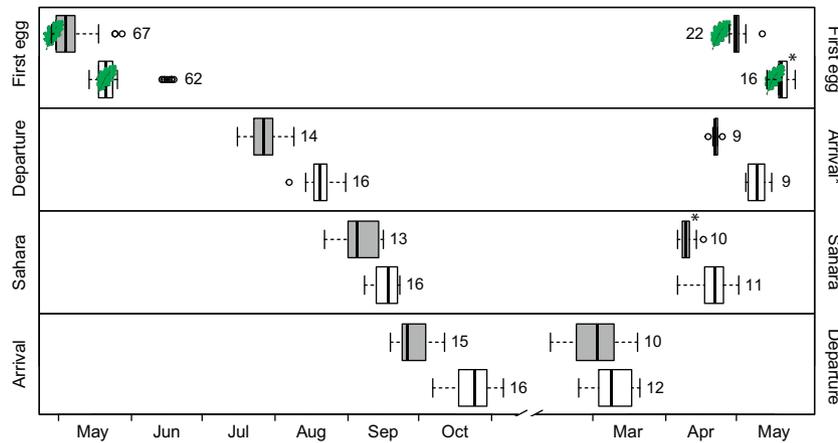


Figure 2. Timing of major events over the collared flycatcher's annual cycle (first egg laid, migratory departure, Sahara crossing and arrival) from the southern (grey box plots) and the northern breeding populations (white box plots). Only geolocator-tagged birds are considered. Sample size for each 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, Supplementary material Appendix 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 non-breeding 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, Ouweland 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 its 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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Supplementary material (Appendix JAV-01002 at <[www.avianbiology.org/appendix/jav-01002](http://www.avianbiology.org/appendix/jav-01002)>). Appendix 1–2.

## Studie 17

Briedis, M., Hahn, S., Krist, M. & Adamík, P. 2018: Finish with a sprint: Evidence for time-selected last leg of migration in a long-distance migratory songbird. *Ecology and Evolution* 8: 6899–6908.

## ORIGINAL RESEARCH

# Finish with a sprint: Evidence for time-selected last leg of migration in a long-distance migratory songbird

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**Abstract**

Under time-selected migration, birds should choose a strategy for outcompeting rivals over securing access to prime resources at the final destination. Thus, migration can be viewed as a race among individuals where winners are arriving first when conditions are suitable. The sprint migration hypothesis predicts that individuals shift from maximum sustained speed to a final burst of sprint to shorten the transition from migration to breeding (Alerstam, 2006). In this study, we test the hypothesis of a final sprint migration in a long-distance Afro-Palaearctic migrant, the collared flycatcher *Ficedula albicollis*, during autumn and spring, and compare migration strategies between the seasons. In both seasons, collared flycatchers evidently exhibited sprint migration by increasing their overall speed over the last leg of migration after the Sahara crossing. This phenomenon was more pronounced in spring, contributing to overall faster spring migration and possibly highlighting higher importance for early arrival at the breeding grounds. In both seasons and particularly in spring, late departing individuals flew at a faster rate, partially being able to catch up with their early departing conspecifics. Differential fueling strategies may play an important role in determining migration speed, especially during the early stages of the migration, and might explain the observed differences in migration speeds between late and early departing individuals. Our findings suggest competition for early arrival at the breeding and at the nonbreeding destinations alike. Sprint migration might be an appropriate strategy to gain advantage over conspecifics and settle in prime territories as well as to cope with the increasingly earlier springs at high latitudes.

**KEYWORDS**

geolocator, long-distance migrant, migration speed, migration-breeding transition, optimal migration, sprint migration

## 1 | INTRODUCTION

The ecological background for why birds migrate differs seasonally (Newton, 2008). In autumn, the drive for migration comes from a self-preservation viewpoint as birds try to increase their chances of survival by escaping the forthcoming unfavorable conditions at

their breeding sites. In spring, however, birds urge to return to the breeding sites to exploit the seasonal increase in food availability for reproduction. Because of these season-specific causes for migration and the variable life history events following the migration, birds may adopt different migration strategies in each of the seasons. The optimal migration theory (Alerstam, 2011) states that birds on the

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move should optimize their energy expenditure (transport costs)—the energy minimization strategy—and they should maximize the total migration speed—the time-minimization strategy (Hedenström, 2008). However, the two strategies may be seen as two endpoints along a continuum and birds may adopt intermediate behaviors depending on the relative importance of energy- and time-selection pressure (Alerstam & Lindström, 1990).

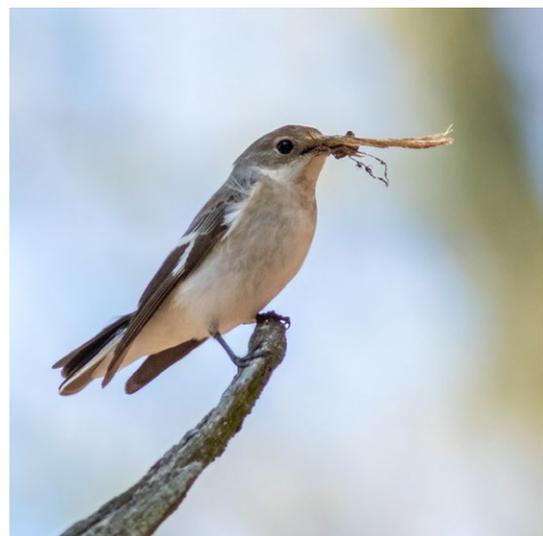
Passerines are typical income breeders (Langin, Norris, Kyser, Marra, & Ratcliffe, 2006) and arrive at the breeding grounds early and use the local resources for reproduction. Earlier arriving individuals, thus, outcompete their rivals for access to important assets, like prime breeding territories (Kokko, 1999). Because early arrival time is of high importance for reproductive success, we may expect the birds to optimize time, rather than energy during the spring migration, that is, to adopt the time-minimization strategy (Alerstam & Lindström, 1990). While advantages of early arrival are evident in spring, the benefits for early arrival at the nonbreeding grounds are less obvious (Gill et al., 2001). If competition for resources, like prime molting sites, at the nonbreeding areas is fierce, we may expect similar migration strategies in respect to timely arrival in both seasons. If arrival time at the nonbreeding sites is of low importance, birds may rather choose to optimize their energy expenditure during the autumn migration, that is, to adopt the energy minimization strategy, and thus, migrate at an overall slower speed as compared to spring (Alerstam & Lindström, 1990).

While theoretical background of the arrival game is strong (Kokko, 1999), we still lack good empirical evidence of the mechanisms how individuals secure early (spring and possibly autumn) arrival to outcompete their rivals. Early arrival could be induced by departing for migration before the competitors and/or by migrating at a faster speed. Earlier tracking studies have shown that the overall migration duration in passerines is shorter and speed is higher in spring than in autumn (McKinnon, Fraser, & Stutchbury, 2013; Nilsson, Klaassen, & Alerstam, 2013; Schmaljohann, 2018). Faster migration can be achieved by flying at higher speeds or by shortening the duration of stopovers. Radar studies revealed that nocturnal migrants fly on average at 12%–16% higher speed in spring compared to autumn (Karlsson, Nilsson, Bäckman, & Alerstam, 2012; Nilsson, Bäckman, & Alerstam, 2014). However, such increase in flight speed contributes relatively little to increasing the overall migration speed, as the vast majority of time during migration is spent on stopovers, rather than actually flying (Hedenstrom & Alerstam, 1997). Therefore, the faster spring migration is more likely to originate from a reduction in stopover time. One way or another, the overall faster spring migration exposes that the importance for early arrival is essentially different in autumn and spring.

How and where migrants adjust their migration speed along the route is still not known. Birds may achieve higher overall speed by increasing the migration speed over the entire migratory journey or increasing the speed of a particular leg of migration. Alerstam (2006) has proposed the “sprint migration” hypothesis: Migratory birds may adopt a variable strategy with optimizing energy expenditure

through the early part of the journey (i.e., energy minimization) followed by a period with increased migration speed to complete the migration (i.e., time-minimization strategy). However, we lack compelling evidence that migratory birds indeed increase the migration speed when approaching their destinations.

In this study, we measure migration speed over different legs of the migratory journey to disentangle the strategies adopted by birds during autumn and spring migration. We use collared flycatcher *Ficedula albicollis* (Figure 1), a small long-distance passerine migrant breeding in Europe and overwintering in south-central Africa (Briedis, Hahn et al., 2016), as our model species. The Afro-Paleartic bird migration system comprises of temperate and tropical-subtropical zones which are separated by a large ecological barrier—the Sahara Desert. Recent evidence from tracking studies shows rapid desert crossing by small passerines (Adamík et al., 2016; Ouweland & Both, 2016; Xenophontos, Blackburn, & Cresswell, 2017), including the collared flycatcher, with the main stopovers typically found before the barrier crossing (Briedis, Beran, Hahn, & Adamík, 2016; Risely, Blackburn, & Cresswell, 2015). Thus, comparing migration speeds and durations prior and after the desert crossing allows for insights into migratory strategies over different legs of the migration journey. We hypothesize that (a) early arrival at the destination is of high importance in both seasons and to attain this, birds adopt the sprint migration strategy (Alerstam, 2006). Thus, we predict that migration speed will be faster for the last migration leg after the Sahara crossing in both autumn and spring. We also hypothesize (b) that the pressure for early arrival is larger in spring than in autumn (Kokko, 1999). Hence, we predict that the overall speed of migration will be higher and birds will advance noticeably more through the last leg of migration during spring compared to autumn. Lastly, we hypothesize that (c) sprint migration is used to outcompete rivals for early arrival at either destination. Therefore, we predict that the arrival date will highly depend on migration speed through the last leg of the migration.



**FIGURE 1** Collared flycatcher female. © Martins Briedis

## 2 | METHODS

### 2.1 | Study site and geolocators

We studied migration of collared flycatchers breeding at two nearby sites in the Czech Republic (Dlouhá Loučka: 49°50'N, 17°13'E and Velký Kosíř: 49°32'N, 17°04'E, distance between the sites = 30 km). Each site hosts a nest box population with ~100 breeding pairs which are monitored throughout the breeding season. In 2013 and 2014, we deployed 69 (33 males and 36 females) and 165 (157 males and 8 females) geolocators (model GDL2.0 with 7 mm light stalk, Swiss Ornithological Institute) on adult birds at Dlouhá Loučka and Velký Kosíř, respectively. Devices were attached on birds' backs using leg-loop silicone harnesses and each device including the harness weighted ~0.6 g (<5% of the body mass of the birds). At Dlouhá Loučka, we deployed all geolocators on breeding adults during the late nestling phase, while at Velký Kosíř, we equipped the birds with the devices upon their arrival at the site before the onset of breeding ( $n = 139$ ) and during the breeding season ( $n = 26$ ). Only 51 of the 139 males equipped with geolocators upon arrival at Velký Kosíř were later observed breeding in the nest boxes that season.

Next year after the deployment, we retrieved 28 geolocators (40.6%, 14 males, 14 females; +1 male 2 years later = 42% total recovery rate) at Dlouhá Loučka and 29 geolocators (17.6%, all males; +1 male 2 years later = 18.2% total recovery rate) at Velký Kosíř. The relatively low recovery rate at Velký Kosíř may at least partially be explained by the deployment of the devices on nonbreeding birds upon their spring arrival as the recovery rate was 43.3% when considering only males that were observed breeding in the nestboxes in 2014. At Dlouhá Loučka, geolocators had no noticeable effect on individual apparent survival compared to the control ringed-only birds (return rate of control individuals = 34.9%,  $\chi^2 = 0.30$ ,  $p = 0.58$ ). Unfortunately, we lack similar data of control birds from site Velký Kosíř as all the captured males were tagged.

