

UNIVERZITA PALACKÉHO V OLOMOUCI

PŘÍRODOVĚDECKÁ FAKULTA

KATEDRA ZOOLOGIE A ORNITOLOGICKÁ LABORATOŘ



**Změny početnosti a rozšíření ptáků ve střední
a východní Evropě: environmentální příčiny a vliv
ochrany přírody**

Doktorská disertační práce

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Abstrakt:

Změny početnosti ptáků jsou významně predikovány především life-history charakteristikami jednotlivých druhů, vlastnostmi ekologické niky, kterou jednotlivé druhy využívají a také činností člověka. Lze je vyjádřit jako prosté změny početnosti, změny rozšíření nebo změny trendů početnosti. Přestože tyto metriky vyjadřují různé aspekty populačních změn, nejsou rozdíly mezi nimi často brány v potaz. Pro znázornění těchto rozdílů jsem srovnal prediktory různě vyjádřených změn početnosti ptáků v České republice mezi lety 1970 a 2003.

Jednotlivá vyjádření změn početnosti spolu pozitivně korelovala, avšak jejich prediktory byly rozdílné.

V Evropě vykazuje dlouhodobě nejvýznamnější – negativní – změny početnosti většina druhů ptáků zemědělské krajiny, habitatoví a potravní specialisté, dálkoví migranti a druhy se severoevropským typem rozšíření. Naopak početnost pozitivně mění převážně některé lesní a mokřadní druhy, habitatoví a potravní generalisté, stálé druhy, migranti na krátkou vzdálenost, druhy s flexibilní migrační strategií a druhy s jihoevropským typem rozšíření. Na modelovém příkladu ptáků České republiky jsem podrobněji analyzoval prediktory změn rozšíření ptáků mezi lety 1985–1989 a 2001–2003. Rozšíření pozitivně změnily lesní a mokřadní druhy, migranti na krátkou vzdálenost a druhy nechráněné zákonem. Druhy s jihoevropským typem rozšíření také pozitivně změnily své rozšíření, ale tento výsledek byl nesignifikantní po zařazení šesti druhů vymizelých v letech 1989–2001 vázaných na ustupující extenzivní zemědělské hospodaření. Příčinou celkově pozitivních

změn rozšíření druhů ptáků hnízdících v České republice bylo pravděpodobně zlepšení stavu životního prostředí po politických změnách v roce 1989.

Zejména v návaznosti na negativní změny početnosti ptáků začaly vznikat červené seznamy ohrožených druhů. Pro plánování účinných opatření na jejich ochranu je rozhodující znalost ekologických vlastností předurčujících míru ohrožení. Analyzoval jsem proto efekt habitatové specializace a life-history znaků jako prediktorů stupně ohrožení 87 druhů pěvců v České republice. Habitatoví specialisté byli více ohroženi než generalisté. Zároveň K-strategie zvyšovala riziko extinkce u habitatových specialistů, toto riziko však snižovala u habitatových generalistů. Výsledky naznačují, že degradace biotopů významně ovlivňuje míru ohrožení druhů, avšak schopnosti druhů reagovat na tyto změny je závislá na jejich life-history strategii.

Přestože je ochrana ohrožených druhů ptáků zakotvena v národních i mezinárodních legislativních předpisech na ochranu přírody, komplexní hodnocení účinnosti legislativní druhové ochrany ptáků v zemích střední a východní Evropy dosud chybí. Srovnal jsem změny početnosti chráněných a nechráněných druhů ptáků v desíti středo- a východoevropských zemích v letech 1970–1990 (před zavedením nových seznamů zvláště chráněných druhů) a 1990–2000 (po jejich zavedení). Zohlednil jsem fylogenetickou příbuznost druhů a life-history a ekologické prediktory změn početnosti. Chráněné druhy změnily v celém regionu početnost v letech 1990–2000 po zařazení na seznamy chráněných druhů pozitivněji než druhy, na které se druhová legislativní ochrana v tomto období nevztahovala. Tyto výsledky mohou být dále využity při vytváření a další optimalizaci národní i mezinárodní legislativy na druhovou ochranu živočichů.

Klíčová slova: červené seznamy ohrožených druhů, ekologické faktory, Evropa, legislativní ochrana, life-history znaky, politické změny, ptáci, změny klimatu, změny početnosti

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Abstract:

Bird population changes are predicted especially by characteristics of species' life histories and ecological niches and by human activity. They can be described as simple change in abundance of individuals, as change of distribution or change in magnitude of population trend. Although these measures describe different aspects of population change, they are often used interchangeably. I compared predictors of the three measures of population changes using data collected in the Czech Republic between 1970 and 2003. Although individual measures of population changes were positively correlated, their predictors were different.

In Europe, long term population declines have been observed in farmland bird species, habitat and dietary specialists, long-distance migrants and species with north European breeding range. In contrast, some forest and wetland species, habitat and dietary generalist, residents, short-distance migrants, species having a less flexible migration strategy and species with north European breeding range have changed their abundance positively. On a model group of birds in the Czech Republic, I analysed predictors of changes in bird distribution between 1985–1989 and 2001–2003. Increasing distribution was observed in species of forest and wetland habitats, in short-distance migrants and in non-protected species. Species with south European breeding range also positively changed their occupancy, but this pattern disappeared after the inclusion of six species dependent on extensively cultivated farmland that went extinct in 1989–2001. The improvement of environmental conditions after political changes in 1989 probably caused the stability of or increased the distribution of common birds in the Czech Republic.

In response to adverse changes in bird populations, the first red lists of endangered species have been established. For development of effective conservation measures, it is crucial to know how the ecological traits relate to the risk of species' extinction. I assessed the relative importance of species' habitat specialization and life history as predictors of species' national threat level. Analysing threat level of 87 central European passerine bird species I found that habitat specialists are always more threatened than the habitat generalists. However, this relationship was affected by species' life history. While the slow life history increases the risk of extinction in habitat specialist species, it reduces such risk in habitat generalists. These results suggest that the habitat deterioration is most likely a principle cause of an elevated extinction risk, but abilities of species to cope with largely depend on their life history.

Although the endangered species protection has been a part of the national as well as international acts on nature conservation, large scale assessments of the effects of species protection on bird populations are lacking in Central and Eastern Europe. I compared changes in population trends of protected and non-protected bird species between 1970–1990 and 1990–2000 (i.e. before and after establishing lists of protected species) in ten Eastern European countries, controlling for effects of species' phylogeny, life history and ecological traits. Within the region, the protected species changed their population trends more positively compared to the non-protected ones. This indicates that the national species protection contributed to preventing population declines of the focal species at a regional scale. The results may be used in establishing and optimizing both national and international legislation on species animal protection.

Keywords: birds, changes in abundance, climate change, ecological factors, Europe, legal protection, life-history traits, political changes, red lists of threatened species

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Prohlašuji, že jsem tuto práci vypracoval samostatně a je mým původním dílem. Výjimku tvoří přiložené články a rukopisy, na nichž se podíleli uvedení spoluautoři. Žádnou část této práce jsem nepředložil k získání dalšího akademického titulu.

V Olomouci dne 9. 5. 2013

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Poděkování

K zájmu o ptáky mě přivedlo krmítko umístěné u babičky za oknem. Od dětství mě tak tyto tvorové provázeli až k doktorskému studiu, kde jsem jim konečně mohl věnovat velkou většinu svého času. Ačkoli mě životní dráha vědce vždy velmi lákala, velmi brzy jsem, ať už v terénu, nebo u počítače, zjistil, že dělat vědu je dřina a k získaným poznatkům vede většinou dlouhá a trnitá cesta. Zcela jistě bych se na ní ztratil, kdybych neměl několik skvělých průvodců. Se základními principy vědecké práce a psaní odborného textu mě při vedení diplomky seznámil Martin Paclík a Karel Weidinger. Jim vděčím za první „prozření“, poznávání vlastních chyb a postupné praktické osvojování poznatků, bez kterých by tato disertační práce zřejmě nikdy nespátřila světlo světa. Díky Karlovi jsem mohl zůstat v Olomouci v prostředí, které je mi blízké. Jako školitel mi obětavě poskytoval podporu a velkou tvůrčí svobodu po celou dobu studia. Můj obrovský dík patří mému konzultantu Jirkovi Reifovi – ujal se mě, ačkoli v Olomouci na počátku mého doktorského studia ještě nepůsobil. Cením si zejména jeho přátelského přístupu – za celou dobu naší spolupráce mě nikdy ani neodbyl, ani nepokáral, přestože jsem mu k tomu nejednou zavládl příčinu. Právě Jirkovo vstřícné a přátelské jednání mě k práci motivovalo i ve chvílích, kdy se řešení některých problémů zdálo být v nedohlednu.

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Seznam příložených příspěvků

Příspěvek I.

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Příspěvek II.

Koleček J. & Reif J. 2011: Differences between the predictors of abundance, trend and distribution as three measures of avian population change. *Acta Ornithologica* 46: 143–153.

Příspěvek III.

Koleček J., Schleuning M., Burfield I. J., Báldi A., Böhning-Gaese K., Devictor V., García J. M. F., Hořák D., van Turnhout C. A. M., Hnatyna O. & Reif J. (rukopis): Species protection by national legislation improves bird population trends in Eastern European countries.

Příspěvek IV.

Koleček J. & Reif J. (rukopis): Interaction between habitat specialization and life history predicts extinction risk in passerine birds.

Úvod

Ptačí společenstva jsou negativně ovlivňována celou řadou faktorů (Ebbinge 1991, Rolland et al. 2010, Williams et al. 2012). Globální úbytek druhového bohatství však nemusí znamenat, že diverzita klesá i na lokální úrovni. Zde je výsledná změna diverzity určena počtem druhů, které danou lokalitu či oblast kolonizují, a tím, kolik druhů z ní vymizí. Lokální kolonizace a extinkce pravděpodobně souvisí s citlivostí jednotlivých druhů vůči současným změnám klimatu a prostředí, které druhy obývají (Donald et al. 2006, Lenzen et al. 2008). Je proto důležité znát vlastnosti jednotlivých druhů, zda jsou spojeny s úbytkem či poklesem lokální diverzity a zda na tento úbytek dokáže účinně reagovat legislativní ochrana přírody.

Změny v druhové bohatosti a početnosti ptáků lze vyjádřit a hodnotit různými způsoby (Magurran & McGill 2011). Většina studií se zabývá prostými (i) změnami početnosti nebo (ii) změnami trendů početnosti (např. Van Strien et al. 2001, Gregory et al. 2009). Zejména na územích o větší rozloze lze analyzovat také (iii) změny rozšíření ptáků (např. Böhning-Gaese & Bauer 1996). Spouštěcími a doprovodnými mechanismy těchto změn byly především intenzifikace zemědělského hospodaření, šíření lesa, snižování rozmanitosti krajiny, urbanizace, znečištění a eutrofizace (viz Reif et al. 2008a). Důležitou roli hrají rovněž globální změny klimatu (především oteplování) a degradace biotopů (Opdam & Wascher 2004, Moreno-Rueda & Pizarro 2008, Schaefer et al. 2008, Yamamura et al. 2008).

V návaznosti na působení těchto faktorů začaly vznikat první červené seznamy ohrožených druhů (Hamblen 2004). Zejména na úrovni jednotlivých zemí slouží jako důležitý podklad pro utváření a kategorizaci legislativy druhové ochrany živočichů (Brito et al. 2010). Jejím hlavním cílem je stabilizace populací ohrožených druhů, ale i ochrana druhů hospodářsky nebo kulturně významných (Ong 1998, Moser 2000, Donald et al. 2007). I přes rostoucí zájem a aktivní zapojení veřejnosti do této problematiky jsou efektivní opatření vedoucí k podpoře ohrožených druhů často významně limitována finančními zdroji a ekonomickými aktivitami, které často účinnost přijatých opatření snižují. Efektivita legislativních nástrojů a na nich založených přímých opatření k druhové ochraně organismů však zpravidla není kompetentně hodnocena a není tudíž jasné, zda jsou omezené finanční prostředky využívány efektivně (Williams et al. 2012).

Budeme-li vycházet z předpokladu, že dlouhodobé změny početnosti legislativně chráněných druhů jsou příznivější než u druhů nechráněných, lze velkoškálová data o změnách početnosti ptáků (viz BirdLife International/European Bird Census Council 2000, BirdLife International 2004) s úspěchem využít při hodnocení efektivity jejich ochrany.

Výsledky studie Donalda a kol. (2007) ukázaly, že druhy ptáků chráněné v zemích Evropské unie prostřednictvím Směrnice o ptácích č. 79/409/EHS zvýšily svou početnost více než ostatní druhy. Pozitivní účinek legislativní ochrany ptáků byl potvrzen také ve Spojených státech amerických (Male & Bean 2005) – podíl zákonem chráněných druhů se stabilním nebo rostoucím populačním trendem zde rostl s časem uplynulým od zařazení druhů mezi zákonem chráněné.

Ačkoli byly populační trendy chráněných a nechráněných druhů ptáků v některých zemích srovnávány (Jiguet et al. 2012), efekt zákonné ochrany na změny početnosti ptáků není ve většině, zejména méně vyspělých zemí, znám. Dosud ojedinělá studie Voříška a kol. (2008) ukázala, že efekt druhové legislativní ochrany ptáků je v České republice diskutabilní. Naopak zvýšení početnosti některých druhů po zavedení ochrany jejich biotopů spojené s aktivním ochranářským managementem bylo prokázáno v různých evropských státech (viz např. Donazar 1990, Ausden & Hirons 2002, Bradbury & Allen 2003, Wilson et al. 2007). Mimo Evropskou unii nebyla dosud v Evropě účinnost národní legislativy na druhovou ochranu ptáků souhrnně hodnocena, přestože má řada regionů ležících mimo Evropskou unii pro zachování evropské biodiverzity klíčový význam. Týká se to zejména zemí střední a východní Evropy, kde po politických změnách v roce 1989 začala v souvislosti s přípravou zemí na vstup do Evropské unie implementace moderní legislativy ochrany přírody. Do Evropské unie tyto státy začaly vstupovat teprve po roce 2000.

V Evropě existuje díky velkému počtu států a různým přístupům k druhové ochraně přírody jedinečná možnost studovat rozdíly ve vlivu legislativních opatření na populační trendy ptáků. Tato disertační práce představuje první hodnocení vlivu ekologických, life-history příčin a národní druhové legislativní ochrany na změny početnosti a na stupeň ohrožení ptáků v postkomunistických státech střední a východní Evropy.

Motivace a cíle disertační práce

V této disertační práci se zabývám vlivem ekologických a life-history vlastností ptáků a jejich druhové ochrany na změny početnosti a ohrožení ve středo- a východoevropských zemích zejména z těchto důvodů:

- Rozdíly mezi jednotlivými vyjádřeními změn početnosti ptáků nejsou často v odborné literatuře brány v potaz. Srovnání jednotlivých metrik změn početnosti ptáků však dosud chybí.

- Pro plánování účinných opatření na ochranu přírody je nutné vědět, zda a do jaké míry mají druhy negativně měnící své rozšíření rozdílné ekologické nároky ve srovnání s druhy, které se šíří. Ve střední a východní Evropě však dosud byly studovány změny rozšíření jednotlivých ekologických skupin druhů ptáků pouze na lokální úrovni (např. Tryjanowski 2000, Verhulst et al. 2004, Goławski 2006, Orłowski and Ławniczak 2009) a generalizace a srovnání těchto výsledků jsou tudíž problematické. Zároveň tak není dostatečně známo, zda rozšíření ptáků ovlivňují podobné mechanismy jako v jiných regionech.
- Pro účinnou ochranu ptáků je důležitá dobrá znalost faktorů, které předurčují ohrožení jednotlivých druhů a riziko extinkce. Analýza vlastností ohrožených druhů ptáků však dosud chybí.
- Studií na téma efektivity legislativy na ochranu ptáků je obecně nedostatek, analýzou problematiky se v postkomunistických zemích dosud nikdo systematicky nezabýval a ani mezinárodní srovnání účinnosti národních legislativních předpisů na druhovou ochranu ptáků dosud nebylo nikde provedeno.
- Výsledky této práce pomohou vysvětlit mechanismy působení legislativy druhové ochrany přírody na změny početnosti ptáků. Zároveň mohou být použity při optimalizaci národní i mezinárodní legislativy ochrany přírody a mohou motivovat ornitology, aby se těmito tématy zabývali intenzivněji především na úrovni jednotlivých států. Pouze dobrá znalost působení lokálních faktorů je předpokladem pro detailní objasnění mechanismů ovlivňujících změny početnosti ptáků a účinnost národní i mezinárodní legislativy na jejich druhovou ochranu.

Cíle mé disertační práce jsou tudíž následující:

- Vytvořit základní přehled problematiky a současného stavu znalostí.
- Na modelové skupině ptáků České republiky porovnat nejčastěji používané způsoby vyjádření změn početnosti ptáků a hodnotit, zda spolu jednotlivá vyjádření změn početnosti ptáků korelují a zda mají podobné prediktory.
- Analyzovat, zda se dlouhodobé změny rozšíření ptáků v České republice v letech 1985–2003 lišily mezi skupinami druhů definovanými na základě typu rozšíření, nároků na prostředí, podle migrační strategie a stupně zákonné ochrany; analyzovat vliv kolonizace a extinkce.
- Analyzovat vliv habitatové specializace a životních strategií na míru ohrožení střeoevropských pěvců.

- Hodnotit efekt národní legislativy na druhovou ochranu ptáků na změny početnosti ptáků v jednotlivých středoevropských a východoevropských zemích, v jejich skupinách i v celém regionu.

Metodické postupy

Výsledky prezentované v příspěvcích zařazených v této disertační práci vycházejí z analýz lokálních (Česká republika) i rozsáhlých mezinárodních datových souborů s údaji o změnách početnosti a ohrožení ptáků. Ve **Příspěvcích I, II a III** jsem analyzoval závislost různými způsoby vyjádřených změn početnosti ptáků na ekologických nárocích, life-history znacích a legislativní druhové ochraně. V **Příspěvku IV** jsem analyzoval vliv habitatové specializace (vyjádřené indexem habitatové specializace) a životní strategie na stupeň ohrožení 87 druhů pěvců v České republice. Stupeň ohrožení jsem převzal z platného Červeného seznamu ptáků České republiky (Šťastný & Bejček 2003). V **Příspěvku I** jsem analyzoval rozdíly mezi změnami rozšíření 215 druhů různých ekologických skupin a s různým stupněm legislativní ochrany hnízdících v České republice. K vyjádření změn rozšíření jsem použil výsledky celostátních atlasových mapování hnízdního rozšíření ptáků v České republice v letech 1985–1989 a 2001–2003 (Šťastný et al. 1996, 2006). V **Příspěvku II** jsem srovnával jednotlivá vyjádření změn početnosti (prostou změnu početnosti, změnu trendů početnosti a změnu rozšíření) a jejich prediktory u 178 druhů ptáků hnízdících v České republice. K vyjádření změn početnosti v letech 1990–2000 a změn trendů početnosti mezi lety 1970–1990 a 1990–2000 jsem použil publikované trendy početnosti ptáků z databázi Birds in Europe v letech 1970–1990 (BirdLife International/European Bird Census Council 2000) a 1990–2000 (BirdLife International 2004). K vyjádření změn rozšíření jsem použil data o hnízdním rozšíření ptáků v České republice v letech 1985–1989 a 2001–2003 (Šťastný et al. 1996, 2006). V **Příspěvku III** jsem analyzoval závislost populačních trendů 306 druhů ptáků z databáze Birds in Europe (BirdLife International/European Bird Census Council 2000, BirdLife International 2004) v deseti zemích střední a východní Evropy v závislosti na jejich legislativní ochraně, ekologických nárocích a life-history znacích.

Pro vyjádření prediktorů změn početnosti (ohrožení) jsem ve všech příspěvcích použil publikovaná data popisující ekologické a life-history vlastnosti a nároky druhů (Cepák et al. 2008, Cramp 1977–1994, Hudec 1983, 1994, Hudec & Šťastný 2005). Typ rozšíření druhu Evropě (**Příspěvek I, II**) jsem vyjádřil z map evropského hnízdního rozšíření ptáků (Hagemeijer & Blair 1997). Klimatická nika druhu byla vyjádřena z map průměrných ročních teplot v hnízdním období jednotlivých druhů (Hagemeijer & Blair 1997, Haylock et al. 2008).

Informace o druhové ochraně ptáků jsem získal ze seznamů chráněných druhů platných v zemích střední a východní Evropy. Abych zjistil efekt legislativní ochrany na populační trendy ptáků v letech 1990–2000, použil jsem pro další analýzy pouze seznamy zvláště chráněných druhů, které vstoupily v platnost mezi lety 1987–1995 v deseti zemích (Bělorusko, Česká republika, Estonsko, Chorvatsko, Maďarsko, Moldávie, Polsko, Slovensko, Slovinsko a Ukrajina). Bližší informace o použitých analýzách jsou podrobně rozvedeny v metodických kapitolách jednotlivých příspěvků.

Life-history a ekologické prediktory změn početnosti a ohrožení ptáků

Ke stanovení početnosti ptáků jsou nejčastěji používány různé metody sčítání – tedy zaznamenávání jedinců v terénu bez nutnosti jejich odchyty (Rosenstock et al. 2002, Bibby et al. 2007, Koleček et al. 2010). Změny početnosti ptáků v prostoru a čase bývají prezentovány jako (i) prostá změna početnosti nebo denzity jedinců daného druhu. Ve větších územích, nejčastěji v rámci jednotlivých států, lze změny početnosti druhů vyjádřit také jako (ii) změnu jejich rozšíření (Böhning-Gaese & Bauer 1996, Lemoine et al. 2007a, Kerbiriou et al. 2009, **Příspěvek I**). Časová variabilita populačních trendů bývá znázorněna jako (iii) změna trendu početnosti (Van Strien et al. 2001, Gregory et al. 2009). Přestože tyto metriky vyjadřují rozdílné aspekty populační dynamiky jednotlivých druhů ptáků, nejsou rozdíly mezi nimi často brány v potaz. Při srovnání výsledků rozdílných studií tak není jasné, zda jsou rozdíly biologického rázu nebo se jedná pouze o metodický artefakt použitého způsobu vyjádření změn početnosti.

Jednotlivá vyjádření změn početnosti spolu korelují, avšak vliv každého z prediktorů může být průkazný pro změnu početnosti vyjádřenou různým způsobem (**Příspěvek II**). V České republice byla v letech 1970–2003 prostá změna početnosti pozitivní zejména u lesních druhů, přičemž k pozitivním změnám rozšíření došlo především u mokřadních druhů, u druhů hnízdících výše nad zemí a u severoevropských druhů. Legislativně přísněji chráněné druhy a druhy s r-strategií pozitivně změnil trend početnosti (**Příspěvek II**).

Změny početnosti ptáků jsou vedle činnosti člověka významně predikovány life-history charakteristikami jednotlivých druhů a také charakteristikami ekologické niky, kterou využívají (Gregory et al. 2007). Tato evoluční a ekologická omezení významně ovlivňují krátko- i dlouhodobé změny početnosti jednotlivých druhů (Böhning-Gaese & Oberrath 2003, Jiguet et al. 2007, van Turnhout et al. 2010, Webb et al. 2010) a mohou limitovat také úspěšnost legislativy na druhovou ochranu ptáků (**Příspěvek III**).

Problematikou vlivu faktorů prostředí a life-history znaků na dlouhodobé změny početnosti ptáků se zejména v uplynulém desetiletí zabývala řada autorů (viz dále). V rámci různých ekologických skupin druhů mají změny početnosti v jednotlivých evropských zemích a regionech různý charakter (BirdLife International/European Bird Census Council 2000, BirdLife International 2004), avšak v některých případech je lze zobecnit. V Evropě tak vykazuje dlouhodobě nejvíce klesající populační trendy většina druhů ptáků zemědělské krajiny (Lenzen et al. 2008, Reif et al. 2008a). Kromě intenzifikace, mechanizace a chemizace zemědělské výroby ohrožuje druhy ptáků otevřené krajiny expanze zemědělského hospodaření do míst s vyšší druhovou bohatostí rostlin a živočichů a opouštění periferních oblastí se zpřírodněnými habitaty příznivými pro výskyt některých specializovaných druhů (Scricciu 2011). Mezi související příčiny můžeme zařadit ústup od extenzivního zemědělského hospodaření spojený s opouštěním otevřených biotopů a jejich postupným zarůstáním. Z těchto změn v krajině naopak profitují lesní druhy a habitatová a potravní generalisté (Lenzen et al. 2008, Kerbiriou et al. 2009, **Příspěvek I**), ačkoli především v západní Evropě byl zaznamenán pokles početnosti také u lesních druhů (Gregory et al. 2007).

Na změny ve využívání zemědělské krajiny měla důležitý vliv politická situace. V transformujících se postkomunistických zemích klesla intenzita zemědělské výroby v letech 1990–1994 v průměru o 20 %, následně se opět začala zvyšovat (Scricciu 2011). Například v Polsku nedošlo v polovině 20. století ke kolektivizaci zemědělství, po roce 1989 tak k zásadním změnám ve struktuře zemědělské krajiny nedošlo. V jiných zemích ale vlivem dekolktivizace a restituce došlo po roce 1989 k výraznějším změnám, případně opětovné částečné fragmentaci krajiny (Scricciu 2011). V České republice, na Slovensku a v Estonsku ale naopak jednotlivé hospodařící subjekty i po roce 1990 nadále spravovaly velké bloky zemědělské půdy (Bański & Bednarek 2008).

Na populační trendy vodních a některých mokřadních druhů ptáků má pozitivní vliv pokles intenzity loveckých aktivit doprovázený přísnější územní ochranou mokřadních lokalit využívaných ptáky (Lemoine et al. 2007a, Orłowski & Ławniczak 2009, van Turnhout et al. 2010, **Příspěvek I**, viz Ramsarská úmluva, soustava NATURA 2000). Naopak u mokřadních druhů vázaných svým výskytem původně zejména na vlhké louky (např. bekasina otavní [*Gallinago gallinago*], břehouš černoocasý [*Limosa limosa*]) došlo k výraznému poklesu početnosti zejména vlivem intenzifikace zemědělského hospodaření (viz Lemoine et al. 2007a).

Také početnost synantropních druhů ptáků je ovlivňována řadou faktorů. Městské mikroklima a s ním spojené vyšší průměrné roční teploty (Lowry 1998) prodlužují období vhodné pro růst rostlin (White et al. 2002) a zvyšují tak dostupnost potravy (Fuller et al. 2008). Potravní nabídka i hnízdní příležitosti některých synantropních druhů ptáků jsou však činností člověka zvyšovány také přímo (Jokimäki & Suhonen 1998, Seather et al. 1999; Boren & Hurd 2005, Robb et al. 2008). Městské prostředí je naopak zatíženo větší mírou znečištění (Sharp 2002) a často i vyšší početností predátorů (Haskell et al. 2001, Sorace 2002, ale viz Anderies et al. 2007), což může mít negativní dopad na fitness synantropních druhů (Møller & Ibáñez-Álamo 2012). Početnost ptáků mohou lokálně snižovat také kolize s transparentními a reflexními plochami nebo s automobily (Klem 2009). Samotný proces urbanizace však způsobuje rozsáhlé změny vedoucí k antropogenním disturbancím, k fragmentaci a degradaci dalších habitatů (Hockin et al. 1992, Crooks et al. 2004, Sorace & Gustin 2010). Některé z těchto změn však mohou vést ke vzniku cenných náhradních stanovišť a mít tak význam pro zvýšení lokální diverzity a pro ochranu ptáků (Eyre et al. 2003, Angold et al. 2006, Strauss & Biedermann 2006, Langner & Endlicher 2007). Různé druhy tak v urbánním prostředí dosahují vyšší početnosti než v primárních habitatech (Šťastný et al. 2006). Ve střední Evropě jsem však signifikantní změny v rozšíření synantropních druhů ptáků nezaznamenal (**Příspěvek I**).

Velmi často diskutovanou příčinou změn početnosti a druhového bohatství ptáků jsou změny klimatu. Spolu s dlouhodobým nárůstem průměrné roční teploty v Evropě mají obecně negativní dopad spíše na početnost a rozšíření druhů se severoevropským typem rozšíření a na dálkové migranty, naopak jihoevropské a stálé druhy ptáků jsou ovlivňovány pozitivně (Bauer et al. 2008, Reif et al. 2008b, Schaefer et al. 2008). Změny klimatu však samy o sobě nejsou dostatečným impulsem pro šíření jihoevropských druhů do střední a východní Evropy, jestliže historicky došlo na území s potenciálem pro jejich šíření k zániku vhodných biotopů (např. drop velký [*Otis tarda*], dytík úhorní [*Burhinus oedicnemus*], mandelík hajní [*Coracias garrulus*] nebo ťuhýk menší [*Lanius minor*], **Příspěvek I**). V případě migrantů je dalším negativním faktorem degradace biotopů na tahových zastávkách, shromaždištích a na zimovištích (desertifikace Středomoří a Sahelu; Opdam & Wascher 2004, Moreno-Rueda & Pizarro 2008, Schaefer et al. 2008, Yamamura et al. 2008). Zejména u hmyzožravých migrantů může být pro reprodukční úspěšnost kritické rovněž správné načasování přiletu na hnízdiště a začátku hnízdění. U populací některých druhů, které nedokázaly datum přiletu optimálně přizpůsobit potravní nabídce vrcholící vlivem klimatických změn dříve, došlo k dlouhodobému poklesu početnosti (Both et al. 2006). Naopak populace stálých druhů ptáků

mají při mírných zimách vyšší míru přežívání a v hnízdním období jsou tak kompetičně zdatnější, což může také vyústit v negativní změny početnosti migrantů (Lemoine & Böhning-Gaese 2003, Lemoine et al. 2007b). V České republice však negativní změna početnosti migrantů nebyla zjištěna (**Příspěvek I, II**). Jedním z důvodů může být skutečnost, že díky geografické poloze hnízdišť ptáci využívají několik migračních tras, zimují na více lokalitách a mohou být proto vůči nepříznivým vlivům na tahových zastávkách a zimovištích i vůči nepříznivému načasování migrace odolnější než západoevropské populace vázané pouze na část těchto tras a zimovišť (viz Cepák et al. 2008, **Příspěvek I**).

V neposlední řadě může mít potenciálně negativní vliv na ptačí společenstva v některých regionech šíření exotických druhů ptáků a patogenů (Drake et al. 1989, Williamson 1996, Duncan et al. 2003). Ve střední a východní Evropě však tento efekt na změny početnosti ptáků na úrovni jednotlivých států dosud nebyl potvrzen (viz Lemoine et al. 2007a).

Měníci se intenzita působení environmentálních faktorů má obecně nepříznivý vliv na habitatové specialisty a druhy s K-strategií, které nedovedou na náhlé změny podmínek reagovat tak pružně jako generalisté a druhy s r-strategií (Henle et al. 2004, **Příspěvek IV**). K-stratégové však mohou být odolnější vůči nepříznivým podmínkám zejména v omezených populacích (Jiguet et al. 2007). Ačkoli mohou r-stratégové početnost obnovit rychleji, čelí vyššímu riziku extinkce z důvodu výraznějších populačních fluktuací (Sol et al. 2012). Naopak druhy, které dovedou více investovat do reprodukce v budoucnu (K-stratégové), mohou vyčkat do dalších let na podmínky příznivější pro rozmnožování (Sol et al. 2012).

Působení faktorů ovlivňujících změny početnosti ptáků se vzájemně prolíná, což může bránit objasnění primárních příčin některých jevů (**Příspěvek II**). Platnost patrností ve změnách početnosti ptáků však často závisí na metodických či jiných okolnostech výzkumu a musí být prověřena dalšími studii (cf. Fox 2004, Wretenberg et al. 2006).