### 2.2 | Geocator data analyses

We defined sunrise and sunset times of the recorded light data using "GeoLocator" software (Swiss Ornithological Institute) and set the light level threshold of 1 unit from the arbitrary scale of 61 to define transition times. Further, we analyzed geolocation data using the R-package "GeoLight" v 2.0.0 following the standard procedure (Lisovski & Hahn, 2012) outlined in Briedis, Hahn et al. (2016). We used a minimal stationary period of 3 days and probability of change ( $q$ -value) 0.85 to determine stationary and movement periods with the "changeLight" function. Beginning and end of the migration periods were validated by visually inspecting changes in longitude over time as birds moved along the east–west axis. Further, geographic coordinates of individual nonbreeding sites were calculated using sun elevation angles derived from Hill-Ekstrom calibration, while the birds were at their nonbreeding residency sites (range: +8.6 to –0.7 for different individuals). Due to the high probability of errors when determining stationary periods of short duration, we did not

define any stopovers during migration. Such data would be of high risk to reflect data quality (which differed substantially among individuals as can be implied from the broad range of sun elevation angles stated above) rather than actual stopover times and sites of the flycatchers. In addition, we determined the date of Sahara crossing using prolonged periods of uninterrupted high light intensities as birds extend their nocturnal flights into the day when crossing the barrier (Adamík et al., 2016).

### 2.3 | Statistical analyses

Migration period is defined as a period starting from predeparture fueling until arrival at the final destination (Alerstam, 2003). Current remote tracking techniques do not allow for quantifying the stationary fueling period before departure. Thus, we excluded this period from our estimations of migration speed, but we examine the possible effects of the predeparture fueling period for migration speeds in the discussion. Therefore, the migration speed here is defined in a conservative way as the rate of movement from the departure until arrival, including stopovers.

We excluded one outlying individual of extraordinary long autumn migration (logger ID: 11PE, 101 days, mean =  $61.1 \pm 10.0$  (SD) days) from further analyses. We used general linear models to identify whether there was an effect of study year (and accordingly study site), birds' age (second calendar year or older), and sex on the migration speeds in autumn and spring. Analyses revealed that neither of the factors were significant predictors for migration speeds in neither of the seasons (Table 1). Thus, we pooled the data across study years, study sites, sexes, and age classes (age 5 and 6, EURING code). We selected the southern and northern edges of the Sahara Desert as the start and end points of specific migration segments generating two main migration legs for each season: (a) first leg—from departure until completion of the Sahara crossing; (b) last leg—from completion of the Sahara crossing until arrival. We included the period of Sahara crossing in the first leg of migration as barrier crossing is typically preceded by prolonged stopovers for fueling (Bayly, Atkinson, & Rumsey, 2012; Briedis, Beran et al., 2016; Risely et al., 2015; Schaub & Jenni, 2000), followed by a rapid desert crossing previously shown in collared flycatchers (Adamík et al., 2016). The duration and migration speed of the Sahara crossing of our tracked birds was  $2.5 \pm 0.4$  days (SD),  $828 \pm 116$  km/day in autumn, and  $3.0 \pm 0.7$  days,  $702 \pm 154$  km/day in spring. We estimated the total migration distance as a great-circle (orthodromic) distance between the breeding site and the median location of the estimated nonbreeding site of each individual. As a result, the migration segments over Europe and over the Sahara Desert were estimated each at 2,000 km long, while the segment in sub-Saharan Africa was ca. 3,000 km long. Please note that as we excluded the predeparture fueling period from calculations of migration speed, we consequently overestimate the overall migration speed across the entire journey, as well as over the first migration leg (see Section 4).

**TABLE 1** Summary statistics of general linear models of study year, birds' sex, and age on migration speed in (a) autumn and (b) spring

	Estimate	SE	t value	p-value
<b>(a) Autumn migration speed (df = 33)</b>				
Intercept	109.4	11.0	9.9	<0.01
Year <sub>(2015)</sub>	16.4	12.7	1.3	0.21
Sex <sub>(male)</sub>	-1.2	15.2	-0.1	0.94
Age <sub>(2nd calendar year)</sub>	3.8	9.4	0.4	0.69
<b>(b) Spring migration speed (df = 22)</b>				
Intercept	148.2	17.3	8.6	<0.01
Year <sub>(2015)</sub>	9.8	17.7	0.6	0.59
Sex <sub>(male)</sub>	-15.0	22.4	-0.7	0.51
Age <sub>(2nd calendar year)</sub>	5.6	13.9	0.4	0.69

Unfortunately, not all the recovered geolocators contained data of full annual schedules, and thus, our analyses are based on 41 individual tracks. Sample sizes for specific migration parts are as following: full autumn migration  $n = 36$ ; autumn first leg  $n = 37$ ; autumn second leg  $n = 38$ ; full spring migration  $n = 26$ ; spring first leg  $n = 28$ ; spring second leg  $n = 26$ ; full annual tracks  $n = 24$ .

We used nested ANOVA to test for differences in migration speed through different parts of the migration irrespective of the season. Two-tailed paired  $t$  tests were used to compare migration

speeds in autumn and spring of individual birds. Further, we used linear models to test whether there is a relationship between departure dates and migration speed of different parts of the migratory journey, as well as between arrival and departure dates.

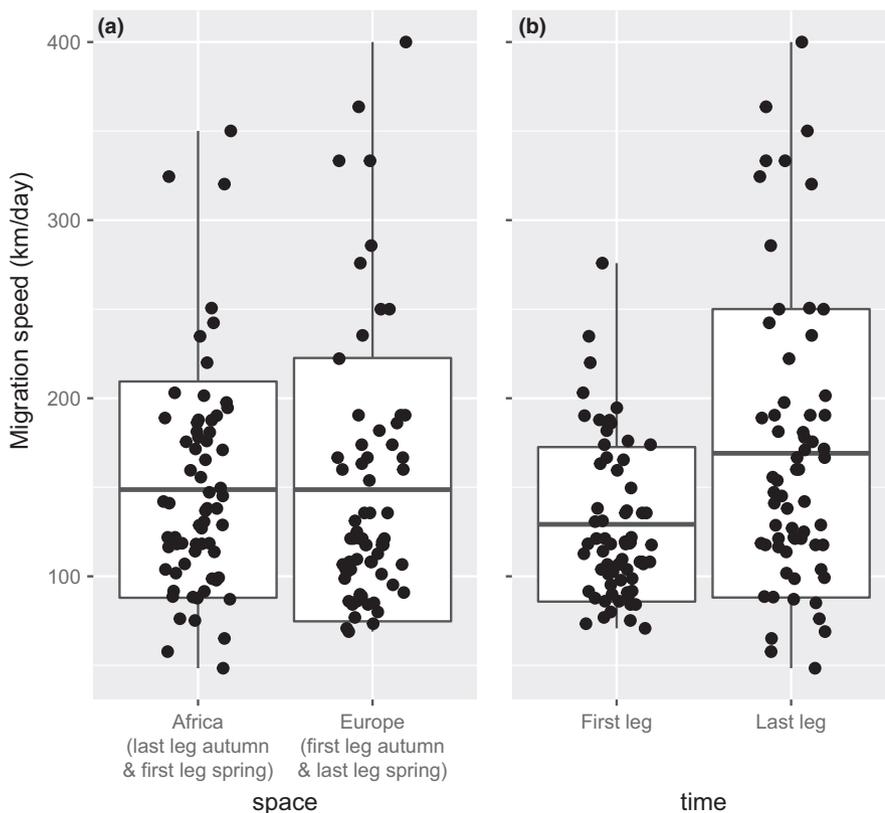
### 3 | RESULTS

#### 3.1 | Migration speed through different parts of the journey

We found no statistical differences in migration speed between the two spatial parts of the migration ( $F_{1,89} = 0$ ,  $p = 1$ ; Figure 2a) when pooling data of both seasons with speeds “through Africa” *sensu lato* (the second leg in spring & the first leg in spring) averaged at  $148.7 \pm 60.7$  km/day (SD) and “through Europe” *sensu lato* (the first leg in autumn and second leg in spring) at  $148.7 \pm 73.9$  km/day. On the contrary, we found the last leg to be significantly faster ( $F_{1,89} = 12.5$ ,  $p < 0.001$ ; Figure 2b), with migration speeds through the first migration leg  $129.2 \pm 43.4$  km/day and through the last migration leg after the Sahara crossing  $169.1 \pm 81.0$  km/day (data pooled for both seasons).

#### 3.2 | Migration speed in autumn and spring

Average migration speed over the entire journey was significantly faster in spring ( $144.2 \pm 30.4$  km/day) compared to autumn ( $120.9 \pm 26.1$  km/day; Figure 3a). We found that for only four individuals (of 24) the average migration speed was lower in spring



**FIGURE 2** Comparison of migration speeds through different parts of the migration irrespective of the season. (a) Migration speeds across spatial scales, (b) migration speeds across temporal scales. Horizontal lines depict mean values, boxes—SD, vertical lines—range of data, and points denote individual data

(Figure 3a), highlighting the overall faster spring migration on the individual level. We also found that birds increased their migration speed over the last leg of migration after the Sahara crossing (Figure 4) in both seasons. Spring migration speeds were typically faster for both migration legs (Figure 3d,e), with particular advancement through Europe (Figure 3c).

We found a positive relationship between departure date and the overall migration speed in both seasons (autumn:  $b = 1.33 \pm 0.35$  (SE),  $F_{1,35} = 14.0$ ,  $p < 0.001$ ,  $r^2 = 0.29$ ; spring:  $b = 2.47 \pm 0.36$ ,  $F_{1,24} = 45.9$ ,  $p < 0.001$ ,  $r^2 = 0.66$ ; Figure 5a,c). This phenomenon was largely caused by faster migration of the late departing individuals through their first leg of migration (autumn:  $b = 1.45 \pm 0.58$ ,  $F_{1,37} = 6.3$ ,  $p = 0.02$ ,  $r^2 = 0.15$ ; spring:  $b = 3.13 \pm 0.63$ ,  $F_{1,26} = 24.3$ ,  $p < 0.001$ ,  $r^2 = 0.48$ ). The speed of the last migration leg was similar for all individuals, irrespective of their departure (autumn:  $b = 0.65 \pm 1.15$ ,  $F_{1,35} = 0.3$ ,  $p = 0.57$ ,  $r^2 = 0.01$ ; spring:  $b = 1.71 \pm 1.79$ ,  $F_{1,24} = 0.9$ ,  $p = 0.35$ ,  $r^2 = 0.04$ ).