Podobně jako početnost, také stupeň ohrožení ptačích druhů má ekologické a life-history prediktory (**Příspěvek IV**). Stupeň ohrožení pěvců hnízdících v České republice silně pozitivně koreloval s habitatovou specializací druhů a s jejich pozicí v r-K kontinuu. Habitatoví specialisté patří mezi více ohrožené skupiny druhů pravděpodobně z důvodu vyšší citlivosti ke ztrátě a změnám habitatů vyvolaným především lidskou činností (Owens & Bennett 2000, Devictor et al. 2008). K poklesu početnosti specialistů však dochází v celé Evropě (Le Viol et al. 2012). Možnou příčinou je využívání omezeného zdroje všemi subpopulacemi druhu, kdy degradace habitatů ve větší oblasti může bezprostředně ohrozit druh na tento habitat specializovaný. Naopak populace habitatových generalistů využívají

širší škálu prostředí, jejichž současná degradace je méně pravděpodobná (Hernandez et al. 2006). Habitatoví generalisté se zároveň lépe dokážou měnícím se podmínkám přizpůsobit a častěji osidlují nově vznikající a urbánní habitaty (Devictor et al. 2007).

Zároveň nejohroženějšími habitatovými specialisty jsou K-stratégové, zatímco specialisté s r-strategií jsou méně ohroženi (**Příspěvek IV**). Jedním z možných vysvětlení je obecně vyšší fekundita r-stratégů (Sæther et al. 2005) spojená se schopností rychleji doplnit případný pokles počtu jedinců v populacích. Naopak u habitatových generalistů může mít pozitivní vliv schopnost K-stratégů přežít nepříznivé podmínky a rozmnožovat se teprve po skončení jejich působení (Sol et al. 2012). Tento mechanismus může být příčinou vyšší odolnosti generalistů vůči degradaci habitatů. Navíc velké druhy pěvců-generalistů (zejména Corvidae) mají lépe rozvinuté kognitivní schopnosti a složitější vzorce chování (Sol et al. 2005), což jim umožňuje lépe reagovat na nepříznivé působení různých faktorů (Reif et al. 2011).

Vliv legislativní druhové ochrany na změny početnosti ptáků

Životní prostředí bylo na konci 80. let 20. století v řadě zemí střední a východní Evropy degradováno intenzivní průmyslovou výrobou a zemědělským hospodařením (Moldan 1990, Haugstad & Wulfhorst 2004). Antropogenní vlivy s nejvíce negativním dopadem však byly po roce 1989 v důsledku ekonomické situace v těchto zemích dočasně utlumeny (Yarnal 1995). Následoval proces zlepšování stavu životního prostředí, který byl urychlen zejména v zemích usilujících o vstup do Evropské unie zaváděním standardů přísnější legislativy na ochranu životního prostředí včetně druhové ochrany přírody (Haugstad & Wulfhorst 2004).

V jednotlivých postkomunistických státech jsou uplatňovány dva základní přístupy k druhové ochraně ptáků. Původnější přístup spočívá v ochraně menšího počtu vybraných, nejčastěji vzácných, ohrožených nebo charismatických, u veřejnosti oblíbených druhů. Toto pojetí druhové ochrany přírody je dodnes uplatňováno, nejčastěji v méně vyspělých zemích (**Příspěvek III**). V 80. a 90. letech 20. století však začalo stále více, zejména ekonomicky rozvinutějších zemí chránit plošně většinu druhů ptáků s výjimkou tradičně lovných druhů (**Příspěvek III**). V prvním případě mohou legislativní nástroje a finanční prostředky alokované pouze na ochranu nejohroženějších druhů, těmto druhům účinněji pomoci. Při ochraně pouze omezeného počtu druhů však může docházet ke zhoršení populačních trendů u nechráněných druhů (**Příspěvek III**). U obou přístupů mohou být v rámci seznamů chráněných druhů vymezeny podkategorie zvláštní druhové ochrany. Zejména v zemích

chránících většinu druhů umožňuje tato kategorizace snazší alokování finančních prostředků a zvýšeného úsilí státních i nevládních organizací na ochranu přírody na přijímání opatření vedoucích k ochraně nejvíce ohrožených druhů (**Příspěvek III**).

Systematická aktivní opatření na podporu populací nejvíce ohrožených a nejpřísněji chráněných druhů (tzv. záchranné programy) patří k moderním nástrojům druhové ochrany přírody. Jejich náplní je zejména posílení populací vypouštěním jedinců z umělých odchovů, reintrodukce, podpora potravních a hnízdních možností, aktivní ochránářský management prostředí, které druh obývá nebo osvětová činnost. Záchranné programy zpravidla realizují vládní nebo nevládní organizace a jednotlivci. Na rozdíl od legislativy jako celku bývá účinnost záchranných programů hodnocena častěji a dosavadní studie ukázaly, že řada přímých opatření funguje úspěšně a mohou hrát v druhové ochraně ptáků velmi důležitou roli (viz Williams et al. 2012). Ačkoli jsou záchranné programy v uplynulých letech realizovány stále častěji, v zemích střední a východní Evropy do roku 2000 vznikaly spíše sporadicky a bez legislativního zázemí (vlastní nepublikovaná data).

Systém druhové ochrany ptáků přijímané na úrovni jednotlivých zemí je různou měrou ovlivněn závazky plynoucími z přijímání mezinárodních úmluv, které se na ochranu jednotlivých skupin druhů vztahují. Mezi nejvýznamnější mezinárodní úmluvy s praktickým dopadem na legislativu ochrany přírody v Evropě patří zejména Úmluva o ochraně evropské fauny, flóry a přírodních stanovišť (Bernská úmluva), Úmluva o mokřadech (Ramsarská úmluva), Úmluva o mezinárodním obchodu s ohroženými druhy volně žijících živočichů a planě rostoucích rostlin (CITES) a Úmluva o ochraně stěhovavých druhů volně žijících živočichů (Bonnská úmluva). Pro ochranu evropských druhů ptáků je klíčová Směrnice o ptácích (Směrnice Rady č. 79/409/EHS o ochraně volně žijících ptáků) platná v zemích Evropské unie. Pouze účinnost této směrnice v ochraně ptáků byla v Evropě komplexně hodnocena a v zemích, kde byla implementována, byl její efekt pozitivní (Donald et al. 2007). Informace o dopadu implementace většiny mezinárodních dohod na efektivitu ochrany přírody však nejsou k dispozici.

Celkový vliv legislativy druhové ochrany přírody na změny početnosti chráněných druhů ptáků v zemích střední a východní Evropy byl v letech 1990–2000 pozitivní, ačkoli v jednotlivých zemích se významněji lišil pravděpodobně z důvodu působení specifických lokálních podmínek (**Příspěvek III**). To je v souladu s výsledky ze západní Evropy a severní Ameriky (Male & Bean 2005, Donald et al. 2007). Pozitivní změny populačních trendů legislativně chráněných druhů pravděpodobně souvisely s rychlou transformací některých

zemí po politických změnách v roce 1989, zaváděním moderní legislativy na ochranu životního prostředí a s rostoucím povědomím veřejnosti (ale viz Voříšek et al. 2008).

V zemích chránících menší podíl celkového počtu druhů došlo po přijetí nové legislativy na druhovou ochranu ptáků v letech 1990–2000 k výraznému zlepšení populačních trendů chráněných druhů ve srovnání s druhy nechráněnými. Naopak v zemích chránících většinu druhů se populační trendy chráněných druhů změnily nevýznamně, ale populační trendy nechráněných druhů se změnily negativně (**Příspěvek III**). Příčinou úbytku nechráněných druhů může být lov nebo přímé pronásledování (Chiron & Julliard 2013). Země chránící pouze omezený počet druhů zařadily mezi chráněné zpravidla pouze druhy nejvíce ubývající a ohrožené. Naopak druhá skupina zemí poskytovala zákonnou ochranu také běžným a neubývajícím druhům. Oba přístupy tedy hrají v druhové ochraně ptáků významnou roli. Lze předpokládat, že pro účinnou legislativní ochranu ptáků je nejvhodnější kombinace obou přístupů (**Příspěvek III**).

Pozitivní efekt druhové ochrany ptáků mohl být u některých druhů maskován jinými faktory, ačkoli vliv potenciálně významných byl v analýzách odfiltrován (**Příspěvek III**). Důležitou roli hrálo výrazné zlepšení stavu životního prostředí po politických změnách v roce 1989 alespoň v některých státech (Goławski 2006, **Příspěvek I**). Například některé druhy ptáků zemědělské krajiny profitovaly z opouštění zemědělské půdy v tomto období (Verhulst et al. 2004, Kamp et al. 2011). Snížení objemu emisí a méně častý výskyt kyselých dešťů vedly k zlepšení stavu lesních porostů a tudíž i některých lesních druhů ptáků (Flousek 1989). Zlepšení životního prostředí ve střední a východní Evropě však působilo na všechny druhy bez ohledu na to, zda byly legislativně chráněny. Proto lze říci, že druhová ochrana ptáků je pro objasnění rozdílů v populačních trendech legislativně chráněných a nechráněných druhů klíčová (**Příspěvek III**).

Závěr

Přestože spolu jednotlivá vyjádření změn početnosti ptáků pozitivně korelují, jejich prediktory jsou rozdílné a tyto rozdíly je nutné brát v potaz při interpretaci výsledků studií změn početnosti ptáků. Prosté změny početnosti, změny rozšíření a změny trendů početnosti ptáků nelze zaměňovat a pouze jejich společná analýza může objasnit mechanismy mající vliv na populační charakteristiky ptáků na určitém území a v určitém čase. Zároveň je však nutné brát v potaz omezení dat – například data o změnách rozšíření ptáků pocházejí často z atlasových mapování a nemohou zachytit změny, k nimž došlo mezi mapováními. Naopak

data vyjadřující dlouhodobé změny početnosti ptáků zpravidla nedovedou zachytit změny rozšíření.

Podobně jako v jiných částech Evropy, kde již byly změny rozšíření ptáků analyzovány (např. Gregory et al. 2007, Kerbiriou et al. 2009), výsledky naznačují, že hlavní příčinou změn rozšíření jednotlivých ekologických skupin druhů ptáků ve střední Evropě je zejména intenzifikace zemědělství, šíření lesa, globální změny klimatu a homogenizace biotopů. Budoucí studie by se měly podrobněji zaměřit na jednotlivé mechanismy ovlivňující změny rozšíření v dalších zemích střední a východní Evropy. Velmi žádoucí je metaanalýza publikovaných výsledků a podrobnější rozbor kontraintuitivních změn početnosti. Ty mohou být zapříčiněny vedle biologických mechanismů také metodickým zázemím studie. Při interpretaci výsledků by měl být brán v potaz výběr modelové skupiny druhů, použitá metrika změn početnosti a způsob vyjádření prediktorů změn početnosti.

Habitatoví specialisté byli ve střední Evropě více ohroženi než generalisté. Zároveň K-strategie zvyšovala riziko extinkce u habitatových specialistů, toto riziko však snižovala u habitatových generalistů. Vyšší míra ohrožení habitatových specialistů ve střední Evropě naznačuje, že důležitým faktorem predikujícím ohrožení jednotlivých druhů je degradace jejich prostředí. Schopnost druhů vyrovnat se s působením těchto změn úzce závisí na jejich životní strategii. Habitatoví specialisté s K-strategií tak v praktické ochraně přírody vyžadují jiná opatření než r-stratégové-specialisté.

Celkový vliv druhové ochrany na změny početnosti ptáků ve střední a východní Evropě byl pozitivní a národní legislativa na ochranu ptáků tak hraje důležitou roli i na regionální úrovni. Velikost tohoto efektu se však mezi jednotlivými státy výrazněji lišila pravděpodobně v důsledku specifických podmínek působících v jednotlivých zemích. Ve státech chránících menší podíl ptačích druhů došlo po přijetí nové legislativy k výraznému zlepšení populačních trendů u chráněných druhů ve srovnání s druhy nechráněnými. Naopak v zemích chránících velkou většinu druhů ptáků se populační trendy chráněných druhů změnilly pouze nevýznamně, ačkoli nechráněné druhy změnilly svou početnost negativně. Pro účinnou legislativní ochranu ptáků je tedy pravděpodobně nejvhodnější kombinace obou přístupů.

Výsledky práce mohou být dále využity při vytváření a další optimalizaci národní i mezinárodní legislativy na druhovou ochranu ptáků a při analýzách její účinnosti. Autoři budoucích studií by se měli ve spolupráci se znalci lokálních podmínek intenzivněji zabývat implementací a dodržováním legislativy, efektivitou přímých opatření na ochranu jednotlivých druhů, podrobnější analýzou účinnosti jednotlivých legislativních nástrojů a

dalšími, zejména lokálními faktory, které mohou mít na efekt legislativní ochrany ptáků vliv. Námětem pro budoucí studie je také efekt implementace Směrnice o ptácích do národní legislativy zemí, které vstoupily do Evropské unie po roce 2000. Data o změnách početnosti z období 2000–2010 (Birds in Europe III) ze všech zemí střední a východní Evropy však budou uceleně zpracována a publikována nejdříve po roce 2014.

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Příspěvek I.

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Changes in bird distribution in a Central European country between 1985–1989 and 2001–2003

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Abstract European birds have been significantly affected by dramatic environmental changes during the last decades. The effects of these changes on species richness and distribution in particular countries are still poorly understood because of a lack of high-quality, large-scale data standardized over time. This is especially true in Central and Eastern Europe. On a model group of birds in the Czech Republic (countrywide atlas mapping data), we examined whether long-term changes of species richness and distribution between 1985–1989 and 2001–2003 differed among groups of species defined by their habitat requirements, type of distribution in Europe, migratory strategy and the degree of national legal protection. Further, we investigated the effects of colonizers and local extinctions on these changes. Whereas the number of species in the whole country remained the same in both periods (208 species), species composition had changed. Increasing occupancy (i.e., number of occupied mapping squares) was observed in species of forest and wetland habitats, in short-distance

migrants and in non-protected species. Southern species also positively changed their occupancy, but this pattern disappeared after the inclusion of six species dependent on extensively cultivated farmland that went extinct between mappings. The overall occupancy of all species together showed positive changes after excluding colonizers and extinct species. We suggest that the improvement of environmental conditions after 1990 caused the stability of or increased the distribution of common birds in the Czech Republic, and it was the disappearance of specific farmland practices that might have caused the loss of several species.

Keywords Bird community · Species richness · Distribution · Central Europe · Global change · Land use

Introduction

Biodiversity conservation is one of the fundamental objectives of current initiatives for nature protection (Primmack 2006). Although most attention is paid to the ongoing decline of global species richness (Swanson 1998), we should bear in mind that management measures are most frequently implemented at local or regional levels, usually within individual states (Lenzen et al. 2008; Yamamura et al. 2008; Orłowski and Ławniczak 2009). Local change in species richness is determined by the number of species that colonize the area and the number of species that disappear. Local colonization and extinction rates are related to the sensitivity of particular species to current changes in the landscape (Donald et al. 2007; Lenzen et al. 2008). For effective conservation management, it is therefore important to see whether species undergoing range retraction have different ecological traits from species with expanding ranges. For this purpose, we can examine the mean

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change in regional distribution of groups of species with defined ecological characteristics (Gregory et al. 2005; Jiguet et al. 2007; Van Turnhout et al. 2010).

Such an “ecological-group” approach has been used successfully for the examination of temporal changes in regional breeding bird distribution in several Western European countries (Gregory et al. 2004; Julliard et al. 2004; Lemoine et al. 2007; Van Turnhout et al. 2007; Bauer et al. 2008). These studies have found prominent effects of various environmental changes on European birds such as the intensification of farming practices, urbanization and global climate change or habitat degradation on stop-over and wintering sites in the Mediterranean region and Sahel zone (Feranec et al. 2000; Jongman 2002; Opdam and Wascher 2004; Moreno-Rueda and Pizarro 2008; Schaefer et al. 2008).

Despite this large body of evidence, our information about factors affecting changes in bird distribution is incomplete due to an apparent regional bias in these studies. Findings from former communist Central and Eastern European countries are based only on a few local scale results (e.g., Tryjanowski 2000; Verhulst et al. 2004; Gołowski 2006; Orłowski and Ławniczak 2009), and their generalization is thus problematic. At the same time, factors affecting bird distribution might differ between Western and Eastern European countries: agriculture was less intensive in the East (Donald et al. 2001), implementation of conservation legislation was delayed (Donald et al. 2007), and many migratory species use different flyways and wintering grounds (Busse 2001; Cepák et al. 2008). The examination of whether the patterns found in Western parts of the European continent also hold true in former communist Central and Eastern European countries is thus of high importance for conservation. In this respect, birds of the Czech Republic represent an ideal opportunity to fill this knowledge gap. Their breeding distribution was mapped using a standardized technique in two mapping sessions during the last decades: in 1985–1989 and 2001–2003. Moreover, their ecological requirements are well known and documented (Hudec 1983, 1994; Hudec and Štátný 2005; Cepák et al. 2008), enabling the sorting of particular species into various ecological groups.