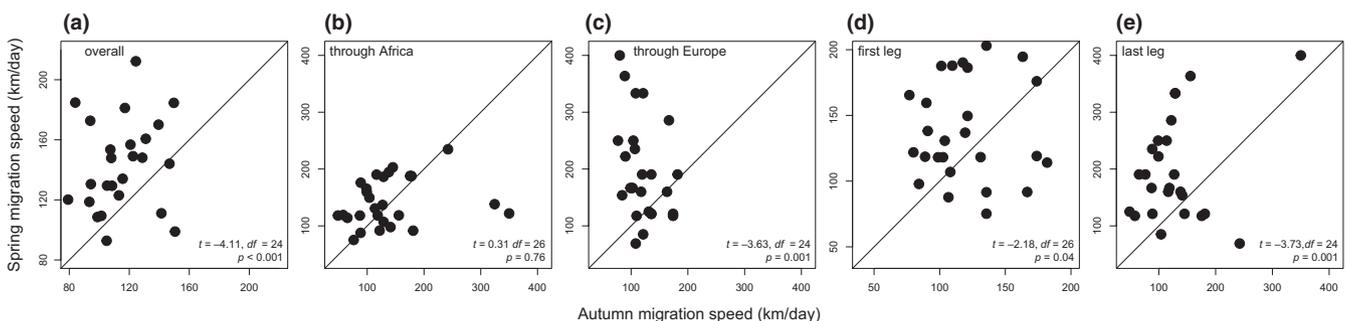
There was a negative relationship between arrival date and migration speed in autumn ( $b = -0.90 \pm 0.42$ ,  $F_{1,35} = 4.5$ ,  $p = 0.04$ ,  $r^2 = 0.11$ ; Figure 5b), but not in spring ( $b = -0.83 \pm 0.99$ ,  $F_{1,24} = 0.7$ ,  $p = 0.41$ ,  $r^2 = 0.03$ ; Figure 5d). However, when excluding one outlying individual whose autumn migration speed was higher than 200 km/day, the relationship between autumn migration speed and nonbreeding arrival date was not significant ( $b = -0.57 \pm 0.36$ ,  $F_{1,34} = 2.5$ ,  $p = 0.12$ ,  $r^2 = 0.07$ ). There was a significant and positive relationship between the departure and the arrival date in autumn ( $b = 0.49 \pm 0.13$ ,  $F_{1,37} = 14.3$ ,  $p < 0.001$ ,  $r^2 = 0.28$ ; Figure 6a), but not in spring ( $b = 0.20 \pm 0.12$ ,  $F_{1,24} = 2.9$ ,  $p = 0.10$ ,  $r^2 = 0.11$ ; Figure 6b). We found a weak positive relationship between autumn arrival date and migration speed of the last migration leg after the Sahara crossing ( $b = -0.04 \pm 0.02$ ,  $F_{1,38} = 3.6$ ,  $p = 0.07$ ,  $r^2 = 0.09$ ), while there was no significant relationship between the speed through the first leg of the migration before Sahara and arrival time ( $b = -0.02 \pm 0.04$ ,  $F_{1,37} = 0.3$ ,  $p = 0.56$ ,  $r^2 = 0.01$ ). Spring arrival date was not significantly related to migration speed of the last migration leg ( $b = 0.01 \pm 0.01$ ,  $F_{1,24} = 0.2$ ,  $p = 0.63$ ,  $r^2 = 0.01$ ), nor with the first migration leg ( $b = 0.01 \pm 0.02$ ,  $F_{1,24} = 0.2$ ,  $p = 0.88$ ,  $r^2 < 0.01$ ).

## 4 | DISCUSSION

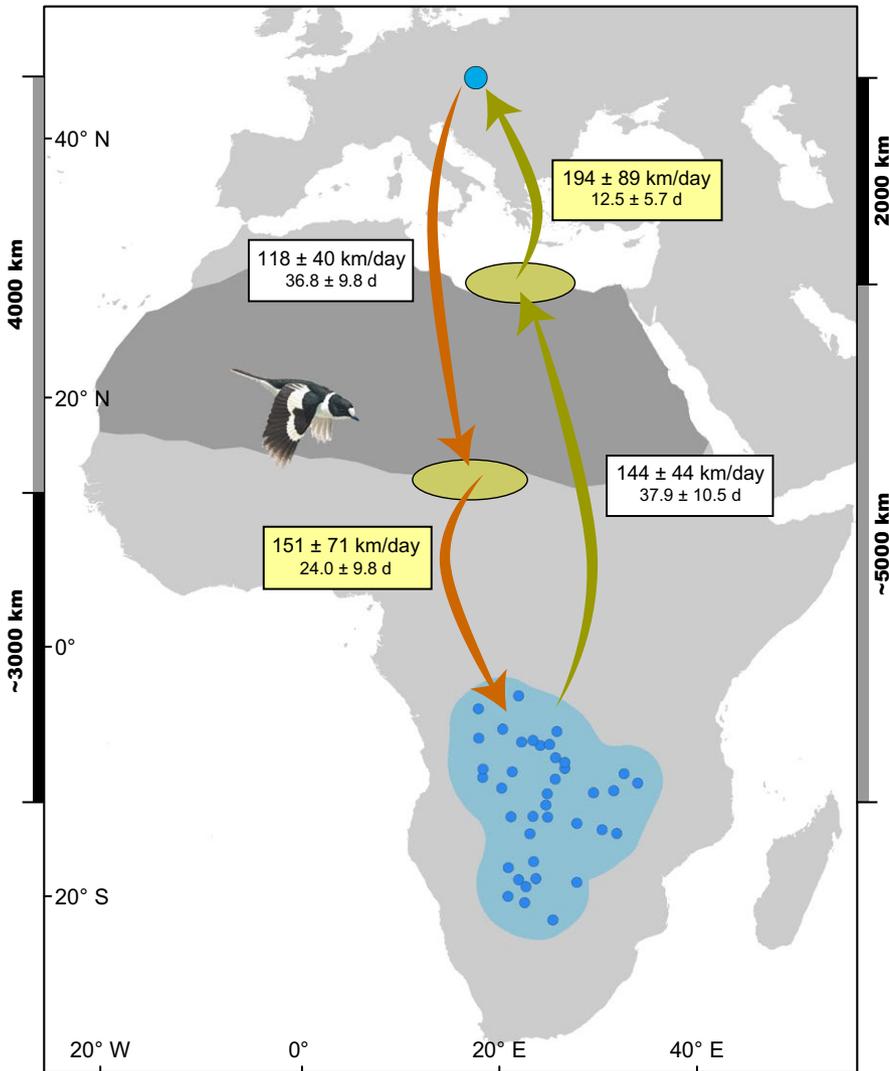
In this study, we first show that long-distance migratory collared flycatchers adopt similar migration strategies in autumn and spring by increasing their migration speed in the last part of the journey after crossing the Sahara Desert. This supports the Alerstam's sprint migration hypothesis (Alerstam, 2006). Second, we reveal that migration through the last leg of the journey is faster in spring than in autumn, largely accounting for an overall faster spring migration and possibly indicating higher pressure for early arrival in spring. We also demonstrate that the overall migration speed in both seasons depends on departure date and late departing individuals are (at least partially) able to catch up with their early departing conspecifics to arrive at the destination at a similar time. Again, this phenomenon is more pronounced in spring, highlighting the possibly higher pressure for early arrival in this season. Our third hypothesis is partially supported—there is a positive trend for relationship between arrival date and migration speed through the last leg in autumn, but not in spring. It may be that in spring, most individuals exhaust themselves to the sustainable limits leaving little room for individual variation.

### 4.1 | Sprint migration

As Alerstam (2006) coined the "sprint migration" hypothesis, he exemplified migration speeds of two male ospreys *Pandion haliaetus* at the tail end of their migrations in autumn and spring. None of the birds exhibited sprint migration in autumn, but results were ambiguous for one in spring. Likewise, GPS-tracked honey buzzards *Pernis apivorus* and Montagu's harriers *Circus pygargus* did not show sprint migration to finish their journeys in either of the seasons (Vansteelant et al., 2015). Nilsson et al. (2013) also report no seasonal differences in the overall migration duration for thermal soaring migrants contrasting the findings in songbird migration. Ring recoveries have shown that songbirds tend to increase their migration speed along the route (Ellegren, 1993; Hedenström & Pettersson, 1987), providing indirect evidence for adoption of sprint migration strategy. Geolocator-tracked swifts *Apus apus* showed



**FIGURE 3** Comparison of individual migration speeds in autumn and spring, including speeds (a) over the entire migration, (b) through Africa, (c) through Europe, (d) the first leg of migration, and (e) the last leg of migration after the Sahara. Values below the diagonal line denote cases when the individual migrated faster in autumn than in spring (summary statistics of two-tailed paired t tests are given within each panel)



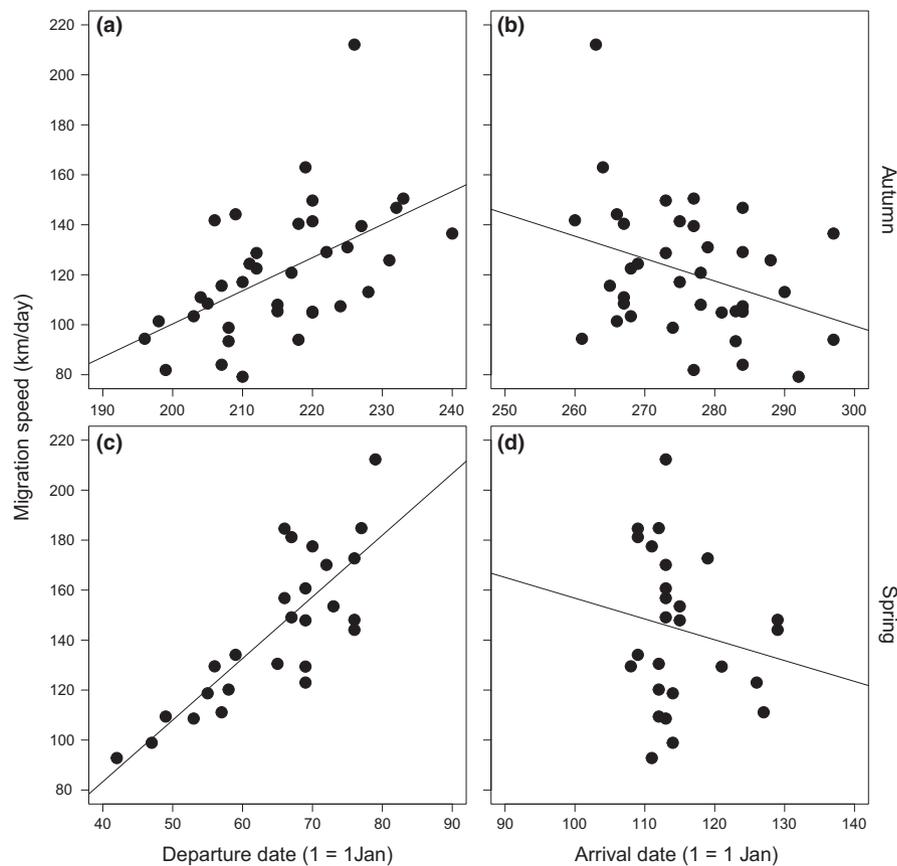
**FIGURE 4** Average migration speed (km/day) and duration (days, d)  $\pm$ SD of the tracked collared flycatchers over different legs of the migratory journey. Sprint migration over the last migration leg is highlighted in yellow. Larger blue circle denotes breeding site, light blue area—nonbreeding range with median coordinates of individual nonbreeding sites depicted as small blue circles. Arrows schematically illustrate different migration legs but do not depict precise migration routes taken. Map is shown in azimuthal equidistant projection centered at 0° latitude and 20°E longitude. The collared flycatcher illustration © Birds of Armenia Project

no clear pattern of changes in travel rate between early and late stages of migration, while, similar to our tracked flycatchers, the swifts showed increased speed during the barrier crossing (Åkesson, Klaassen, Holmgren, Fox, & Hedenström, 2012). Rapid crossing of ecological barriers have also been demonstrated in other songbirds (Adamík et al., 2016; Ouwehand & Both, 2016) as well as waders (Klaassen, Alerstam, Carlsson, Fox, & Lindström, 2011; Pakanen et al., 2018). However, a comprehensive comparison of migration speeds in songbirds over different parts of their journey is still lacking due to former weight limitations of tracking devices.