Based on the results of studies of European bird communities, we can formulate the following predictions about recent changes in distribution of particular ecological groups of Czech birds. First, landscape changes, such as the loss of extensively cultivated farmland because of agricultural intensification or land abandonment followed by forest spread, should reduce the distribution of farmland birds and increase the distribution of forest species (Lenzen et al. 2008; Reif et al. 2008a; Orłowski and Ławniczak 2009). Second, the increase in the average annual temperature should have a positive effect on the distribution of

south European species and a negative impact on the north European ones (Bauer et al. 2008; Reif et al. 2008b). Third, global warming, along with the degradation of wintering habitats, should lead to an increase in the distribution of resident species and to a decrease of migrants (Schaefer et al. 2008). Fourth, legal protection should have a positive impact on protected species compared to unprotected ones (Donald et al. 2007).

The aim of the study was to examine these predictions comparing particular ecological groups of Czech birds between the two mapping periods. For each species group, we have focused on changes in breeding distribution. We have paid special attention to the species that colonized the country or went extinct between the mappings and how these species influenced the observed patterns.

Methods

Bird distribution data

We used data from the two atlases of breeding bird distribution (hereafter Atlases) in the Czech Republic covering the period 1985–1989 (Štátný et al. 1996) and 2001–2003 (Štátný et al. 2006). Data were collected in a unified network of 628 squares of 10' longitude and 6' latitude (roughly 12 × 11.1 km) evenly covering the entire territory of the country. The method of fieldwork was based on the contributions of a large number of volunteers (750 and 532 in the first and second mapping periods, respectively) and was the same in both Atlases. Each volunteer was requested to survey all habitats in a selected square. It was recommended that they start with the most frequent habitats (fields, meadows, forests, towns, villages, etc.) and then move on to rarer ones (water bodies, wetlands, streams, etc.). Finally, a targeted search was carried out for individual species in appropriate environments or at appropriate times—e.g., at dusk in case of the owls, crakes, nightingales, etc. Field observations of each bird species in the particular mapping squares were recorded using 17 numerical breeding codes with respect to the probability of its breeding occurrence, according to the standards used in Europe (Hagemeijer and Blair 1997).

The distribution of each species (hereafter occupancy) was expressed as the number of occupied squares with categories of “probable” or “confirmed breeding” (breeding codes 3–16 in Hagemeijer and Blair 1997) in respective mapping periods. There were 215 species conforming to these criteria.

Definition of explanatory variables

We have recognized the following species groups (Appendix) differing in (1) habitat requirements, i.e., forest

species (78 species in the first and 80 in the second mapping), wetland species (61/65), farmland species (50/44) and urban species (19/19), (2) migration strategy, i.e., resident species (45/44), partial migrants (22/23), short-distance migrants (71/74) and long-distance migrants (70/67), (3) breeding distribution in Europe, i.e., northern species (68/69), southern species (53/51), central species (22/22) and widespread species (65/66), and (4) legal protection in the Czech Republic, i.e., critically endangered (30/28), highly endangered (56/55), endangered (28/28) and species without any special legal protection (94/97). The terms like “endangered” do not describe the real level of threat, but they are the title of the official categories of legal protection listed in Czech conservation law (Anonymus 2008). Therefore, a “critically endangered” species is under the highest conservation concern according to Czech conservation law, but in reality it may not be more threatened than other species. The real levels of threat to a particular bird species in the Czech Republic are currently unknown as no one has performed any formal analysis (Voříšek et al. 2008).

Most of the species used for further analyses were already sorted into these categories in Reif et al. (2006, 2008b) and Voříšek et al. (2008). For the categorization of the remaining species, we used the following literature sources: Hudec (1983, 1994) and Hudec and Štastný (2005) for the habitat requirements, anonymus (2008) for legal protection status and Hagemeyer and Blair (1997) for the breeding distribution in Europe.

Determination of particular groups defined by different breeding distributions in Europe followed the two-step assessment procedure described in Reif et al. (2008b). First, we divided Europe into three large regions with respect to the location of the Czech Republic: the northern region had its southern boundary five geographical degrees north of the latitudinal midpoint of the Czech Republic, the southern region had its northern boundary five degrees south of the midpoint of the Czech Republic, and the central region laid between the northern and southern regions. These regions broadly correspond to the biogeographical divisions of Europe. The Mediterranean region is in the south, the boreal region is in the north, and the continental region is in the central part (European Environmental Agency 2006). In the second step, we measured the area of the breeding range of each species in each region and calculated the proportion of a region covered by the range of the focal species. Based on these proportions, we defined four species groups differing in the latitudinal distributions of their breeding ranges in Europe. As nearly all species occurring in the Czech Republic have relatively large European breeding ranges distributed in all three regions, we could not use strict criteria such as “northern species are those confined solely to the northern region.”

Instead, we used criteria focused on the avoidance of a region in which a species has the lowest proportion of its range. We thus recognized: (1) northern species whose ranges cover <30% of the southern region (e.g., *Turdus pilaris*); (2) southern species whose ranges cover <30% of the northern region (e.g., *Luscinia megarhynchos*); (3) central species whose ranges cover <30% of southern and northern regions (e.g., *Parus palustris*); (4) widespread species whose ranges cover more than 30% of the area of each region (e.g., *Passer domesticus*). Although such species sorting is arbitrary to some extent, and indeed 30% has no biological meaning, we trust that it mirrors the real latitudinal preferences of a particular species.

Migratory strategy of each particular species was excerpted from the new Czech and Slovak migration atlas (Cepák et al. 2008), which is based on all known ringing recoveries of Czech birds up to 2002.

Statistical analysis

We calculated the change in occupancy (C) of each particular species between the two mapping periods using the formula introduced by Lemoine et al. (2007):

$$C = (N_2 - N_1) / ((N_2 + N_1) / 2)$$

$N_{1,2}$ is the occupancy of a given species in the first and second mapping period, respectively. Positive values of C indicate increasing occupancy, negative values decreasing occupancy and where $C = 0$ there is an indication of no change (Lemoine et al. 2007).

To test whether mean occupancy of particular species groups increased or declined, we performed the one-sample t -tests. Each test tested the null hypothesis that the mean change in occupancy of a given group is zero. Performance of 16 repeated tests using the same dataset would result in an elevated risk of a type I error (Zar 1996). To account for this factor, we have applied the Bonferroni correction, adjusting the 0.05 level of significance (α) to 0.0031.

To test whether mean changes in occupancy differ among the focal species groups, we have applied analysis of variance (ANOVA). First, we have performed one-way ANOVAs for each factor (i.e., habitat, European distribution, migratory strategy and protection status) separately. Tukey's HSD post hoc test was used to compare means where significant differences were found with the ANOVA. Second, we have examined the effects of each factor, controlling the influence of the others, using main effects ANOVA.

Finally, we were interested in the influence of colonization/extinction processes on changes in the distribution of birds in the Czech Republic. For this purpose, we excluded all species ($n = 14$) present only in one of the mapping periods and then repeated all the tests described

above. Comparison of the outcome of the tests with and without such species revealed their possible influence.

Results

The number of species in the Czech Republic remained the same in both periods—208 species. Seven species went extinct in the Czech Republic during the time between the mappings (*Falco vespertinus*, *Otis tarda*, *Burhinus oedipnemus*, *Charadrius hiaticula*, *Coracias garrulus*, *Lanius minor* and *L. senator*), and, at the same time, seven species colonized the country (*Egretta alba*, *Anas penelope*, *Tadorna tadorna*, *Pandion haliaetus*, *Aquila heliaca*, *Chlidonias hybridus* and *Otus scops*). The prevailing characteristics of the species that were not registered in the second mapping period were: farmland habitat (six species), long-distance migratory strategy (six species), southern distribution (five species) and critically endangered

protection status (four species). The colonizers were characterized by wetland habitat (five species), long-distance (three species) or short-distance migratory strategy (three species), southern distribution (three species) and no legal protection (four species).

The overall mean change in occupancy between both mappings was not significantly different from zero (Table 1a). Regarding particular species groups, we found a positive change in occupancy in forest and wetland species, short-distance migrants and non-protected species. After application of the Bonferroni correction, the result remained significant in the wetland species only (Table 1a). No group showed a significantly negative change in mean occupancy, although the result in farmland birds approached the 0.05 significance level (Table 1a).

We applied analysis of variance to test whether some ecological characteristics would predict differences among the species groups in their mean changes in occupancy. We have found that habitat requirements were the only

Table 1 Changes in species richness (total number of species in the country) and occupancy (number of occupied mapping squares) of birds in the Czech Republic between 1985–1989 and 2001–2003 as revealed by the country-wide breeding distribution atlas mapping

	Species richness		(a) Change in occupancy (\pm SE)	<i>N</i>	<i>t</i>	<i>P</i>	(b) Change in occupancy (\pm SE)	<i>N</i>	<i>t</i>	<i>P</i>
	1985–1989	2001–2003								
<i>Habitat requirements</i>										
Farmland	50	44	−0.21 (\pm 0.11)	50	−1.92	0.0614	0.04 (\pm 0.06)	44	0.58	0.5626
Forest	78	80	0.14 (\pm0.05)	80	2.74	0.0076	0.09 (\pm0.04)	78	2.33	0.0220
Urban	19	19	−0.09 (\pm 0.06)	19	−1.42	0.1742	−0.09 (\pm 0.06)	19	−1.41	0.1742
Wetland	61	65	0.28 (\pm0.06)	66	3.10	0.0029	0.19 (\pm0.07)	60	2.63	0.0107
<i>Migratory strategy</i>										
Resident	45	44	0.02 (\pm 0.08)	45	0.24	0.8127	0.06 (\pm 0.06)	44	1.03	0.3096
Partial migrants	22	23	0.14 (\pm 0.10)	23	1.34	0.1934	0.05 (\pm 0.06)	22	0.87	0.3934
Short-distance migrants	71	74	0.19 (\pm0.07)	74	2.64	0.0102	0.11 (\pm 0.06)	71	1.90	0.0619
Long-distance migrants	70	67	0.01 (\pm 0.10)	73	0.08	0.9328	0.10 (\pm 0.05)	64	1.94	0.0571
<i>European distribution</i>										
Central	22	22	0.02 (\pm 0.17)	23	0.09	0.9271	0.02 (\pm 0.13)	21	0.13	0.8947
Northern	68	69	0.13 (\pm 0.08)	70	1.70	0.0930	0.11 (\pm 0.06)	67	1.70	0.0882
Southern	53	51	0.10 (\pm 0.12)	56	0.86	0.3951	0.20 (\pm0.06)	48	3.14	0.0029
Widespread	65	66	0.05 (\pm 0.04)	66	1.23	0.2239	0.02 (\pm 0.03)	65	0.73	0.4708
<i>Protection status</i>										
Non-protected	94	97	0.12 (\pm0.05)	98	2.43	0.0168	0.06 (\pm0.02)	93	3.29	0.0014
Endangered	28	28	0.03 (\pm 0.06)	28	0.43	0.6692	0.03 (\pm 0.06)	28	0.43	0.6692
Highly endangered	56	55	0.10 (\pm 0.09)	57	1.02	0.3137	0.14 (\pm 0.07)	54	1.86	0.0679
Critically endangered	30	28	0.03 (\pm 0.20)	32	0.16	0.8769	0.19 (\pm 0.16)	26	1.21	0.2344
<i>Total</i>	208	208	0.09 (\pm 0.05)	215	1.91	0.0576	0.09 (\pm0.03)	201	3.00	0.0030

Species were sorted into groups defined by their habitat requirements, migratory strategy, European distribution and legal protection status in the Czech Republic. Statistics refer to single sample *t* tests that tested the significance of change in occupancy of each group between the mapping periods. Significant differences ($P < 0.05$) are in bold type, and those significant after the Bonferroni correction ($P < 0.0031$) are underlined. Tests were performed with (a) and without (b) 14 species that colonized the country or went extinct between the mapping periods. See “Methods” section for a detailed description of the calculation of change in occupancy and for more details on the sorting of species into the ecological groups

Table 2 The effects of ecological characteristics of bird species expressed as four factors on changes in their mean occupancy between 1985–1989 and 2001–2003 tested by one-way ANOVAs (separate tests for each factor) with (a) and without (c) 14 species

Factor	(a)		(b)		(c)		(d)	
	$F_{3,211}$	P	$F_{3,202}$	P	$F_{3,197}$	P	$F_{3,188}$	P
Habitat requirements	6.6040	0.0003	5.7691	0.0008	2.4741	0.0628	2.1731	0.0926
Migratory strategy	1.1359	0.3355	0.2256	0.8785	1.1795	0.9102	0.1149	0.9512
European distribution	0.2533	0.8589	0.3632	0.7796	1.8702	0.1471	1.6522	0.1789
Protection status	0.2152	0.8858	0.3402	0.7963	1.0695	0.3631	0.2533	0.8589

See Table 1 for identification of the levels of each factor

Significant differences ($P < 0.05$) are in bold type

significant predictor of these changes, as shown by both one-way and main effects ANOVAs (Table 2a, b, Fig. 1). Post hoc comparisons using Tukey’s HSD tests showed that both forest ($P = 0.0138$) and wetland ($P = 0.0001$) species extended their distribution more than farmland species.

After exclusion of the 14 species present only in one of the two mappings, we found that the overall mean change in occupancy between the mappings was positive (Table 1b). Further, the results showed increasing occupancy in southern species (Table 1b). Excluding colonizers and extinct species did not qualitatively change the results for forest, wetland and non-protected species (Table 1b). In contrast, change in short-distance migrants was no longer significant (Table 1b). After the Bonferroni correction, the overall average change in occupancy and change in southern and non-protected species remained significant (Table 1b).

Exclusion of the 14 species, present only in one of both mappings, did not reveal any significant results in both one-way and main effects ANOVAs (Table 2c, d).

Discussion

Our results based on the analysis of the large-scale mapping data showed four striking patterns of changes in breeding bird distribution in the Czech Republic between 1985–1989 and 2001–2003: (1) dominant effect of habitat over all other factors, (2) weaker but significant effects of European distribution, migratory strategy and protection status in some tests, (3) influence of rare species on most of the observed patterns and (4) prevalence of positive changes in bird distribution over the negative ones. The effects of habitat and European distribution were in congruence with our initial predictions, but the legal protection status showed the opposite pattern to what we had expected. The effect of migratory strategy did not support our

prediction of decline in long-distance migrants and increase of residents.

present in only one of the mappings, and by main effects ANOVAs (all factors included into one model) with (b) and without (d) 14 species present in only one of the mappings

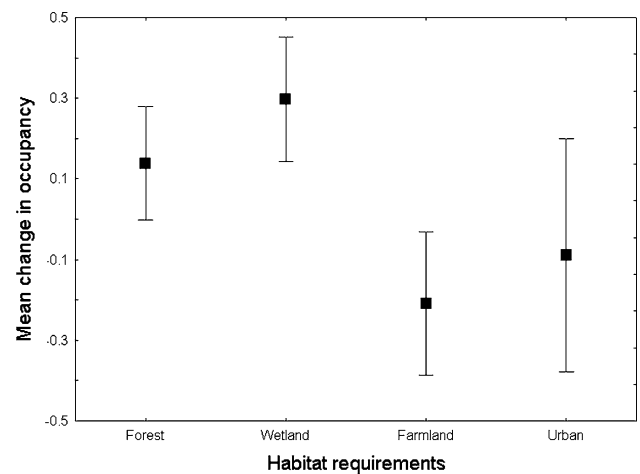


Fig. 1 Mean changes in the occupancy of Czech birds between 1985–1989 and 2001–2003 according to their habitat requirements. The vertical bars denote 0.95 confidence intervals. In one-way ANOVA, $F_{3,211} = 6.6040$ and $P = 0.0003$. Pairwise comparisons of means by the Tukey test gave the following results: Forest different from Farmland ($P = 0.0138$) and Wetland different from Farmland ($P = 0.0001$)

prediction of decline in long-distance migrants and increase of residents.

The effect of habitat was caused by expansion of forest and wetland species in contrast to farmland birds. Since this contrast was not significant after excluding species detected in one mapping only, the marked difference between these habitat-defined species groups is probably caused by the extinction of six farmland species between the mapping periods: *Falco vespertinus*, *Otis tarda*, *Burhinus oedicnemus*, *Coracias garrulus*, *Lanius minor* and *L. senator*. Their disappearance from the Czech Republic indicates a possible adverse impact of the recent land use practices on these species. This result is somewhat surprising as the decrease in agricultural intensity after the fall of communism probably reduced the rate of population decline of common farmland birds in the Czech Republic (Reif et al. 2008a), Poland (Goławski 2006) and Hungary

(Verhulst et al. 2004). This land use change obviously did not prevent more sensitive farmland species from extinction. The exact causes of the loss of these species remains unexplored. We can only speculate about the switch from an extensively cultivated agricultural landscape providing a heterogenous mosaic of habitats to either highly intensive agriculture or the complete abandonment of arable land in the key areas for populations of these species (Konvička et al. 2006, 2008; Ludwig et al. 2009; see also Štastný et al. 1996). The disappearance of these highly specialized species is consistent with Kerbiriou's et al. (2009) findings on the spread of tolerant species with a broad ecological niche leading to biotic homogenization of bird communities in France (Devictor et al. 2008) and the Netherlands (Van Turnhout et al. 2007).

The increasing occupancy of forest and wetland birds was found even if the species detected in only one mapping were excluded (although with lower significance). Therefore, we suggest that these patterns were caused mainly by extending distribution of common species already breeding in the Czech Republic, and the colonization of the country by new species has only strengthened this effect. In the case of forest birds, this result is in accordance with studies based on annual monitoring of populations of common species in the Czech Republic (Reif et al. 2007) and other parts of Europe (Gregory et al. 2007; Van Turnhout et al. 2007). It might be attributed to forest expansion, the alteration of forest age class composition towards older classes and/or by the impact of forest recovery after the reduction of imissions in the 1990s (Reif et al. 2007, 2008c). The increase of wetland birds was also confirmed in local bird communities in central and western Europe (Lemoine et al. 2007; Van Turnhout et al. 2010; Orłowski and Ławniczak 2009) and was probably caused by lower hunting pressure and the fact that many newly established nature reserves in the country protected wetland habitats (Málková and Lacina 2002).

Southern species that bred in the Czech Republic in both mapping periods extended their occupancy, corresponding with findings of an earlier study focused on annual changes in abundance of common birds in the Czech Republic (Reif et al. 2008b). This result is consistent with the observations of climate change impact on bird species (Julliard et al. 2004; Jiguet et al. 2007; Bauer et al. 2008). It also corroborates predictions of future breeding bird distribution patterns modeled under various scenarios of climatic warming (Huntley et al. 2007). Increasing occupancy of southern species, however, vanished after the inclusion of the species which became extinct between the mappings. A more detailed focus on particular species uncovered the fact that the decrease was caused by the extinction of the farmland species that were probably more affected by unfavorable land use practices than by the climate. This

result implies that global warming itself is not a sufficient impetus for range expansion of the southern species if their habitat is destroyed.

Regarding changes of distribution of birds with different migratory strategies, we have found two unexpected results: increased occupancy in short-distance migrants and no change in occupancy in long-distance migrants. The first pattern was driven by the expansion of several colonizers of wetland birds (*Egretta alba*, *Anas penelope* and *Tadorna tadorna*), and it was probably caused by habitat effects. The second pattern contrasts with observations of population decline of long-distance migrants in several western European countries (e.g., Lemoine et al. 2007; Heldbjerg and Fox 2008) and might be attributable to the use of different migratory routes and/or wintering sites by the Czech populations (Busse 2001; Cepák et al. 2008).

Increasing occupancy was found in non-protected species, and the same result was found in all species grouped together after the exclusion of species detected in one mapping only. These results imply that common birds probably benefited from changes in the Czech landscape after 1990. In fact, components of the environment, including water, air, forests and farmland, were heavily affected by human activity within all of Europe in the late 1980s (Moldan 1990). During the 1990s, the water quality and air pollution greatly improved, and there was also a sharp decrease in agricultural intensity. These positive changes were also documented in Poland (Goławski 2006) and Hungary (Verhulst et al. 2004). Moreover, forests, defoliated in extensive areas because of air pollution, started to recover (Anonymus 1996; Reif et al. 2007, 2008a). At the same time, we have failed to find any significant positive effect of legal protection on the occupancy of species. The reason may lie in the low effectiveness of direct conservation actions (Kumstátová et al. 2005). Czech nature conservation is probably not able to take care of problematic bird species (Voříšek et al. 2008). Further studies are needed to ensure that existing protected areas create suitable conditions for endangered birds' existence (e.g., Kollar and Wurm 1996).

To our knowledge, our study is the first attempt to examine the patterns of changes in breeding bird distribution on a country-wide level within the former Eastern block. Compared to the previous studies based on population trends from annual monitoring schemes (e.g., Gregory et al. 2007; Reif et al. 2008a, b, c), our breeding distribution mapping data involve information about uncommon species (Van Turnhout et al. 2007). They are, therefore, less biased, and the observed patterns are more general. Our results imply that the major drivers of changes (agricultural intensification, forest expansion, global climate change, biotic homogenization) are probably similar across European regions, although local specificities of

several aspects emerged (e.g., poor performance of legal protection). Future studies should focus in more detail on the investigation of particular drivers.

Zusammenfassung

Veränderungen in der Vogelverbreitung in einem mitteleuropäischen Land zwischen 1985–1989 und 2001–2003

Europäische Vögel sind in den letzten Jahrzehnten signifikant von dramatischen Umweltveränderungen betroffen worden. Die Effekte dieser Veränderungen auf den Artenreichtum und die Verbreitung in bestimmten Ländern sind nach wie vor schlecht verstanden, da hochwertige, großräumige Daten fehlen, die über die Zeit standardisiert sind. Dies trifft besonders auf Mittel- und Osteuropa zu. Anhand einer Modellgruppe von Vögeln in Tschechien (landesweite Atlaskartierungsdaten) haben wir untersucht, ob sich Langzeitveränderungen in Artenreichtum und Verbreitung zwischen 1985-1989 und 2001-2003 zwischen Artengruppen unterschieden, die anhand ihrer Habitatansprüche, ihrem Verbreitungstyp in Europa, ihrer Zugstrategie und ihrem nationalen Schutzstatus voneinander abgegrenzt sind. Außerdem haben wir die Effekte von Erstbesiedlungen und lokalen Ausrottungen auf diese Veränderungen untersucht. Während die Artenzahl im gesamten Land in beiden Zeiträumen gleich blieb (208 Arten), hat sich die Artenzusammensetzung verändert. Zunehmende Besiedlung (d.h. Zahl besetzter Kartenquadrate) wurde für in Wald- und Feuchtlandhabitaten vorkommende Arten, Kurzstreckenzieher und nicht geschützte Arten beobachtet. Im Süden vorkommende Arten veränderten ihre Besiedlung ebenfalls zum Positiven, doch dieses Muster verschwand nach der Einbeziehung von sechs Arten, die auf extensiv bewirtschaftetes Ackerland angewiesen sind und zwischen den Kartierungen ausstarben. Die gesamte Besiedlung aller Arten zusammengenommen zeigte positive Veränderungen, nachdem Erstbesiedler und ausgestorbene Arten ausgeschlossen worden waren. Wir schlagen vor, dass die Verbesserung der Umweltbedingungen nach 1990 die Verbreitung von häufigen Vögeln in Tschechien stabilisierte oder ansteigen ließ, und der Verlust mehrerer Arten könnte durch das Verschwinden spezifischer Ackerbautechniken verursacht worden sein.

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Appendix

See Table 3.

Table 3 List of species and their habitat requirements, migratory strategy, European distribution and legal protection status in the Czech Republic

Species	Habitat	Migration	Distribution	Protection
<i>Accipiter gentilis</i>	F	R	W	E
<i>Accipiter nisus</i>	F	P	W	H
<i>Acrocephalus arundinaceus</i>	W	L	S	H
<i>Acrocephalus palustris</i>	A	L	N	N
<i>Acrocephalus scirpaceus</i>	W	L	W	N
<i>Acrocephalus schoenobaenus</i>	W	L	N	N
<i>Actitis hypoleucos</i>	W	L	W	H
<i>Aegithalos caudatus</i>	F	R	W	N
<i>Aegolius funereus</i>	F	R	N	H
<i>Alauda arvensis</i>	A	S	W	N
<i>Alcedo atthis</i>	W	P	S	H
<i>Anas acuta</i>	W	S	N	C
<i>Anas clypeata</i>	W	S	N	H
<i>Anas crecca</i>	W	S	N	E
<i>Anas penelope</i>	W	S	N	N
<i>Anas platyrhynchos</i>	W	P	W	N
<i>Anas querquedula</i>	W	L	N	H
<i>Anas strepera</i>	W	S	C	E
<i>Anser anser</i>	W	S	N	N
<i>Anthus campestris</i>	A	L	S	H
<i>Anthus pratensis</i>	A	S	N	N
<i>Anthus spinoletta</i>	A	S	S	H
<i>Anthus trivialis</i>	F	L	W	N
<i>Apus apus</i>	U	L	W	E
<i>Aquila heliaca</i>	F	P	C	N
<i>Aquila pomarina</i>	F	L	C	C
<i>Ardea cinerea</i>	W	S	W	N
<i>Ardea purpurea</i>	W	L	S	C
<i>Asio flammeus</i>	A	S	N	H
<i>Asio otus</i>	A	P	W	N
<i>Athene noctua</i>	U	R	S	H
<i>Aythya ferina</i>	W	S	N	N
<i>Aythya fuligula</i>	W	S	N	N
<i>Aythya nyroca</i>	W	S	C	C
<i>Bonasa bonasia</i>	F	R	N	H
<i>Botaurus stellaris</i>	W	S	C	C
<i>Bubo bubo</i>	F	R	W	E
<i>Bucephala clangula</i>	W	S	N	H
<i>Burhinus oedienemus</i>	A	L	S	C
<i>Buteo buteo</i>	F	P	W	N
<i>Caprimulgus europaeus</i>	F	L	W	H

Table 3 continued

Species	Habitat	Migration	Distribution	Protection
<i>Carduelis cannabina</i>	U	S	W	N
<i>Carduelis carduelis</i>	U	P	S	N
<i>Carduelis flammea</i>	F	R	N	N
<i>Carduelis chloris</i>	U	P	W	N
<i>Carduelis spinus</i>	F	S	N	N
<i>Carpodacus erythrinus</i>	A	L	N	E
<i>Certhia brachydactyla</i>	F	R	S	N
<i>Certhia familiaris</i>	F	R	N	N
<i>Ciconia ciconia</i>	U	L	S	E
<i>Ciconia nigra</i>	F	L	S	H
<i>Cinclus cinclus</i>	W	R	W	N
<i>Circus aeruginosus</i>	W	L	C	E
<i>Circus cyaneus</i>	F	S	N	H
<i>Circus pygargus</i>	A	L	S	H
<i>Coccothraustes coccothraustes</i>	F	S	S	N
<i>Columba livia f. domestica</i>	U	R	W	N
<i>Columba oenas</i>	F	S	W	H
<i>Columba palumbus</i>	F	S	W	N
<i>Coracias garrulus</i>	A	L	S	C
<i>Corvus corax</i>	F	R	W	E
<i>Corvus cornix</i>	A	R	W	N
<i>Corvus corone</i>	A	R	S	N
<i>Corvus frugilegus</i>	U	P	C	N
<i>Corvus monedula</i>	U	P	W	H
<i>Coturnix coturnix</i>	A	L	S	H
<i>Crex crex</i>	A	L	N	H
<i>Cuculus canorus</i>	A	L	W	N
<i>Cygnus olor</i>	W	P	C	N
<i>Delichon urbica</i>	U	L	W	N
<i>Dendrocopos leucotos</i>	F	R	W	H
<i>Dendrocopos major</i>	F	R	W	N
<i>Dendrocopos medius</i>	F	R	C	E
<i>Dendrocopos minor</i>	F	R	N	N
<i>Dendrocopos syriacus</i>	F	R	S	H
<i>Dryocopus martius</i>	F	R	N	N
<i>Egretta alba</i>	W	S	S	H
<i>Egretta garzetta</i>	W	L	S	H
<i>Emberiza citrinella</i>	A	R	W	N
<i>Emberiza hortulana</i>	A	L	W	C
<i>Emberiza schoeniclus</i>	W	S	N	N
<i>Erithacus rubecula</i>	F	S	W	N
<i>Falco cherrug</i>	F	P	C	C
<i>Falco peregrinus</i>	A	P	W	C
<i>Falco subbuteo</i>	F	L	W	H
<i>Falco tinnunculus</i>	U	P	W	N
<i>Falco vespertinus</i>	A	L	C	C
<i>Ficedula albicollis</i>	F	L	C	N
<i>Ficedula hypoleuca</i>	F	L	N	N
<i>Ficedula parva</i>	F	L	N	H
<i>Fringilla coelebs</i>	F	S	W	N
<i>Fulica atra</i>	W	S	W	N
<i>Galerida cristata</i>	A	R	S	E
<i>Gallinago gallinago</i>	W	S	N	H

Table 3 continued

Species	Habitat	Migration	Distribution	Protection
<i>Gallinula chloropus</i>	W	S	W	N
<i>Garrulus glandarius</i>	F	P	W	N
<i>Glaucidium passerinum</i>	F	R	N	H
<i>Grus grus</i>	W	S	N	C
<i>Haliaeetus albicilla</i>	W	R	N	C
<i>Himantopus himantopus</i>	W	L	S	N
<i>Hippolais icterina</i>	F	L	N	N
<i>Hirundo rustica</i>	U	L	W	E
<i>Charadrius dubius</i>	W	L	W	N
<i>Charadrius hiaticula</i>	W	L	N	N
<i>Charadrius morinellus</i>	A	S	N	C
<i>Chlidonias hybridus</i>	W	L	S	N
<i>Chlidonias niger</i>	W	L	C	C
<i>Ixobrychus minutus</i>	W	L	S	C
<i>Jynx torquilla</i>	A	L	W	H
<i>Lanius collurio</i>	A	L	N	E
<i>Lanius excubitor</i>	A	P	W	E
<i>Lanius minor</i>	A	L	S	H
<i>Lanius senator</i>	A	L	S	H
<i>Larus cachinnans</i>	W	S	S	N
<i>Larus canus</i>	W	S	N	N
<i>Larus melanocephalus</i>	W	S	C	H
<i>Larus ridibundus</i>	W	S	N	N
<i>Limosa limosa</i>	W	L	C	C
<i>Locustella fluviatilis</i>	A	L	C	N
<i>Locustella luscinioides</i>	W	L	C	E
<i>Locustella naevia</i>	A	L	N	N
<i>Loxia curvirostra</i>	F	P	N	N
<i>Lullula arborea</i>	F	S	S	H
<i>Luscinia luscinia</i>	A	L	N	H
<i>Luscinia megarhynchos</i>	A	L	S	E
<i>Luscinia svecica cyanecula</i>	W	S	S	H
<i>Luscinia svecica svecica</i>	W	S	N	C
<i>Mergus merganser</i>	W	S	N	C
<i>Merops apiaster</i>	A	L	S	H
<i>Miliaria calandra</i>	A	P	S	C
<i>Milvus migrans</i>	F	L	S	C
<i>Milvus milvus</i>	F	S	S	C
<i>Motacilla alba</i>	U	S	W	N
<i>Motacilla cinerea</i>	W	S	S	N
<i>Motacilla flava</i>	A	L	W	H
<i>Muscicapa striata</i>	F	L	W	E
<i>Netta rufina</i>	W	S	S	H
<i>Nucifraga caryocatactes</i>	F	R	N	E
<i>Numenius arquata</i>	W	S	N	C
<i>Nycticorax nycticorax</i>	W	L	S	H
<i>Oenanthe oenanthe</i>	A	L	W	H
<i>Oriolus oriolus</i>	F	L	S	H
<i>Otis tarda</i>	A	R	S	C
<i>Otus scops</i>	F	L	S	C
<i>Pandion haliaetus</i>	W	L	N	C
<i>Panurus biarmicus</i>	W	P	S	H
<i>Parus ater</i>	F	R	W	N