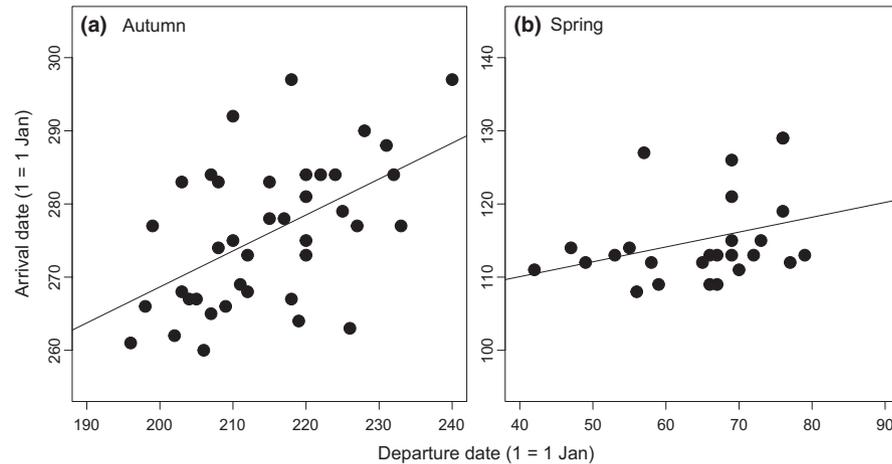
The changes in speed over different legs of migration found in collared flycatchers may alternatively be explained by a reduction in migration speed over the first migration leg rather than advancement over the last leg. The overall slower speed during the first migration leg might arise due to prolonged stopovers for fuel accumulation before the cross-desert flight or simply by weather-induced delays of Sahara crossing. However, the latter should affect the migration speed both ways as some individuals may delay the Sahara crossing, while others may rush it to catch the optimal conditions. Furthermore, it has been recently shown that collared flycatchers

routinely cross the Sahara Desert in flights reaching speeds of up to 1,000 km/day (Adamík et al., 2016; see Section 2). Therefore, we included the Sahara crossing in the first migration leg to diminish the effect of the lengthy pre-desert stopovers on the overall speed of the first migration leg.

It is to be noted that our calculated migration speeds through the first leg are likely an overestimation due to the exclusion of predeparture fueling period (Alerstam, 2003). While accurate measure of individual predeparture fueling times is currently not possible using remote tracking techniques, Zhao et al. (2018) estimated that predeparture fueling in waders of various body sizes can take longer than the actual movement period between breeding and nonbreeding sites, leading to overestimation of migration speed by up to 60%. Unfortunately, we lack similar data on predeparture fueling durations in flycatchers before either autumn or spring migrations. In the Zhao et al. (2018) study, they also found a positive relationship between predeparture fueling duration and lean body mass of the species. Following their calculations, the predeparture fueling in collared flycatchers may range roughly between 5 and 10 days (depending on the on-site specific intake rates). In such



**FIGURE 5** Ordinary least squares regression between overall migration speed and (a, c) migratory departure and (b, d) arrival dates in autumn and spring



**FIGURE 6** Ordinary least squares regression between migratory departure and arrival dates in (a) autumn and (b) spring

case, our migration speed for the first leg would be overestimated by 14%–25% in autumn and 13%–23% in spring. After the flight across the Sahara Desert and the completion of the first migration leg, flycatchers' fuel reserves are presumably depleted and need to be renewed before continuing the migration. The last migration leg therefore may reflect nearly true migration speed including both fueling and flight to the final destination. Therefore, the difference in the observed migration speeds between the first and the last legs of migration is likely even larger with more pronounced sprint migration when considering the predeparture fueling as part of the first migration leg.

## 4.2 | Seasonal differences in time-selected migration

It is widely accepted that pressure for timely arrival in spring is higher due to the strong relationship between early arrival, breeding time, and subsequent reproductive success (Kokko, 1999; Wiggins, Pärt, & Gustafsson, 1994). We have also shown that there is such positive relationship between early arrival and early breeding in our study population ( $b = 1.26 \pm 0.28$ ,  $F_{1,21} = 20.73$ ,  $p < 0.001$ ,  $r^2 = 0.50$ ; Briedis et al. 2018). Differences between spring and autumn migration durations are largely induced by reduction in stopover duration;

the increase in flight speeds contributed relatively little (Nilsson et al., 2013; Schmaljohann, 2018). As the stopover durations are tightly linked to fueling rates (Schaub, Jenni, & Bairlein, 2008), it may be that the environmental conditions like food abundance and day length (i.e., the time available for foraging) at least partially explain the higher migration speeds observed in spring. Disentangling the intrinsic behavioral adaptations of individuals from those induced by changes in the environment is challenging and remains to be accomplished. However, at least in the case of collared flycatchers, the feeding conditions should be better during the autumn migration with higher food abundance along the route, while having similar daylight hours for feeding in both seasons (Bauchinger & Klaassen, 2005). Thus, we propose that competition for resources at the final destination rather than improved environmental conditions *en route* may better explain the faster overall spring migration as well the sprint finishes observed in the collared flycatchers.

Competition for resources at the nonbreeding sites (Lindström & Ålerstam, 1992; Price, 1981) may also explain why autumn migration schedules of long-distance migrants are tightly linked to the time of completion of breeding (Briedis, Hahn et al., 2016; Conklin, Battley, Potter, & Fox, 2010). Many long-distance migrants likely begin the autumn migration as soon as their respective breeding cycles are over and they are in a physiological condition required for migration. With the progression of autumn, the Northern Hemisphere experiences depletion in resources for long-distance migrants, while on the contrary, autumn marks the onset of rainy season in the Sahel where conditions are getting increasingly better. Thus, Afro-Palaearctic migrants would benefit from early and fast migration through Europe but, in case there is no competition for early arrival at the nonbreeding sites, could afford prolonged stopovers after the Sahara crossing as the prey abundance flourishes. Though, the observed sprint migration of collared flycatchers during autumn may suggest competition at the nonbreeding grounds. Long-distance migrants spend several months at the nonbreeding sites where many species undergo full or partial feather molt and high-quality molting sites may be the limited resource that birds compete for (Greenberg, 1986; Sherry & Holmes, 1996; Studds & Marra, 2005; Stutchbury, 1994).

The predeparture fueling (not considered in our calculations of the overall migration speed) should similarly affect the overall migration speed in autumn and spring given the fueling rates at breeding and nonbreeding destinations are similar. We found that spring migration was on average  $11 \pm 14$  days (SD) shorter than autumn migration. If the observed pattern of faster spring migration originates solely by the amount of fat stored during the fueling, individual fat scores at departure in autumn would have to be much lower than at departure in spring. This would slow down the early parts of the migration as birds need to stop more often and/or for more extended periods to fuel for migratory flights. Even though this fits the pattern found in collared flycatchers where the migration speed through the first leg was slower in autumn compared to spring, it remains to be tested in the field by measuring fuel loads of birds upon migratory departure.

### 4.3 | What determines arrival time?

Migration schedules of long-distance migrants seem to be under tight endogenous control in autumn and spring alike (Berthold, 1991; Gwinner, 1996). In the closely related pied flycatcher *Ficedula hypoleuca*, spring arrival largely depends on the departure time from Africa, rather than migration speed (Ouwehand & Both, 2017). On the contrary, semicollared flycatcher *Ficedula semitorquata* spring arrival at breeding sites in Bulgaria differed significantly between years and was related to the environmental conditions *en route* and spring green-up at the breeding site (Briedis, Hahn, & Adamík, 2017; Briedis, Träff et al., 2016). Thus, migration speed through the last leg of migration reflected the arrival time more closely than departure time in semicollared flycatchers. Our results show that both strategies, that is, early departure and slow migration, and late departure and fast migration, are used by the collared flycatchers possibly reflecting differences in fueling strategies for the early parts of migration.

None of our geolocator-tracked birds adopted the strategy of early departure and fast migration speed. This may be due to physiological constraints and early departing individuals might recognize that they should depart earlier to arrive on time as they may be incapable of sustaining high migration speed throughout the journey. Unfavorable conditions *en route* or at the breeding sites may also be of high relevance in this regard (Briedis et al., 2017; Tøttrup et al., 2012). Migrating in spring before the environment is suitable implies high mortality risk. Late departing individuals might spend the extra time before the onset of migration to store additional fuel reserves for the early stages of migration. Such strategy would allow completing the first leg of migration without stopping-over for extensive fueling. If this is the case, we may expect to see the pattern shown by the collared flycatchers when late departing individuals are those migrating faster through the first leg of the migration. Such pattern has also been found in several warbler species of genus *Sylvia* (Fransson, 1995) as well as in a number of other short- and long-distance migrants (Ellegren, 1993) highlighting the importance of predeparture fueling as a determinant for migration speed through early stages.

Evidence suggests that in long-distance migrants the onset of migration is less flexible (Doren, Liedvogel, & Helm, 2017; Gwinner, 1989), while the migratory journey itself has a great potential for flexible adjustments (Briedis et al., 2017; Marra, Francis, Mulvihill, & Moore, 2005; Tøttrup et al., 2012; van Wijk et al., 2012). Within the Afro-Palaearctic bird migration system, cues about the environmental conditions at the destination can be obtained only after crossing the Sahara Desert (and possibly Mediterranean Sea). Such circumstances present a situation when speed through the first leg of migration may offer limited adjustments in accordance with the environmental conditions at the breeding grounds. Acceleration of migration speed through the last leg of the journey may play an important role not only in intraspecific competition but also in adjusting migration timing in accordance with phenology of each

particular spring as well as for climate change (Schmaljohann & Both, 2017).

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## CONFLICT OF INTEREST

None declared.

## AUTHOR CONTRIBUTIONS

MB conceived the idea and study design. SH provided geolocators. MB, MK, and PA collected data. PA organized and coordinated work in the field. MB with help of SH analyzed the data. MB wrote the manuscript with substantial contributions from all other authors.

## DATA ACCESSIBILITY

Raw sun events of geolocator data: Dryad: <https://doi.org/10.5061/dryad.v51p331>.