Table 3 continued

Species	Habitat	Migration	Distribution	Protection
<i>Parus caeruleus</i>	F	P	W	N
<i>Parus cristatus</i>	F	R	W	N
<i>Parus major</i>	F	P	W	N
<i>Parus montanus</i>	F	R	N	N
<i>Parus palustris</i>	F	R	C	N
<i>Passer domesticus</i>	U	R	W	N
<i>Passer montanus</i>	A	R	S	N
<i>Perdix perdix</i>	A	R	C	E
<i>Pernis apivorus</i>	F	L	N	H
<i>Phalacrocorax carbo</i>	W	S	N	E
<i>Phasianus colchicus</i>	A	R	C	N
<i>Phoenicurus ochruros</i>	U	S	S	N
<i>Phoenicurus phoenicurus</i>	F	L	W	N
<i>Phylloscopus collybita</i>	F	S	W	N
<i>Phylloscopus sibilatrix</i>	F	L	N	N
<i>Phylloscopus trochiloides</i>	F	L	N	N
<i>Phylloscopus trochilus</i>	F	L	N	N
<i>Pica pica</i>	A	R	W	N
<i>Picoides tridactylus</i>	F	R	N	H
<i>Picus canus</i>	F	R	N	N
<i>Picus viridis</i>	F	R	S	N
<i>Platalea leucorodia</i>	W	S	S	C
<i>Podiceps cristatus</i>	W	S	N	E
<i>Podiceps grisegena</i>	W	S	N	H
<i>Podiceps nigricollis</i>	W	S	C	E
<i>Porzana parva</i>	W	L	C	C
<i>Porzana porzana</i>	W	L	N	H
<i>Prunella collaris</i>	A	S	S	H
<i>Prunella modularis</i>	F	S	W	N
<i>Pyrrhula pyrrhula</i>	F	P	N	N
<i>Rallus aquaticus</i>	W	S	S	H
<i>Recurvirostra avosetta</i>	W	S	S	C
<i>Regulus ignicapillus</i>	F	S	S	N
<i>Regulus regulus</i>	F	S	N	N
<i>Remiz pendulinus</i>	W	S	S	E
<i>Riparia riparia</i>	A	L	W	E
<i>Saxicola rubetra</i>	A	L	N	E
<i>Saxicola torquata</i>	A	S	S	E
<i>Scolopax rusticola</i>	F	S	N	E
<i>Serinus serinus</i>	U	S	S	N
<i>Sitta europaea</i>	F	R	W	N
<i>Sterna hirundo</i>	W	L	N	H
<i>Streptopelia decaocto</i>	U	R	S	N
<i>Streptopelia turtur</i>	A	L	S	N
<i>Strix aluco</i>	F	R	W	N
<i>Strix uralensis</i>	F	R	N	C
<i>Sturnus vulgaris</i>	F	S	W	N
<i>Sylvia atricapilla</i>	F	S	W	N
<i>Sylvia borin</i>	F	L	W	N
<i>Sylvia communis</i>	A	L	W	N
<i>Sylvia curruca</i>	U	L	N	N
<i>Sylvia nisoria</i>	A	L	C	H

Table 3 continued

Species	Habitat	Migration	Distribution	Protection
<i>Tadorna tadorna</i>	W	S	W	N
<i>Tachybaptus ruficollis</i>	W	S	S	E
<i>Tetrao tetrix</i>	A	R	N	H
<i>Tetrao urogallus</i>	F	R	N	C
<i>Tringa ochropus</i>	F	S	N	H
<i>Tringa totanus</i>	W	S	N	C
<i>Troglodytes troglodytes</i>	F	S	W	N
<i>Turdus iliacus</i>	F	S	N	H
<i>Turdus merula</i>	F	P	W	N
<i>Turdus philomelos</i>	F	S	W	N
<i>Turdus pilaris</i>	F	S	N	N
<i>Turdus torquatus</i>	F	S	N	H
<i>Turdus viscivorus</i>	F	S	W	N
<i>Tyto alba</i>	U	R	S	H
<i>Upupa epops</i>	A	L	S	H
<i>Vanellus vanellus</i>	A	S	N	N

habitat requirements (habitat): A—farmland, F—forest, U—urban, W—wetland; migratory strategy (migration): R—resident, P—partial migrants, S—short-distance migrants, L—long-distance migrants; European distribution (distribution): C—central, N—northern, S—southern, W—widespread; legal protection status (protection): N—non-protected, E—endangered, H—highly endangered, C—critically endangered

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Příspěvek II.

Koleček J. & Reif J. 2011: Differences between the predictors of abundance, trend and distribution as three measures of avian population change. *Acta Ornithologica* 46: 143–153.

Differences between the predictors of abundance, trend and distribution as three measures of avian population change

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Abstract. Changes in bird populations can be described as simple changes in abundance or density of individuals or, in larger areas, as changes of distribution or population indices. Although these measures describe different aspects of population change, they are often used interchangeably when discussing the relationships between various predictors of bird population changes found in different studies. This hampers a meaningful comparison of results, because it is unclear which differences between studies are biologically relevant and which are just methodological artifacts, caused by the different nature of measures used to quantify population changes. We compared predictors of the three measures of population changes: (i) change in abundance, (ii) change in magnitude of population trend and (iii) change in distribution, using data collected in a single region, the Czech Republic, and over similar time periods. We also aimed to identify significant drivers of population changes of Czech birds, using a large set of predictor variables and virtually all species regularly breeding in the region. No significant predictors were common across the three measures of population change tested. Abundance increased mostly in forest birds, while the change in magnitude of population trend was positive in species with a higher level of legal protection and in r-selected species. Species extending their distribution include wetland birds, above-ground nesters and north European species. Although individual measures of population changes are positively correlated, their predictors are different. This limits possibilities of simple comparisons, but also offers a better insight into forces shaping bird population changes in time and space.

Key words: abundance, distribution, population trend, population changes, land-use change

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INTRODUCTION

Biodiversity dynamics could be evaluated based on a wide array of measures (Magurran & McGill 2011), pertaining to species assemblages, individual species or genes. On the level of individual species, the majority of studies addressing dynamics of species in space and time, focus on analyses of long-term population changes. Such temporal changes in bird populations are best described as simple changes in abundance or density of individuals, but these are often quite difficult to quantify over larger areas. Therefore, other measures are frequently used as proxies for the population change, including changes in species distribution (or occupancy) or changes in various population indices (Böhning-Gaese & Bauer 1996, Lemoine et al. 2007, Kerbirou et al. 2009, Koleček

et al. 2010). One can also look at indices measuring the amount of population change over time to quantify the rate of population change (trend) and its temporal variation, i.e. dynamics of population change (Van Strien et al. 2001, Gregory et al. 2009). In summary, for a given time period, bird population changes are being characterized as change in (i) abundance, (ii) magnitude of population trend or (iii) distribution. These measures have been frequently used in the studies aiming to found the trait-based predictors of bird population changes (e.g. Donald et al. 2001, 2007, Sanderson et al. 2006, Lemoine et al. 2007, Bauer et al. 2008, Reif et al. 2008a, Kerbirou et al. 2009, Van Turnhout et al. 2010).

Although they describe different aspects of population change, these measures are often used interchangeably when discussing various

predictors of bird population changes revealed in diverse studies. This makes comparison of the results among the different studies difficult, because it is unclear what are the biologically relevant differences among the studies and what are the methodological artifacts caused simply by the different nature of the measures used. At the same time, however, such a comparison may contribute to a better understanding of forces driving population changes. To explore this subject further, we examined similarities and differences among the predictors of these three different measures of population changes, calculated for the same set of species, in the same region and over the similar time period. We expected here a positive correlation between change in distribution and change in abundance, given the general validity of the abundance-range size relationship (Gaston et al. 1997, Zuckenberg et al. 2009). On the other hand, the distribution of individual species should be more affected by a possible range shift, driven by climatic changes (Reif et al. 2008b), while abundance tends to be more influenced by habitat changes (Henle et al. 2004, Borregaard & Rahbek 2010) and thus their predictors might well differ accordingly. As the change in magnitude of population trend (as defined here; see "Methods") is based on the change in abundance in different periods, we also hypothesize that the two measures will show a positive correlation and similar predictors, which, in turn, would differ from the predictors of change in distribution.

Irrespective of the actual measure of population change, one of the most important questions is, what actually are the major drivers of changes observed recently in avian populations. Several studies have addressed this issue recently, by relating population changes to characteristics of species' ecological niches (i.e. species-habitat associations; e.g. Gregory et al. 2007). Farmland birds have long been recognized as the group suffering a widespread, and perhaps the most severe decline across the Europe. A continuing loss of extensively cultivated farmland due to agricultural intensification or land abandonment, connected with forest spread, has led to population declines in birds of open habitats, as well as diet and habitat specialists. The same process has promoted population increases among forest birds and species being diet and habitat generalists (Lenzen et al. 2008, Kerbiriou et al. 2009, Koleček et al. 2010). However, various factors related to bird population changes, including habitat preferences and life-history traits, are in fact interlinked,

hampering our identification of primary drivers of observed changes. For example, species building open nests, situated on the ground are more frequent among birds inhabiting extensively cultivated open habitats, now in decline. Therefore, also birds having open nests show generally more negative population changes, compared to species breeding in habitats with a higher vegetation density and to birds nesting in tree cavities (Thaxter et al. 2010). Furthermore, changing environmental conditions have more adverse impact on populations of 'K-selected' species, which are not able to track habitat changes as fast as 'r-selected' ones (Henle et al. 2004). On the other hand, lowering hunting pressure, together with the legislation enabling to establish many new wetland nature reserves and improve the conditions on wintering grounds, have a positive impact on populations of wetland species (Lemoine et al. 2007, Orłowski & Ławniczak 2009, Van Turnhout et al. 2010). The increase in average annual temperature has more negative effects on species with north European breeding range and on migrants, than for the south European breeders and residents (Bauer et al. 2008, Reif et al. 2008b, Schaefer et al. 2008). Finally, population changes in protected species are more positive in recent decades, compared to unprotected ones (Donald et al. 2007, Voříšek et al. 2008). However, the generality of these findings is yet to be supported, and importance of some widely recognized drivers is clearly context-dependent (cf. Fox 2004, Wretenberg et al. 2006). We therefore wanted to test the importance of various environmental and life-history variables for recent bird population changes in the Czech Republic, via species-specific trends.

Our goals in this paper were thus twofold: (1) to test, if different measures of population change correlate with the same predictors, and (2) to identify the important predictors of population change for Czech breeding birds.

METHODS

Measures of population changes and bird population data

We focused on population changes of 178 species breeding in the Czech Republic in the last four decades for which data are available (see Supporting Information — available via web page of the journal as well as on request from authors — for details). We expressed population changes of the focal bird species within the country in

three different ways: as (i) the change in abundance, (ii) change in the magnitude of population trend (or rate of change in abundance), (iii) change in distribution (occupancy) of the species.

The relevant data were extracted from two comprehensive data sources. Firstly, the Birds in Europe database, which provides estimates of the population trends of individual species in the Czech Republic in 1970–1990 and 1990–2000 (BirdLife International/European Bird Census Council 2000, BirdLife International 2004). Estimates of population sizes and trends were derived here from a combination of published and unpublished survey data, as well as expert opinion. This combined approach improved data quality, which is consistent across the species. Moreover, the reliability of Czech bird population changes data is generally high in the species we selected for this study due to a long tradition of various types of bird monitoring in this country (Hora & Kaňuch 1992, Klvaňová & Voříšek 2007, Reif et al. 2009). Prior to further analyses, we standardized categories of change in abundance in the period of 1990–2000 to the same categories used in the period of 1970–1990, using a simple coding introduced by Donald et al. (2007) and obtaining values from -2 to $+2$ ($0 = < 20\%$ change, $1 = 20\text{--}49\%$ change, $2 = > 50\%$ change). Although the codes for the change in magnitude of population trend are discrete values, in line with other studies (Møller et al. 2008) we have used them as continuous variables in the linear models, because they show unimodal distribution and are closely correlated with more detailed measures of population trend based on annual monitoring data. We excluded all species with unknown or fluctuating trend at least in one of the respective periods. The second source of data were two atlases of breeding bird distribution (hereafter Atlases) in the Czech Republic, covering the periods 1985–1989 (Štátný et al. 1996) and 2001–2003 (Štátný et al. 2006). The method of fieldwork was based on the contributions of a large number of volunteers and was the same in both Atlases. The distribution of each species was expressed as the number of occupied grid squares (roughly 12.0×11.1 km) with categories of “probable” or “confirmed breeding” (breeding codes 3–16 in Hagemeyer & Blair 1997) in individual mapping periods. For further details see Voříšek et al. (2008) or Koleček et al. (2010).

As a measure of the change in abundance we used standardized values of population trends (see above) reflecting change in overall population size between 1990 and 2000, extracted from

BirdLife International (2004). We did not use the difference in raw abundance estimates between 1970–1990 and 1990–2000 to express the change in abundance, because these estimates of the overall population size often change due to improved accuracy in evaluating many species. This methodological artifact may mask the genuine changes in species' abundance potentially caused by the environmental drivers we are interested in.

We obtained the change in the magnitude of population trend between 1970–1990 and 1990–2000 from the Birds in Europe database using the following formula:

$$T = \text{BiE2} - \text{BiE1}$$

where T is the magnitude of population trend change index, BiE is the standardized category of change in abundance (see above) in the period of 1970–1990 (BiE1) and 1990–2000 (BiE2), respectively. Positive values of T indicate positive change in magnitude of population trend and vice versa.

Furthermore, we calculated the change in distribution (D) of each particular species between the two mapping periods, using the formula introduced by Lemoine et al. (2007):

$$D = (N_2 - N_1) / ((N_2 + N_1) / 2)$$

where N_1 and N_2 are numbers of occupied atlas grid squares for a given species in the first and second mapping period, respectively. Positive/negative values of D indicate increasing/decreasing distribution and where $D = 0$ there is an indication of no change (Lemoine et al. 2007). These data have already been used in Koleček et al. (2010) and Reif et al. (2010a). Particular measures of population changes were used as dependent variables in further analyses.

Definition of explanatory variables

To predict the interspecific variability in population changes, we selected an assortment of predictors, which have been successfully used in recent studies (e.g. Böhning-Gaese & Oberrath 2003, Reif et al. 2011). Accordingly, we first defined 10 species' traits, characterizing habitat niche, dietary niche, latitudinal distribution as a surrogate for species' climatic niche (for these measures we used data from the breeding season), nest type and location and migratory strategy (see Supporting Information for the complete list of individual species and the respective traits). For habitat and dietary niche, we distinguished between niche position (i.e. mean value of the respective variable) and niche breadth (i.e. range

of the respective variable). Habitat niche position was based on a classification of species' habitat requirements along a gradient of decreasing complexity of vegetation structure and density (see Böhning-Gaese & Oberrath 2003): closed forest (1), open forest (2), forest edge (3), savannah, orchard, garden (4), scrubland or human settlement (5), open country with solitary trees or shrubs (6) and open country without solitary trees or shrubs (7). Species were given up to three different values and habitat niche position was calculated as the mean of these values. Habitat niche breadth was determined as the difference between extreme values. Another expression of habitat requirements we used was along a gradient of increasing habitat humidity: non-humid (1), wetland (2) and water (3) habitats. Dietary niche position was based on a classification of species into four different trophic levels as either herbivorous (1), herbivorous and insectivorous, or omnivorous (2), insectivorous (3) or carnivorous (4). Dietary niche breadth was based on a classification of species into obligatory herbivorous or obligatory insectivorous/carnivorous (1), herbivorous and insectivorous/carnivorous (2), or omnivorous (3), both (dietary niche and position) using data from Böhning-Gaese et al. (2000), Hudec (1983, 1994) and Hudec & Štátný (2005). Latitudinal distribution was calculated from maps of European breeding bird distribution (Hagemeyer & Blair 1997) as a latitudinal midpoint of individual species' breeding range. Nest type was scored along the gradient of the increasing nest hiddenness: open cup nests outside cavities (e.g. *Sylvia* sp.) (1), semi-closed nests either outside cavities (e.g. *Phylloscopus* sp.) or open nests in semi-cavities (e.g. *Phoenicurus* sp.) (2) and cavity nests (e.g. *Parus* sp.) (3). Nest location described the height of the nest above the ground: on the ground or close to the ground (1), middle high — i.e. shrubs and lower trees (2) and high (3). Migration distance was defined as the distance to the wintering grounds distinguishing between residents (1), short-distance migrants (2), and long-distance migrants (3). Moreover, we defined migratory flexibility as the variation in migratory behavior within a species. We thus recognized obligatory migrants and obligatory residents (0), and facultative migrants (1) using data from Cepák et al. (2008).

Furthermore, we chose six species' life-history traits — body mass, egg mass, number of broods per year, laying date (julian date of the beginning of laying in the first breeding), clutch size and

length of incubation expressed as mean values from published data (Hudec 1983, 1994, Hudec & Štátný 2005, for several species with a lack of data Cramp 1977–1994).

In addition to the ecological traits, we also investigated the effect of legal protection in the Czech Republic. The respective legislative act has recognized four levels of increasing protection: species without any special legal protection (0), endangered (i.e. least protected; 1), highly endangered (2) and critically endangered species (i.e. most protected; 3). This legislation has been in force since 1992 (Anonymous 1992). These terms do not describe the actual level of threat, but they reflect labeling of official categories of legal protection used in the Czech conservation law (Anonymous 1992). Therefore, the species classified merely as “endangered” is under the lowest conservation concern according to Czech conservation law, although it may in fact be more threatened than some other species. The real levels of threat to a particular bird species in the Czech Republic are currently unknown (Voříšek et al. 2008).

Most of the explanatory variables were coded as discrete values along a specific gradient, except for habitat niche position, latitudinal distribution and species' life-history traits, which have continuous distributions.

Data analysis

As the six life-history traits mentioned above are closely correlated (e.g. Sæther 1988, Stearns 1992), we used principal component analysis (PCA) to reduce many correlated variables into a smaller number of independent axes (see Reif et al. 2010b). Each species revealed its position (score; see Supporting Information) along two most important ordination axes, and these scores were used for further analyses. PCA identified two clear patterns in life-history traits within the assemblage of analyzed species (Fig. 1). The first ordination axis (PC 1, explaining 47.1% of the variability among species) expressed a gradient from 'r-selected' species (i.e. those having small eggs, small body mass, multiple broods and large clutch sizes) to 'K-selected' species (hereafter the 'first life-history axis'). The second axis (PC 2, explaining 17.5% of variability) depicted an independent gradient from late breeding species with single brood and bigger clutch sizes to earlier breeding species with multiple broods and smaller clutch sizes. The PCA performed on the life-history traits reduced the total number of explanatory variables used in the analyses from 17 to 13.

Table 2. Results of the linear models analyzing effects of life-history traits, ecological traits and the level of legal protection predicting on changes in abundance (A), magnitude of population trend (B), and distribution (C) of 178 species breeding in the Czech Republic. PC 1 and PC 2 denote species' scores along the first and second ordination axes from PCA on 6 life-history traits. Significant results are in bold type. Minimum adequate model was selected from full (saturated) model using AIC (as implemented by *step* function in R platform). See "Methods" section for a detailed description of individual traits and measures. Measures of overall performance of particular models are provided in Table 1.

Species trait	Full model				Minimum adequate model			
	Estimate	SE	t	p	Estimate	SE	t	p
Habitat niche position	-0.108	0.062	-1.736	0.0845	-0.113	0.051	-2.245	0.0260
Habitat niche breadth	0.006	0.063	0.101	0.9194				
Habitat humidity	0.048	0.138	0.345	0.7308				
Dietary niche position	0.033	0.114	0.291	0.7711				
Dietary niche breadth	-0.143	0.169	-0.846	0.3985				
Latitudinal distribution	0.015	0.022	0.692	0.4898				
Nest type	0.023	0.135	0.167	0.8675				
Nest location	0.170	0.133	1.278	0.2031	0.169	0.110	1.541	0.1251
Migration distance	0.099	0.130	0.766	0.4451	0.153	0.105	1.459	0.1464
Migratory flexibility	-0.051	0.191	-0.265	0.7912				
PC 1 (life history)	-0.057	0.096	-0.594	0.5532				
PC 2 (life history)	0.040	0.086	0.464	0.6432				
Legal protection	0.014	0.087	0.161	0.8724				

Species trait	Full model				Minimum adequate model			
	Estimate	SE	t	p	Estimate	SE	t	p
Habitat niche position	0.023	0.067	0.352	0.7253				
Habitat niche breadth	0.008	0.068	0.125	0.9004				
Habitat humidity	-0.160	0.148	-1.084	0.2797				
Dietary niche position	-0.078	0.121	-0.646	0.5189				
Dietary niche breadth	-0.164	0.180	-0.912	0.3632				
Latitudinal distribution	-0.010	0.024	-0.404	0.6870				
Nest type	0.183	0.144	1.271	0.2055	0.192	0.108	1.784	0.0762
Nest location	-0.076	0.142	-0.533	0.5947				
Migration distance	0.020	0.139	0.145	0.8848				
Migratory flexibility	0.024	0.204	0.115	0.9085				
PC 1 (life history)	-0.337	0.102	-3.290	0.0012	-0.369	0.087	-4.230	< 0.0001
PC 2 (life history)	-0.098	0.092	-1.068	0.2871				
Legal protection	0.291	0.094	3.110	0.0022	0.325	0.080	4.088	< 0.0001

Species trait	Full model				Minimum adequate model			
	Estimate	SE	t	p	Estimate	SE	t	p
Habitat niche position	-0.034	0.027	-1.280	0.2025				
Habitat niche breadth	-0.027	0.027	-0.978	0.3297				
Habitat humidity	0.148	0.060	2.478	0.0142	0.128	0.047	2.759	0.0064
Dietary niche position	0.004	0.049	0.091	0.9275				
Dietary niche breadth	-0.095	0.073	-1.313	0.1911				
Latitudinal distribution	0.024	0.010	2.516	0.0128	0.027	0.009	3.070	0.0025
Nest type	-0.050	0.058	-0.855	0.3941				
Nest location	0.140	0.057	2.451	0.0153	0.157	0.043	3.629	0.0003
Migration distance	-0.020	0.056	-0.350	0.7269				
Migratory flexibility	0.105	0.082	1.279	0.2026				
PC 1 (life history)	-0.049	0.041	-1.192	0.2349				
PC 2 (life history)	0.010	0.037	0.262	0.7933				
Legal protection	-0.016	0.038	-0.416	0.6780				

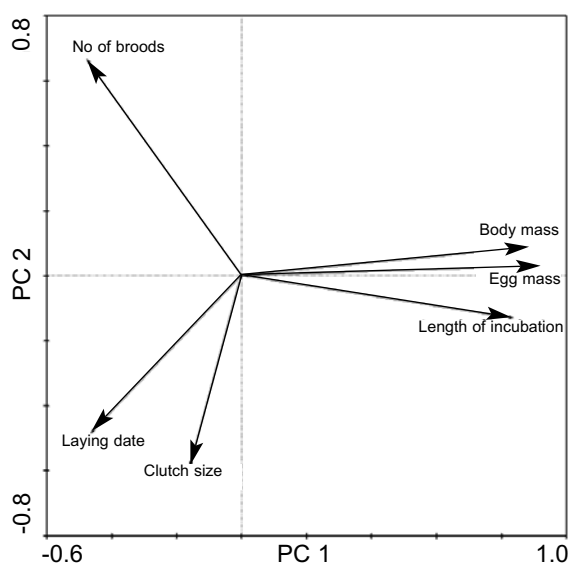


Fig. 1. The two most important ordination axes (PC 1 and PC 2), revealed by a principal component analysis, explaining the largest proportion of variability among six life-history traits (i.e. body mass, egg mass, number of broods per year, laying date, clutch size and length of incubation) in 178 bird species breeding in the Czech Republic.

To find out which predictors have a significant effect on particular dependent variables (i.e. change in abundance, magnitude of population trend and distribution), we used linear models (every response variable has been involved in just one model). We fitted two types of the linear models: (i) models including all explanatory variables entered together (i.e., full models), and (ii) minimum adequate models, identified applying the backward stepwise selection using the R function “step”, which uses AIC values as the elimination criterion (Crawley 2007). Finally, to elucidate relationships between individual dependent variables, we calculated the correlations between each pair of these variables.

RESULTS

Comparison of individual measures of population change

All the measures of population changes showed positive correlations among each other. Change in abundance strongly correlated with change in distribution ($r = 0.66$, $n = 178$, $p < 0.001$), and also (less markedly but still highly significantly) with change in magnitude of population trend ($r = 0.56$, $n = 178$, $p < 0.001$). However, correlation of change in magnitude of population trend and change in distribution was rather weak, but still significant ($r = 0.17$, $n = 178$, $p = 0.020$).

No significant predictors were common for individual types of measures (Table 1, 2). While the sole significant predictor of change in abundance was the habitat niche position of the species, the life-history traits (expressed as scores along the PC 1) and the legal protection were the most significant predictors of change in population trend. Change in distribution was significantly affected by habitat humidity, latitudinal distribution and nest location.

We did not find any significant effect of dietary niche and migratory strategy on any measure of population change (Table 2).

Significance and gradient direction of individual predictors

The most significant predictors of population changes of Czech birds were position of species in the r-K continuum (PC 1) and legal protection, which explained almost 16% of variation in the magnitude of population trend. Species protected under domestic law showed more positive changes in their population trends than the non-protected ones. Similarly, the r-selected species tended to improve their situation more than the K-selected species (Table 2). Changes in distribution were more positive in water birds (scoring

Table 1. Summary statistics for the models analyzing effects of life-history traits, ecological traits and legal protection on the individual measures of population changes for 178 species breeding in Czech Republic. Statistics provided for full models and minimum adequate models (after backward stepwise selection, in all cases with 3 predictors retained) include coefficient of multiple determination R^2 and F-statistics. See “Methods” section for further details.

Measure of population change	Full model			Minimum adequate model		
	R^2_m	$F_{13,164}$	p	R^2_m	$F_{3,174}$	p
Change in abundance	0.104	1.463	0.137	0.091	5.790	0.001
Change in magnitude of population trend	0.176	2.703	0.002	0.156	10.720	< 0.001
Change in distribution	0.155	2.320	0.008	0.122	8.061	< 0.001

higher along the gradient of habitat humidity), the above-ground nesters (nest location) and species with more northern distribution in Europe (latitudinal distribution) than in the case of the terrestrial birds, the birds building their nests on the ground and the birds with south European distribution (Table 2). The least important (but still significant) predictor of population changes identified in our data set was species' position along the gradient of habitat use (habitat niche position) ranging from forest interior to open steppe: birds associated with open, farmland habitats tended to decline in abundance, while the forest species increased. This result was significant only in the model identified using backward stepwise procedure (Table 2).

DISCUSSION

Differences in predictors among three measures of population change

All the measures of population change were positively correlated, but their predictors selected from the same set of candidate variables were not the same. In fact, ecological and life history variables explaining the variation found in three measures of population changes differ remarkably among these measures. Abundance increases were largest for forest birds, while the change in the magnitude of population trend was most positive in protected and *r*-selected species. Distribution expanded most for wetland birds, species nesting above-ground and north European birds.

A positive relationship between changes in distribution and changes in abundance is in accordance with a general macroecological rule describing a positive correlation of local abundance and regional distribution (Brown 1984, Gaston et al. 1997). However, in our data set, no predictor affects changes in abundance and distribution in the same way. Whereas a change in abundance was influenced mostly by species' association with the forest-farmland habitat gradient, a change in distribution depended on species' affinity to wetland habitats and latitude of species' breeding range in Europe. This may be caused by the fact that abundance is more sensitive to major land use changes — e.g. open habitat degradation decreases immediately local population abundance, although the species is still present on a site (Borregaard & Rahbek 2010). On the contrary, species' range position within Europe, which is

assumed to reflect the climatic tolerance of species, could affect the regional distribution more considerably, because climate change enables species to colonize new areas (Huntley et al. 2007, Reif et al. 2010a).

A positive relationship was also found between changes in the magnitude of population trend and changes in abundance. This pattern shows that a change from a negative to a positive population trend is related mainly to species increasing their abundance in the latter time period. In this context, it is noticeable that additionally analyzed relationship between change in abundance in 1970–1990 and change in magnitude of population trend was negative ($r = -0.56$, $n = 178$, $p < 0.001$). Consequently, populations initially decreasing their abundance, faster improve their trends and vice versa. This limitation of population growth for species showing a rapid initial increase may be explained by a negative density dependence, related to population sizes approaching the environmental carrying capacity. However, species could also simply respond to fluctuating changes in the environment and climate (e.g. land abandonment followed by intensification, patterns of winter weather) and these factors can produce alternating change points in temporal trends of bird populations. The state of bird populations in the Czech Republic has been improving, because the positive change in magnitude of population trend has been affected by increasing species' abundance and not slowing the rate of population decline. This is in accordance with an overall positive change in the distribution of Czech birds reported by Koleček et al. (2010).

Despite a strong correlation with change in abundance, change in distribution is only weakly related to change in the magnitude of population trend. The above-discussed differences in the factors affecting the abundance and distribution are probably responsible for this relationship.

Explanations of the effects of particular predictors

A positive change in abundance was found in forest birds, confirming a long-term forest spread in the Czech Republic and the other parts of southern and eastern Europe (Gregory et al. 2007, Reif et al. 2007, Gil-Tena et al. 2009). A possible positive effect of legal protection should date back to 1992, when the new Czech national act on nature conservation passed. A positive effect of protection status may be driven primarily by the

spread of very rare species, which are generally protected (Koleček et al. 2010). However, it is difficult to say whether this is effect of effective national legislation and conservation management or rather reflects improvement of environmental conditions in central Europe after 1989 (Verhulst et al. 2004, Gołowski 2006). Many protected species decreased continuously before and also between 1990 and 2000. Effectiveness of national conservation legislation is thus ambiguous (Voříšek et al. 2008) and pattern found in our study requires further analysis. Nevertheless, implementation of European legislation has been related to a positive change in the magnitude of population trends in several European countries as well (Donald et al. 2007).

The positive change in magnitude of population trends in r-selected species is contrary to results obtained in the analysis of 68 Czech passerines, which showed an opposite pattern (Reif et al. 2010b). This incongruence could be explained by a clear taxonomic bias in that study, which included only passerines, representing only a limited spectrum of r-K selection gradient, and lacking the true K-selected species (Reif et al. 2010b). These species were found to be at a higher risk of extinction at the global scale (Henle et al. 2004) and our results confirm this finding also for the national level. Limited ability to track rapidly changing environmental conditions, coupled with increased mortality are probably the crucial reasons of negative population changes in 'K-selected' species. It means that many Czech K-selected species (mostly non-passerines — e.g. *Botaurus stellaris* and *Otis tarda*) are highly endangered and decreasing because they cannot react fast enough e.g. to increasing nest predation or to growing mortality due to traffic collisions (Voříšek et al. 2009).