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## Studie 18

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# Linking events throughout the annual cycle in a migratory bird—non-breeding period buffers accumulation of carry-over effects

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## Abstract

Annual cycles of animals consist of distinct life history phases linked in a unified sequence, and processes taking place in one season can influence an individual's performance in subsequent seasons via carry-over effects. Here, using a long-distance migratory bird, the collared flycatcher *Ficedula albicollis*, we link events throughout the annual cycle by integrating breeding data, individual-based tracking, and stable-carbon isotopes to unravel the connections between different annual phases. To disentangle true carry-over effects from an individuals' intrinsic quality, we experimentally manipulated the brood size of geolocator-tracked males prior to tracking. We did not find unambiguous differences in annual schedules between individuals of reduced and increased broods; however, in the following spring, the latter crossed the Sahara and arrived at the breeding grounds earlier. Individuals with higher absolute parental investment delayed their autumn migration, had shorter non-breeding residency period but advanced spring migration compared to individuals with lower breeding effort. Neither the local non-breeding conditions (as inferred from  $\delta^{13}\text{C}$  values) nor the previous breeding effort was linked to the timing of the following breeding period. Furthermore, while on migration, collared flycatchers showed a pronounced "domino effect" but it did not carry over across different migration seasons. Thus, the non-breeding period buffered further accumulation of carry-over effects from the previous breeding season and autumn migration. Our results demonstrate tight links between spatially and temporally distinct phases of the annual cycles of migrants which can have significant implications for population dynamics.

## Significance statement

Timing is everything! This holds true also for migratory animals which must time their annual movements, breeding and non-breeding seasons according to the environment they live in. However, perfect timing of a particular event can be hampered by past events. We studied connections between spatially and temporarily distinct annual phases in collared flycatchers, a small bodied bird which twice a year migrates between Europe and sub-Saharan Africa. We found tight links between individual's parental investment and timing of autumn migration, but not spring migration. Similarly, the timing of autumn migration did not translate to influence the timing of spring migration. Thus, our results demonstrate that the non-breeding period may serve as a buffer to overcome high energy expenditure during the previous breeding season and prevent further accumulation of carry-over effects in migratory birds.

**Keywords** Autumn migration · Geolocator · Phenology · Spring migration · Seasonal interactions · Stable isotope

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## Introduction

Annual cycles of migratory animals consist of various spatially and temporally distinct phases, such as 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; Catry et al. 2013; Low et al. 2015). 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).

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).

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); but it is important to note that the interaction between individual quality and the environment may also play a significant role (Souchay et al. 2018). 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. On the other hand, carry-over effects of delayed autumn migration could also be

overcome during the non-breeding period as found in Hudsonian godwits *Limosa haemastica* (Senner et al. 2014). Hence, we still lack a comprehensive assessment of carry-over effects across full annual cycles.

Just as parental effort influences migration and the non-breeding period, experiences at the non-breeding areas have consequences for the following spring migration and breeding season. Non-breeding conditions are known to influence spring migration phenology and individual fitness (Marra et al. 1998; Norris et al. 2004; Saino et al. 2004; Gunnarsson et al. 2005; Balbontín et al. 2009; Drake et al. 2013; López-Calderón et al. 2017). For instance, individuals residing in better 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 ( $\delta^{13}\text{C}$ ) signatures have been used most often to discriminate between higher (i.e. mesic) and lower quality (i.e. xeric) sites (e.g. Bearhop et al. 2004; Norris et al. 2004; Procházka et al. 2008) as  $\delta^{13}\text{C}$  values allow for the discrimination between habitats with C3 and C4 plants.

Collared flycatchers *Ficedula albicollis* are long-distance Afro-Palaearctic migrants which breed across large areas of the Western Palearctic and migrate to Southern-Central Africa during the Northern Hemisphere winter (Briedis et al. 2016). During their annual cycle, flycatchers spend about 3 months at breeding sites where birds reproduce and undergo a complete body moult before departing for autumn migration (Stresemann and Stresemann 1966). For the greater part of the year, birds reside in sub-Saharan Africa, where approximately 5 months are spent at the non-breeding residency sites (Briedis et al. 2016). During the non-breeding period, the species is assumed 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; López-Calderón et al. 2017).

With this study, we aim to narrow the gap in our understanding of full annual cycles in animal ecology by linking summer–winter–summer events in a long-distance migratory bird (Marra et al. 2015). We couple an experimental approach with observational data to unravel the links between different parts of the annual cycle by integrating breeding monitoring, tracking by light-level geolocators, and stable isotope analyses of winter-grown feathers. By doing so, we are able to follow individual birds throughout the full annual cycle and assess the magnitude of carry-over effects from the breeding season to autumn migration, 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 week 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. The flycatchers at Dlouhá Loučka are under heavy predation pressure by edible dormouse *Glis glis*; therefore, we protected the nest boxes by applying approximately 50 cm wide plastic foil around the trees roughly 50 cm above and below the nest boxes.

**Data availability** The datasets analysed during the current study are available upon request from the MoveBank data repository (project ID 166151488).

## Geolocator deployment and retrieval

Field work was carried out during three breeding seasons from 2013 to 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 automatically—thus with a blind method—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 (40.6%, 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 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. The recovery rate was 43.3% when considering only males that were observed breeding in the nestboxes in 2014. 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, but typical return rates at this site range between 30% and 50% (MK unpublished data). 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 (tagged:  $28/69 = 40.6\%$ ; control:  $29/83 = 34.9\%$ ;  $\chi^2 = 0.30$ ,  $p = 0.58$ ).

## 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 2 or 3 after the eggs had hatched. In total, 104 nests (52 pairs) were experimentally manipulated. At the manipulated nest, we trapped adult males and equipped them with geolocators. In total, we tagged males 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 were caught on two nests. We obtained migration and non-breeding residency data from the geolocators of seven males with reduced broods (reduced from 8 to 7 chicks = 1 case, 7/6 = 1, 6/5 = 1, 5/4 = 1, 4/3 = 2, 3/2 = 1) and nine males with increased brood size (increased from 5 to 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 carbon ( $\delta^{13}\text{C}$ ) measured from tertial feathers moulted at the

non-breeding sites (Svensson 1992) to assess the non-breeding conditions. Lower  $\delta^{13}\text{C}$  values identify cooler and moister habitats which accommodate increased quantities of invertebrates providing better feeding opportunities, while higher  $\delta^{13}\text{C}$  values are associated with hotter and drier habitats with more  $\text{C}_4$  plants (Marra et al. 1998; Marshall et al. 2007). Lab procedures of stable isotope analyses are detailed in the Online Resource 1.

## 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 the R-package ‘GeoLight’ v 1.03 following the standard procedures outlined by Lisovski and Hahn (2012) and setting the ‘changeLight’ function parameters to  $q = 0.85$ , days = 3. Unfortunately, due to high variability in the recorded light data during the migration and proximity of the equinox, we were not able to identify specific migratory stopover sites. Geographic coordinates of the individual non-breeding sites were calculated using Hill-Ekstrom calibration. The derived sun elevation angles ranged between +8.6 and  $-0.7$ . We determined time of Sahara crossing 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 (Adamik et al. 2016; Ouweland and Both 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 coordinates within the non-breeding residency period).

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 (Online Resource 2), 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.

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, and a skewed distribution (but see Online Resource 3 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 ( $5.4 \pm 1.4$  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 (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 differ 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).

We used confirmatory path analyses (R-package ‘lavaan’; Rosseel 2012) to examine direct and indirect effects of how timing of one annual cycle event is linked to the timing of all subsequent events. Path analysis is a type of structural equation models where only the measured variables are considered ignoring latent variables. In structural equation models, components can appear both as predictors and response variables generating a causal network. We included timing of eight annual cycle events in our model: onset of egg laying in the first year, breeding site departure, Sahara crossing in autumn, non-breeding site arrival, non-breeding site departure, Sahara crossing in spring, breeding site arrival, and onset of egg laying in the second year. Since the timing of all events in the animals’ annual cycle are linked in a unified sequence via carry-over effects (Harrison 2011), we structured the path model so that the timing of each event was dependent on the timing of all preceding events. The final path diagram was plotted using R-package ‘semPlot’ and one-headed arrows represent causal relationship between the variables. The given path coefficients are standardized partial regression coefficients.

Due to multiple testing,  $p$  values should be interpreted against a threshold level of  $\alpha = 0.008$  for the timing of migration, and  $\alpha = 0.017$  for the duration of annual stages (autumn migrations, non-breeding residency, and spring migration). We assessed the timing of spring events in relation to the non-breeding conditions ( $\delta^{13}\text{C}$  values) and previous parental investment using general linear models (GLM) with normal error structure and an identity link function:

Timing/duration of migration event  $\sim \delta^{13}\text{C}$  + previous parental investment.

We calculated the unbiased Cohen's  $d$  values and their confidence intervals according to Nakagawa and Cuthill (2007) accounting for small sample sizes. Statistical tests were performed in R version 3.3.1 (R Core Team 2016).

## Results

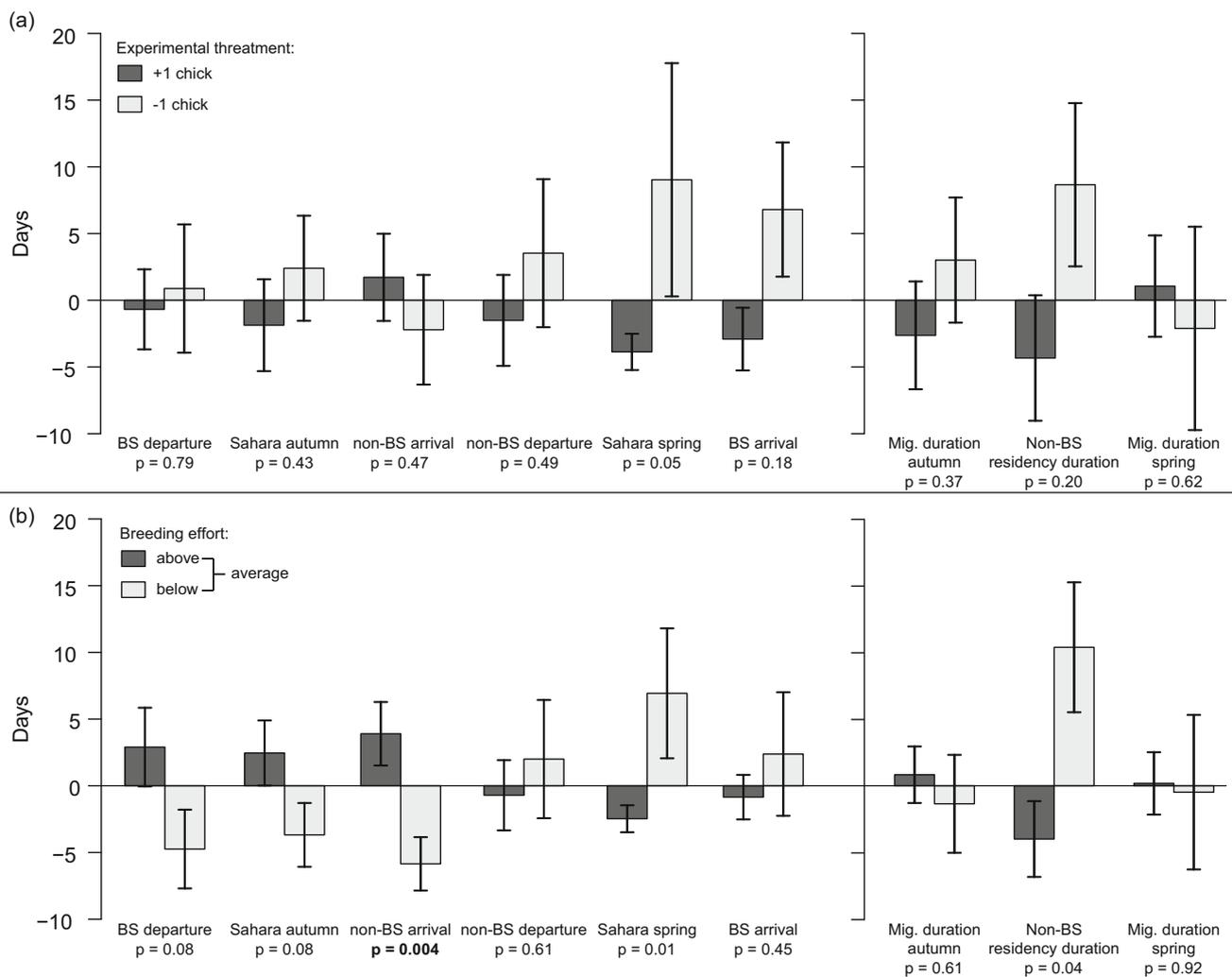
### Brood size manipulation

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:  $6.1 \pm 0.9$  SD,  $n = 9$ ) and those with reduced broods (averaged fledged:  $4.1 \pm 1.9$  SD,  $n = 7$ ; Fig. 1a, Online Resource 4). 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.

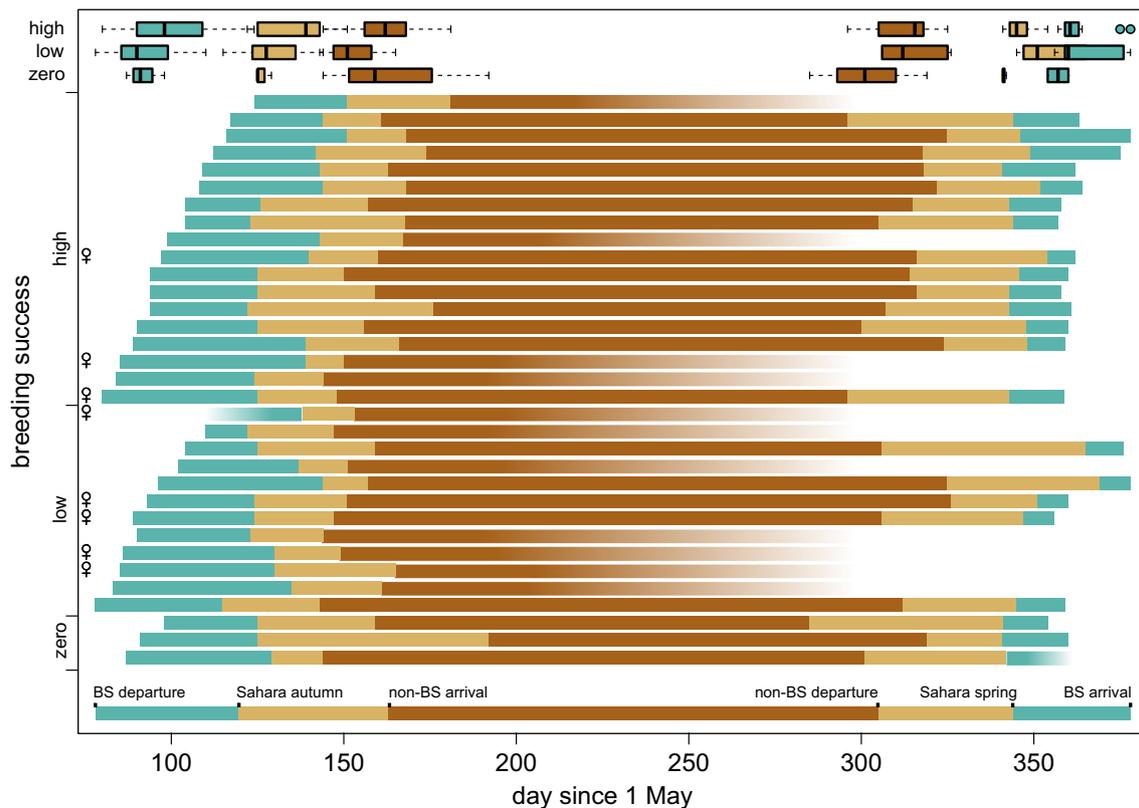
### Absolute breeding effort

When looking at the absolute fledgling numbers (not considering brood manipulation) as a proxy for breeding effort, we found that individuals that fledged higher than average number of fledglings ( $6.3 \pm 0.5$  SD,  $n = 18$ ) underwent all stages of autumn migration later than those fledging fewer than average fledglings ( $4.0 \pm 1.0$  SD,  $n = 12$ ; Fig. 1b, Online Resource 5). The timing difference between the two groups was significant for arrival at the non-breeding site (unpaired  $t$  test:  $t = 3.1$ ,  $p = 0.004$ ) with birds fledging more young arriving on average 10 days later. The opposite was observed regarding the timing of spring migration—birds that fledged more young in the previous year underwent all



**Fig. 1** Average deviation of migration timing in collared flycatchers depending on **a** experimental treatment of brood size manipulation, and **b** absolute breeding effort (expressed as below or above the study average

of 5.4 fledglings). Bars denote the average difference in timing of migration events relative to the mean of the compared groups. Error bars denote standard errors



**Fig. 2** 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 showing median, interquartile range (IQR)—boxes; whiskers extend to values within 1.5 times the IQR and dots depict outliers) data are presented. Migration schedules include departure from the

breeding site, Sahara crossing in autumn, arrival at the non-breeding site, departure from the non-breeding site, Sahara crossing in spring, and arrival at the breeding site. 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

stages of the spring migration earlier. 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 less at the non-breeding residency areas (unpaired  $t$  test:  $t = -2.5$ ,  $p = 0.04$ , Fig. 1b, Online Resource 5) and, thus, on average migrated earlier in spring (individual schedules are summarized in Fig. 2).

Confirmatory path analyses between the timing of different annual events revealed no significant effects of the breeding time on the timing of any of the further stages throughout the annual cycle, nor the timing of breeding next year (Fig. 3). There was a significant positive effect of breeding site departure, non-breeding site arrival, and breeding site arrival on the timing of following breeding, while timing of Sahara crossing in autumn had a negative effect on the timing of breeding the following year. Significant positive effects were also found between timing of breeding site departure and Sahara crossing in autumn, as well as Sahara crossing in spring and breeding site arrival (Fig. 3; Online Resource 6).

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

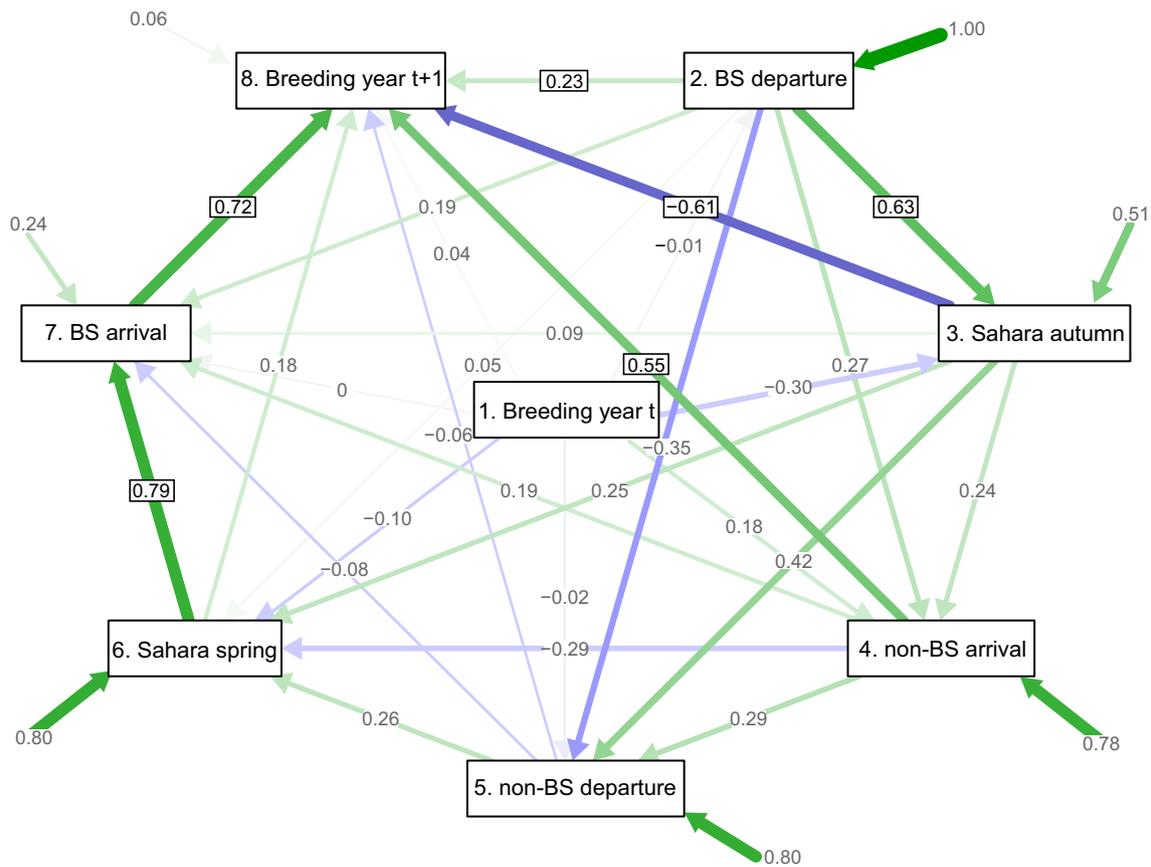
increasing timespan between the events ( $F_{1,26} = 11.48$ ,  $r^2 = 0.28$ ,  $p = 0.002$ , Fig. 4; individual linear regressions are available at Online Resource 7). Thus, there was a stronger relationship in timing of intra-seasonal events compared to timing of inter-seasonal events (autumn–spring).

### Stable isotopes

GLM analyses relating spring migration schedules to local habitat conditions at the non-breeding areas and previous breeding effort revealed that  $\delta^{13}\text{C}$  values were strong predictors only for the non-breeding site departure (Fig. 5, Table 1). There was no indication that either of the factors carried over to influence the timing of the following breeding (Fig. 5d, Table 1d).

### Discussion

In this study, we linked events across the entire annual cycle in the long-distance migratory collared flycatcher and evaluated carry-over effects of parental investment and local non-



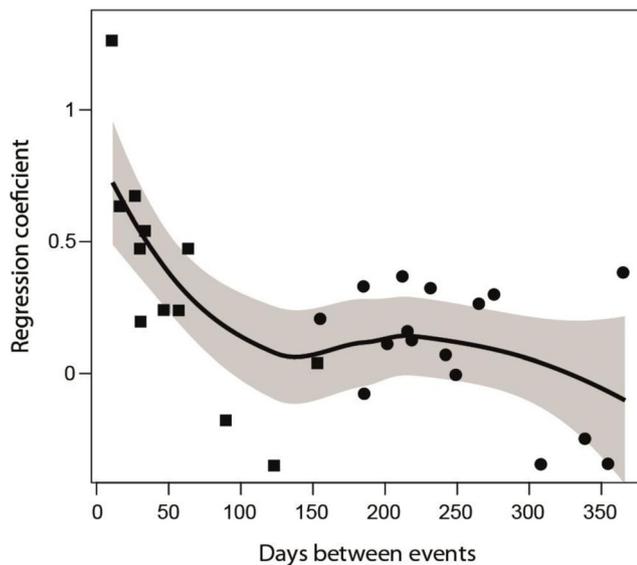
**Fig. 3** Path diagram of the model showing causal relationship between different parts of the annual cycle in collared flycatchers. Arrows indicate casual effects of one event (independent variable) on the subsequent events (dependent variables). Green arrows indicate positive effects,

blue arrows—negative effects. The width and colour intensity of the arrows represent the values of standardized path coefficients. The significant interactions are highlighted with standardized path coefficients given in boxes

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 in migration schedules between the males whose brood sizes were reduced and males with enlarged brood sizes. However, when looking at the absolute 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 and the non-breeding period served as a buffer not allowing for carry-over effects to accumulate. Hereof, we also showed that neither local non-breeding conditions nor the previous breeding effort was linked to the timing of spring migration and the following breeding period.

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). 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 south-bound 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 the 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 through provisioning of young may differ between the sexes.



**Fig. 4** The strength of the “domino effect” between consecutive parts of the annual cycle expressed as the relationship between regression coefficients of the timing of different parts of the annual cycle and the timespan between the events. Squares (■) denote regression coefficients of intra-seasonal events and circles (●) denote regression coefficients of inter-seasonal events. The black line depicts fitted loess curve  $\pm$  SE (shaded area)

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 significant relationship between the timing of breeding and other parts of the annual cycle (Fig. 3, Online resources 7). Mitchell et al. (2012), Saino et al. (2017), and van Wijk et al. (2017) reported positive correlation between the completion of breeding and autumn migration departure in savannah sparrows *Passerculus sandwichensis*, barn swallows *Hirundo rustica*, and hoopoes

**Table 1** Summary statistics of models showing a relationship between the timing and duration of spring events and non-breeding conditions ( $\delta^{13}\text{C}$ ) and parental investment (above or below the population average) in the previous breeding season

	Estimate	SE	<i>t</i>	<i>p</i>
(a) Departure non-breeding site (df = 15)				
Intercept	194.6	57.88	3.36	< 0.01
$\delta^{13}\text{C}$	6.85	3.00	2.29	0.04
Breeding effort <sub>(below)</sub>	5.42	4.56	1.19	0.25
(b) Sahara crossing spring (df = 15)				
Intercept	143.15	43.37	3.3	< 0.01
$\delta^{13}\text{C}$	2.39	2.25	1.06	0.3
Breeding effort <sub>(below)</sub>	10	3.42	2.93	0.01
(c) Arrival breeding site (df = 15)				
Intercept	135.19	45.3	2.98	0.01
$\delta^{13}\text{C}$	1.18	2.35	0.5	0.62
Breeding effort <sub>(below)</sub>	4.71	3.57	1.32	0.21
(d) Onset of egg laying year <i>t</i> + 1 (df = 22)				
Intercept	124.67	63.75	1.96	0.06
$\delta^{13}\text{C}$	0.03	3.31	0.01	0.99
Breeding effort <sub>(below)</sub>	3.03	3.94	0.77	0.45
(f) Timespan arrival breeding site–onset of egg laying (df = 14)				
Intercept	− 54.95	98.56	− 0.56	0.59
$\delta^{13}\text{C}$	− 6.08	5.12	− 1.19	0.25
Breeding effort <sub>(below)</sub>	0.15	7.72	0.02	0.98
(e) Timespan departure non-breeding site–onset of egg laying (df = 14)				
Intercept	3.84	47.92	0.08	0.94
$\delta^{13}\text{C}$	− 0.44	2.49	− 0.18	0.86
Breeding effort <sub>(below)</sub>	0.82	3.75	0.22	0.83

*Upupa epops*, 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 in the tropics (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 shorter non-breeding residency neglecting the delays in autumn migration schedules. Fayet et al. (2016) have shown that experimentally increasing the duration of provisioning for young delayed autumn migration

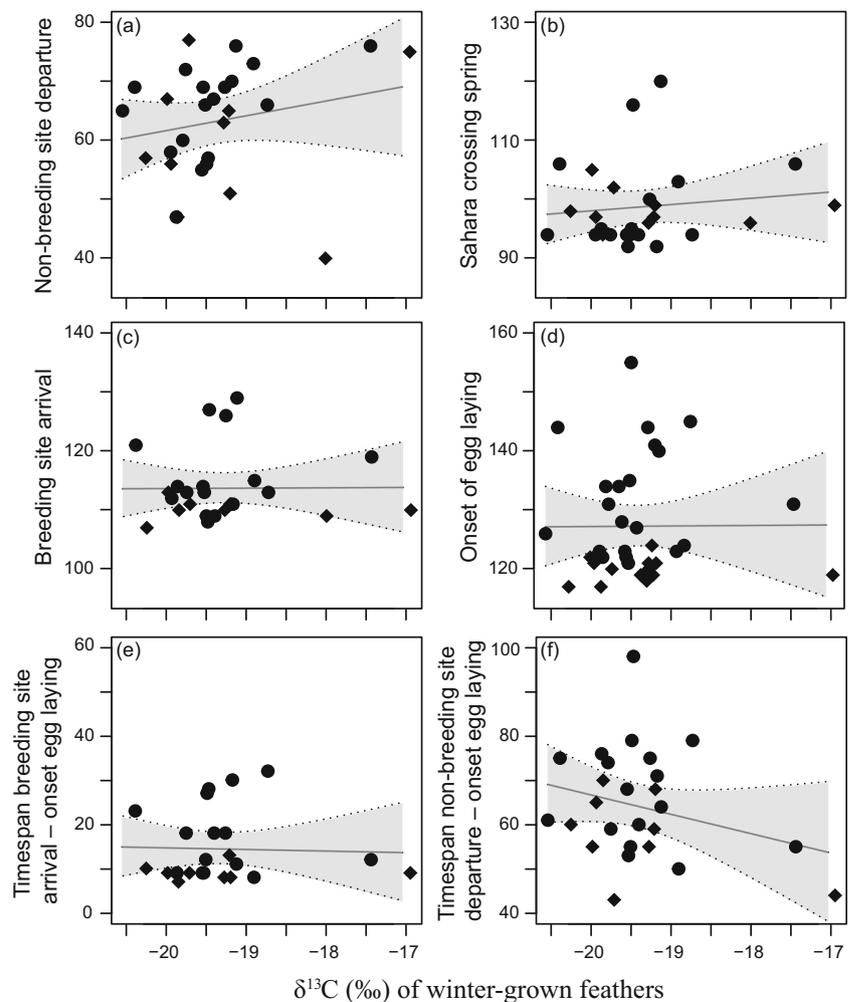
departure and resulted in a shorter non-breeding residency period in Manx shearwaters. The length of the non-breeding residency period might not be as time-constrained as other parts of the annual cycle and thus could be a subject to adjustments if needed. We have shown earlier that collared flycatchers breeding in Sweden spend ca. 10% less time at the non-breeding sites than birds from our study site in the Czech Republic, suggesting more relaxed schedules and the buffering effect of this period on other parts of the annual cycle (Briedis et al. 2016).

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 within a single migration season. 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. 4). The strong links found within rather than across migration seasons suggest that the domino effect and carry-over effects from the breeding season can be overcome during the non-breeding season. Collared flycatchers that had higher breeding effort migrated later in autumn, but earlier in spring, supporting the hypothesis that non-breeding period buffers accumulation of carry-over effects. Van Wijk et al. (2017) also reported strong relationship between the timing of annual stages directly following each other in hoopoes. The dependencies of the timing decreased with increasing timespan between the annual cycle events. Similarly to our results, van Wijk et al. (2017) found the strongest relationship between the timing of breeding site arrival and the onset of breeding, highlighting the importance for timely spring arrival (Kokko 1999).

Conditions at the non-breeding areas have been shown to influence the spring migration schedule and following breeding period in several species (Marra et al. 1998; Norris et al. 2004; Saino et al. 2004; Studds and Marra 2005; Tonra et al.

**Fig. 5** Relationship between  $\delta^{13}\text{C}$  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 to 2014 and circles (●) denote data from 2014 to 2015 non-breeding seasons. Linear models are depicted by solid lines with 95% CI (shaded area)



2011; Rockwell et al. 2012; Paxton and Moore 2015; López-Calderón et al. 2017), while we found no such links in our study system (Fig. 5). Pedersen et al. (2016) also found no carry-over effects of local non-breeding habitat conditions on the late stages of spring migration and the following breeding period in red-backed shrikes *Lanius collurio* using  $\delta^{13}\text{C}$  values as a proxy. Similarly, no carry-over effects of non-breeding habitat quality were found in yellow warblers *Setophaga petechial* (Drake et al. 2014), magnolia warblers *S. magnolia* (Boone et al. 2010), and Hudsonian godwits (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 via isotope signatures in winter-grown tissues.

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 the previous breeding effort and local non-breeding habitat conditions had negligible influence on the timing of the following breeding period. Similarly, Bogdanova et al. (2011) reported no differences in spring migration schedules caused by previous breeding experience. Ouweland 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*. On the contrary, long-lasting carry-over effects of previous breeding effort have been shown to influence following breeding attempts in long-lived migratory birds (Inger et al. 2010; Catry et al. 2013). 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 energetic and time-dependent costs of reproduction play a key role in altering autumn migration schedules and defining individual variation via carry-over effects but we also highlight the importance of non-breeding period as a buffer for further accumulation of the carry-over effects. Linking events throughout the entire annual cycle 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 research with respect to full annual cycles.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This study was carried out in accordance with the Ethical Committee of Palacký University and approved by the Ministry of Education, Youth and Sports of the Czech Republic (Licence number: MSMT-56147/2012-310). All applicable institutional and national guidelines for the care and use of animals were followed.

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## Studie 19

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RESEARCH ARTICLE

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

Martins Briedis<sup>1\*</sup> , Steffen Hahn<sup>2</sup> and Peter Adamík<sup>1,3</sup>

## 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, Geocator, 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].

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Here we examine how long-distance migrating semi-collared 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  $4.6 \pm 0.3\%$  (SD) of the bird's body mass. There was no difference in the average load of the geocator

between the birds that returned and those that did not return (average  $\pm$  SD; returned:  $4.7 \pm 0.3\%$ ,  $n = 18$ ; not returned:  $4.6 \pm 0.3\%$ ,  $n = 71$ ;  $t$  test:  $t_{87} = -1.19$ ,  $p = 0.25$ ).

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 geocator 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.

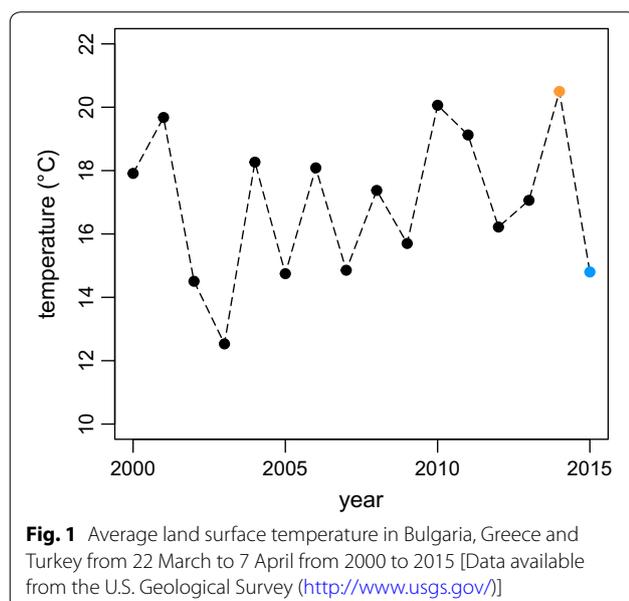
### Data analysis

We processed the light recording data using the R-package 'GeoLight' v2.0 [15], having determined sunrise and sunset times with 'Geocator' software (Swiss Ornithological Institute) beforehand. We filtered the datasets for outlying sun events using the 'loessFilter' function ( $k$  value = 2). We determined departure from the non-breeding 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 geocator'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

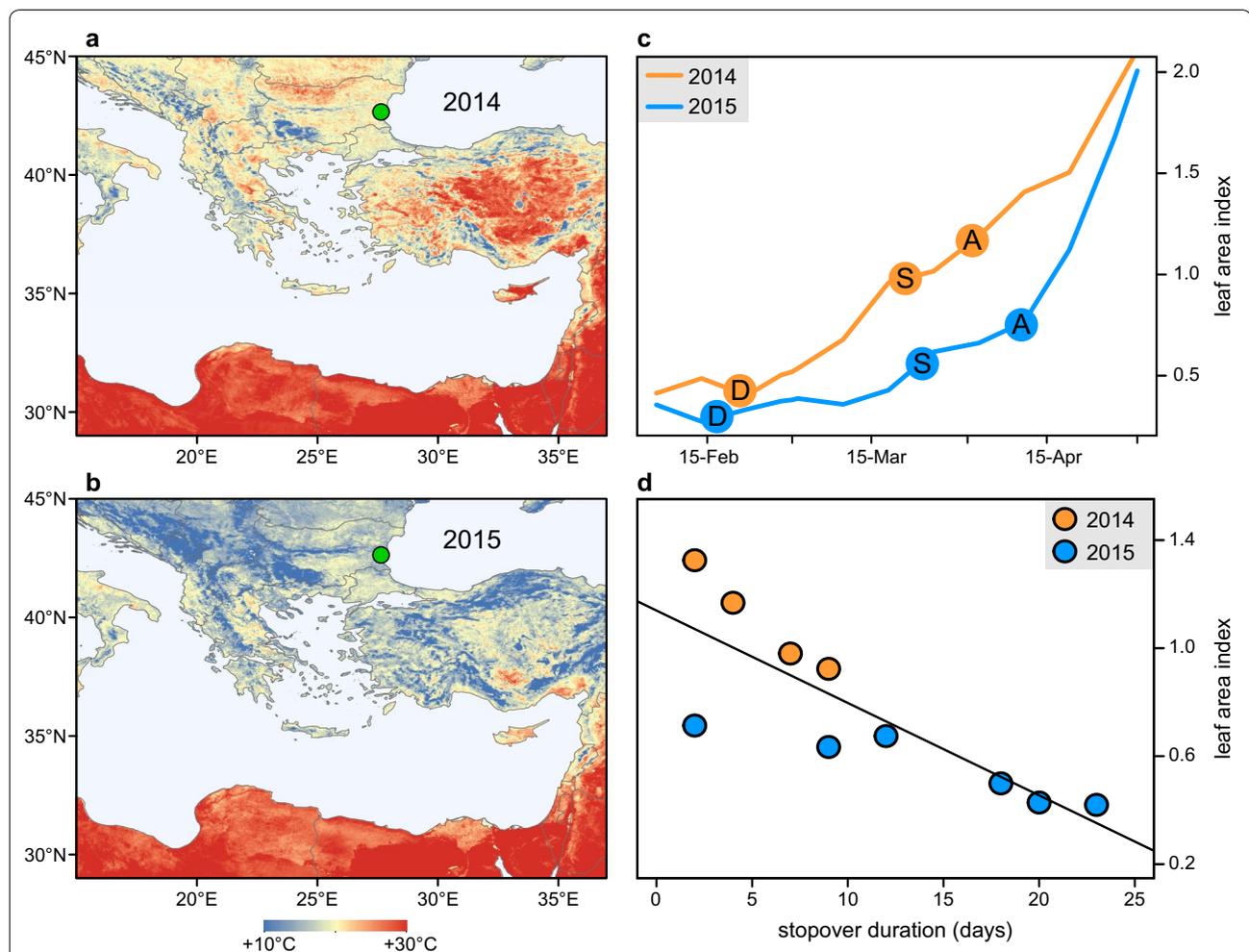


Resources Observation and Science (EROS) Center (<https://lpdaac.usgs.gov/>). We obtained wind data for the 850 mb pressure level (approximately 1500 masl) from the National Center for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) Reanalysis dataset [17] using R-package '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].

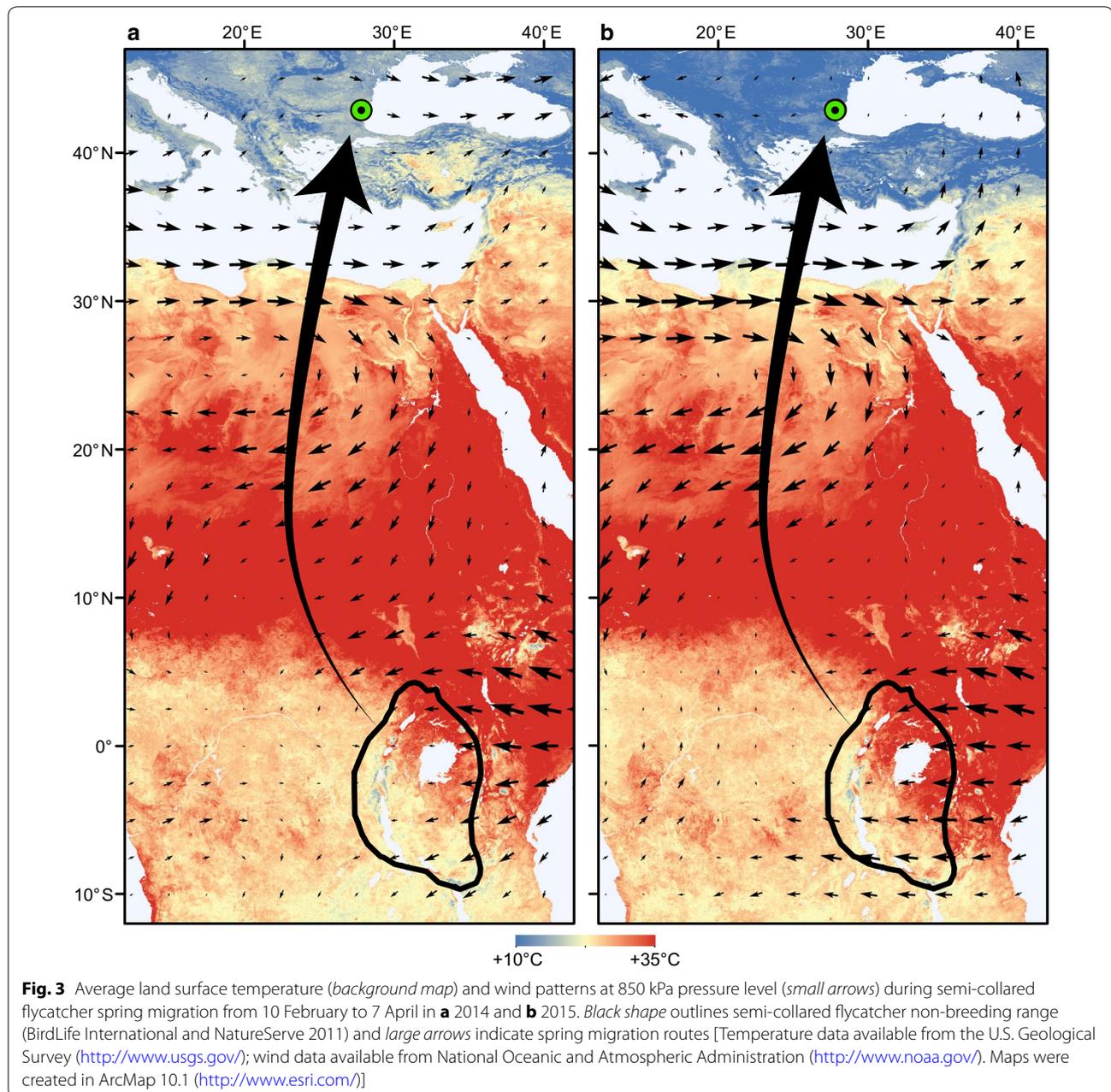
## Results

### 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).



**Fig. 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 ( $\text{m}^2$  of leaf area per  $\text{m}^2$  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 from data available from the U.S. Geological Survey (<http://www.usgs.gov/>); maps were created in ArcMap 10.1 (<http://www.esri.com/>)]



### Responses of migrants

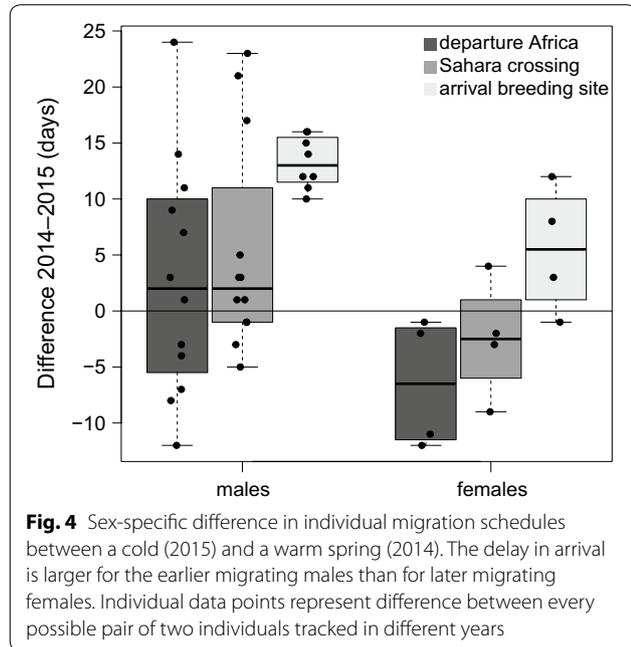
During both years, flycatchers departed from their non-breeding grounds in Eastern-Central Africa in the second half of February {median date 2014: 21 February [interquartile range (IQR) = 17–22 Feb], 2015: 16 February (11–19 Feb), Fig. 2c} and crossed the Sahara desert in late March [2014: 23 March (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 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).

We also observed prominent sex differences in migration timing, with males crossing the Sahara and arriving at the breeding site earlier than females in both years. The distinct protandry resulted in stronger delays in males' migration schedule than in females'. In 2015 males

arrived at the breeding site on average 13 days later than in 2014, while the difference for females was only 5.5 days (Fig. 4).

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).

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 is used by different populations than ours, and those populations migrating through Antikythira

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

	2014	2015	$\chi^2$	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
	<b>Control</b>	<b>Tagged</b>	<b><math>\chi^2</math></b>	<b>p value</b>
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

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 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-Palaearctic flyway, while collared and semi-collared flycatchers migrate along the central Afro-Palaearctic flyway. Migrants using the central Afro-Palaearctic 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-Palaearctic 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-Palaearctic 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.

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.

## 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.

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## Competing interests

The authors declare that they have no competing interests.

## 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 (Additional file 2) of this published article.

## Ethics approval and consent to participate

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

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