Change in distribution of Czech birds was affected significantly by three predictors — habitat humidity, nest location and European distribution. Concerning the first pattern, represented by the increase of wetland birds, the same finding has been confirmed also in local bird communities in other parts of central and western Europe (Lemoine et al. 2007, Orłowski & Ławniczak 2009, Van Turnhout et al. 2010) and was probably caused by a lower hunting pressure or better conditions on wintering grounds (more rainfall). An important role in the increase of waterfowl populations could play decreasing concentrations of chemical pollutants in water bodies coupled with widespread eutrophication of waters (due to farming intensification), which should result in

improving food conditions (Van Turnhout et al. 2010). Moreover, wetland birds could particularly benefit from establishing many new wetland nature reserves in the country (Málková & Lacina 2002). The effect of nest location was caused by a negative change in distribution of the ground nesters. Similar pattern was found in many studies of North American bird communities (e.g. Böhning-Gaese et al. 1993) and could be caused by the recent spread of mammalian mesopredators (Schmidt 2003) such as American Mink *Neovison vison* or Raccoon Dog *Nyctereutes procyonoides*. These two species became invasive in the Czech Republic in recent years (Pyšek & Hulme 2011). An interesting pattern was found along the gradient of European distribution, where south European species decreased and north European increased their distribution within Czech Republic. The negative trend found among south European birds may be related to the regional extinction of several species using extensively cultivated farmland habitats such as *Otis tarda*, *Burhinus oedicephalus*, *Falco vespertinus*, *Lanius minor* and *Lanius senator* (Koleček et al. 2010). Since we were unable to include this habitat x distribution interaction among our predictors, this effect could be captured by the effect of latitudinal distribution in statistical analysis. A positive change in distribution of north European species is somewhat contra-intuitive, given the frequently reported effect of climate warming on European birds (Lemoine et al. 2007, Bauer et al. 2008, Reif et al. 2008b) which should cause decline of these species in the Czech Republic. However, several northern species have isolated populations in central Europe (e.g. *Mergus merganser*, *Bucephala clangula*, *Glaucidium passerinum* or *Luscinia svecica*) and these populations recently expand to north (Štátný et al. 2006), which is consistent with the predicted climate change effects. This process can thus produce the increase in the distribution of the northern species in the Czech Republic, without contradicting simple predictions of climate change at the same time. However, we do not have any strong evidence supporting these explanations which are, therefore, rather speculative. Another explanation for this pattern may relate to the fact that distribution in our study was defined as the occupancy, registered using rather small grid size (slightly larger than 10x10 km). Given this and relatively small area of the Czech Republic, we expect that the discovered changes in distribution may be caused rather by changes in occupancy within the stable area defined as extent

of occurrence, than by the range shifts. The intensity of the mappings in both atlas periods was comparable (Št'astný et al. 1996, 2006). Therefore the registered changes in distribution should represent rather genuine changes than methodological artifacts.

CONCLUSION

Although individual measures of population changes are positively correlated, their predictors are different and it is necessary to be aware of this when interpreting results of bird population studies. Moreover, different population change measures are not exchangeable and only their joint use may reveal the real mechanisms driving bird population changes in the given area and time interval. Furthermore, it is necessary to take into account the data limitation — e.g. atlas distribution data usually only cover specific time periods and it is easy to neglect the population changes which happen in the meantime. In contrast, long-term population trend data provide continual information on population changes, but are often inappropriate for evaluation of spatial patterns.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article. This document contains complete list of species, their population and distribution data, ecological traits and life-history scores obtained from the PCA used in analysis.

STRESZCZENIE

[Od czego zależą zmiany wielkości populacji ptaków? Zróznicowanie predyktorów zmian liczebności, trendu i zasięgu]

Zmiany wielkości populacji ptaków mogą być mierzone jako zmiany liczebności lub zagęszczeń osobników, a w przypadku większych obszarów –

jako zmiany zasięgu występowania lub wskaźników liczebności. Choć wymienione miary odnoszą się do różnych aspektów zmian wielkości populacji, to jednak często są one używane zamiennie w dyskusjach na temat możliwych czynników odpowiedzialnych za zachodzące zmiany. Taka sytuacja utrudnia wiarygodne porównania wyników uzyskiwanych w różnych badaniach. Nie wiadomo bowiem, jaka część obserwowanych różnic odzwierciedla realne zjawiska biologiczne, a jaka jest artefaktem metodycznym, wynikającym z różnic w charakterystykach miar wykorzystywanych do opisu zmian wielkości populacji. W publikacji weryfikowano tezę, że takie same zmienne mogą być dobrymi predyktorami trzech różnych miar zmian wielkości populacji: (i) zmian liczebności, (ii) zmian trendu liczebności, (iii) zmian zasięgu. Analizowane dane odnoszą się do awifauny lęgowej Republiki Czeskiej (178 gatunków) i oceniane były w zbliżonych przedziałach czasu w ostatnich czterech dekadach (1970–2003). Celem publikacji jest również identyfikacja czynników znacząco wpływających na wymienione wyżej trzy miary zmian wielkości populacji. Wśród parametrów analizowanych jako potencjalne predyktory zmian w trzech miarach wielkości populacji znajdowały się zmienne opisujące m. in. wymogi siedliskowe gatunku, jego niszę pokarmową, strategię migracji, umiejscowienie gniazda, czy

rozmieszczenie w Europie. Ponadto, wśród potencjalnych predyktorów uwzględniono również zmienne opisujące strategię życiową gatunku: masę ciała, liczbę lęgów w roku, termin przystępowania do lęgów, wielkość zniesienia, wielkość jaj, długość inkubacji, podsumowane za pomocą dwóch składowych głównych, Fig. 1).

Trzy analizowane w pracy miary zmian wielkości populacji były ze sobą dodatnio skorelowane, ale ich istotne predyktory były różne (Tab. 1, 2). Zmiany ogólnej liczebności populacji były kształtowane przede wszystkim przez wzrosty liczebności ptaków leśnych. Natomiast zmiany trendu liczebności były pochodną pozytywnych zmian wśród gatunków objętych wyższym reżimem ochronnym oraz gatunków podlegających selekcji typu r. Poszerzanie zasięgu dotyczyło głównie gatunków mokradlowych i wodnych, ptaków gniazdujących nad ziemią oraz gatunków, których europejski zasięg był obejmował głównie północ kontynentu.

Powyższe wyniki wskazują, że możliwości bezpośrednich porównań zmian wielkości populacji mierzonych z użyciem różnych zmiennych (liczebność, trendy, zasięg) są ograniczone. Z drugiej strony, znajomość czynników kształtujących dynamikę różnych miar wielkości populacji pozwala lepiej zrozumieć mechanizmy zmian wielkości populacji ptaków w czasie i przestrzeni.

SUPPLEMENTARY MATERIAL
 Koleček J., Reif J. 2011. Differences between the predictors of abundance, trend and distribution as three measures of avian population change. Acta Ornithol. 46: 00–00.

Table 1. List of species; their population (1970–1990 and 1990–2000) and distribution (1985–1989 and 2001–2003) data, ecological traits and life-history scores obtained from the PCA. See “Methods” section of the paper for a detailed description of individual traits and measures.

Species	abundance	Change in trend mag.	distribution	position	Habitat breadth	humidity	position	Diet breadth	Latitudinal distribution	Nest type	Nest loc.	Migration distance	flexibility	PC 1	PC 2	Legal protection
<i>Accipiter gentilis</i>	0	1	-0.15	2.3	3	1	4	1	53.18	1	3	1	0	1.62	0.47	1
<i>Accipiter nisus</i>	0	0	0.02	2.7	3	1	4	1	51.37	1	3	2	1	0.62	-0.75	2
<i>Acrocephalus arundinaceus</i>	0	2	-0.01	7.0	0	3	3	1	47.81	1	2	3	0	-0.57	-0.74	2
<i>Acrocephalus palustris</i>	0	1	0.14	5.5	1	2	3	1	51.57	1	2	3	0	-0.63	-0.89	0
<i>Acrocephalus schoenobaenus</i>	0	0	0.18	6.5	1	3	3	2	54.69	1	2	3	0	-0.65	-0.53	0
<i>Acrocephalus scirpaceus</i>	0	0	0.02	7.0	0	3	3	2	48.85	1	2	3	0	-0.80	-0.72	0
<i>Actitis hypoleucos</i>	-1	-1	-0.10	6.5	1	3	3	1	53.91	1	1	3	0	0.10	-0.15	2
<i>Aegithalos caudatus</i>	0	0	0.06	3.0	2	1	3	1	49.72	2	2	1	0	-0.41	-1.11	0
<i>Aegolius funereus</i>	2	1	0.42	3.5	5	1	4	1	58.20	3	3	1	0	0.55	-0.15	2
<i>Alauda arvensis</i>	0	1	0.02	7.0	0	1	1	2	57.80	1	1	2	0	-0.68	1.71	0
<i>Anas clypeata</i>	-2	0	-0.17	7.0	0	3	2	2	53.96	1	1	2	1	0.47	-1.80	2
<i>Anas crecca</i>	-2	0	-0.24	7.0	0	3	2	2	56.08	1	1	2	1	0.18	-1.66	1
<i>Anas platyrhynchos</i>	-1	0	0.04	7.0	0	3	2	2	52.04	1	1	2	1	0.82	-1.22	0
<i>Anas querquedula</i>	-1	1	-0.01	7.0	0	3	2	2	52.24	1	1	3	0	0.19	-1.66	2
<i>Anas strepera</i>	1	0	0.37	7.0	0	3	1	1	51.03	1	1	2	1	0.53	-2.11	1
<i>Anser anser</i>	0	-2	0.69	5.0	5	3	1	1	53.68	1	2	2	1	2.92	0.41	0
<i>Anthus campestris</i>	-1	1	-0.33	7.0	0	1	3	1	45.45	1	1	3	0	-0.69	-0.11	2
<i>Anthus pratensis</i>	0	-2	-0.06	7.0	0	2	3	2	56.11	1	1	2	1	-0.71	1.03	0
<i>Anthus spinoletta</i>	-2	-2	-0.10	7.0	0	1	3	2	44.94	1	1	2	1	-0.73	0.86	2
<i>Anthus trivialis</i>	0	-1	0.00	4.5	3	1	3	1	53.44	1	1	3	0	-0.86	0.54	0
<i>Apus apus</i>	0	0	0.02	6.0	0	1	3	1	50.71	3	3	3	0	-0.19	-0.32	1
<i>Ardea cinerea</i>	2	0	0.66	4.5	3	3	4	1	50.68	1	3	2	1	1.65	0.78	0
<i>Ardea purpurea</i>	-2	-1	-0.29	7.0	0	3	4	1	46.08	1	2	3	0	0.80	-0.65	3
<i>Asio otus</i>	0	0	-0.08	2.3	3	1	4	1	51.25	1	3	2	1	0.68	0.59	0
<i>Athene noctua</i>	-2	-1	-1.10	5.0	2	1	4	1	46.51	3	3	1	0	0.39	-0.21	2
<i>Aythya ferina</i>	0	1	-0.10	7.0	0	3	2	2	51.93	1	1	2	1	0.68	-1.74	0
<i>Aythya fuligula</i>	-1	0	0.02	7.0	0	3	2	2	57.04	1	1	2	1	0.46	-2.12	0
<i>Bonasa bonasia</i>	0	1	-0.23	1.5	1	1	2	2	56.75	1	1	1	0	0.24	-1.70	2

Species	Change in		Habitat			Diet		Latitudinal		Nest		Migration		PC 1	PC 2	Legal
	abun- dance	trend mag.	distri- bution	position	breadth	humidity	position	breadth	distribution	type	loc.	distance	flexi- bility			
<i>Botaurus stellaris</i>	1	2	0.50	7.0	0	3	4	1	50.97	1	1	2	1	0.72	-0.25	3
<i>Bubo bubo</i>	0	-2	-0.09	2.0	2	1	4	1	51.57	1	2	1	0	2.40	1.34	1
<i>Bucephala clangula</i>	0	1	0.74	6.0	0	3	3	1	59.69	3	3	2	1	1.04	-1.74	2
<i>Burhinus oedicnemus</i>	-1	1	-2.00	6.5	1	1	3	1	41.70	1	1	3	0	0.66	0.18	3
<i>Buteo buteo</i>	0	0	0.02	4.0	4	1	4	1	49.76	1	3	2	1	1.49	0.62	0
<i>Caprimulgus europaeus</i>	-1	0	-0.63	3.5	1	1	3	1	49.22	1	1	3	0	-0.61	0.95	2
<i>Carduelis cannabina</i>	0	1	0.05	5.0	2	1	2	2	48.75	1	2	2	1	-0.86	0.85	0
<i>Carduelis carduelis</i>	0	0	0.02	4.3	3	1	2	2	47.95	1	3	2	1	-0.85	0.61	0
<i>Carduelis chloris</i>	0	1	0.01	4.3	3	1	2	2	50.46	1	3	2	1	-0.72	0.88	0
<i>Carduelis flammea/cabaret</i>	0	-1	0.06	3.7	3	1	2	2	60.39	1	2	1	0	-0.85	0.93	0
<i>Carpodacus erythrinus</i>	2	0	0.31	5.5	1	2	2	1	56.09	1	2	3	0	-0.78	-1.20	1
<i>Certhia brachydactyla</i>	0	0	0.02	2.0	2	1	2	2	45.35	2	3	1	0	-0.51	1.18	0
<i>Certhia familiaris</i>	0	1	0.10	2.0	2	1	3	2	54.43	2	3	1	0	-0.64	0.96	0
<i>Charadrius dubius</i>	0	0	0.03	7.0	0	2	3	1	50.39	1	1	3	0	0.10	-0.47	0
<i>Chlidonias niger</i>	-2	0	-0.74	7.0	0	3	4	1	50.99	1	1	3	0	-0.07	-0.31	3
<i>Ciconia ciconia</i>	1	1	0.01	6.0	0	2	4	1	48.58	1	3	3	0	2.55	0.39	1
<i>Ciconia nigra</i>	1	-1	0.20	3.5	5	2	4	1	50.23	1	3	3	0	2.51	0.31	2
<i>Cinclus cinclus</i>	0	0	0.00	7.0	0	3	3	1	52.43	2	2	1	0	-0.11	0.22	0
<i>Circus aeruginosus</i>	1	-1	0.30	7.0	0	3	4	1	61.74	1	1	3	0	1.07	-0.32	1
<i>Circus cyaneus</i>	-1	-1	-0.18	4.5	5	2	4	1	63.78	1	1	2	1	0.75	-0.48	2
<i>Circus pygargus</i>	2	2	0.87	7.0	0	2	4	1	61.15	1	1	3	0	0.44	-0.68	2
<i>C. coccythraustes</i>	0	0	0.08	2.5	3	1	1	2	49.42	1	3	2	1	-0.40	-0.33	0
<i>Columba oenas</i>	1	2	0.38	1.0	0	1	1	1	50.92	3	3	2	0	-0.44	2.31	2
<i>Columba palumbus</i>	1	1	0.05	2.5	3	1	1	1	51.27	1	3	2	0	-0.22	1.71	0
<i>Coracias garrulus</i>	-1	1	-2.00	3.0	2	1	3	1	46.62	3	3	3	0	-0.20	-0.66	3
<i>Corvus corax</i>	2	0	0.76	2.0	2	1	2	3	52.29	1	3	1	0	0.94	0.91	1
<i>Corvus cornix</i>	0	0	-0.14	6.0	0	1	2	3	51.94	1	3	1	0	0.31	0.19	0
<i>Corvus corone</i>	0	0	0.01	6.0	0	1	2	3	51.94	1	3	1	0	0.31	0.19	0
<i>Corvus frugilegus</i>	0	0	-0.25	4.0	4	1	4	3	50.98	1	3	2	1	0.42	0.86	0
<i>Corvus monedula</i>	0	2	-0.42	5.0	2	1	2	2	50.13	3	3	2	1	0.06	0.10	2
<i>Crex crex</i>	2	3	0.86	7.0	0	2	3	2	52.41	1	1	3	0	-0.72	-1.02	2
<i>Cuculus canorus</i>	0	0	0.03	4.0	4	1	3	1	51.01	1	2	3	0	-0.67	-1.87	0
<i>Cygnus olor</i>	-1	-3	-0.04	7.0	0	3	1	1	50.94	1	1	2	1	6.96	0.66	0
<i>Delichon urbica</i>	0	0	0.02	6.0	0	1	3	1	50.72	2	3	3	0	-0.83	0.39	0
<i>Dendrocopos leucotos</i>	0	0	0.20	1.0	0	1	2	2	52.82	3	3	1	0	-0.22	-0.23	2
<i>Dendrocopos major</i>	0	0	0.03	2.5	3	1	2	2	51.58	3	3	1	0	-0.43	-0.48	0
<i>Dendrocopos medius</i>	2	2	0.37	1.0	0	1	2	2	49.03	3	3	1	0	-0.40	-0.39	1

Species	Change in abundance	trend mag.	distribution	Habitat position	Habitat breadth	humidity	position	Diet breadth	Latitudinal distribution	Nest type	Nest loc.	Migration distance	flexibility	PC 1	PC 2	Legal protection
<i>Dendrocopos minor</i>	1	1	0.09	3.0	2	1	3	1	53.81	3	3	1	0	-0.52	-0.52	0
<i>Dendrocopos syriacus</i>	2	1	0.84	4.0	0	1	2	2	46.36	3	3	1	0	-0.49	-0.47	2
<i>Dryocopus martius</i>	1	1	0.07	1.0	0	1	3	1	53.75	3	3	1	0	-0.13	0.18	0
<i>Emberiza citrinella</i>	0	0	0.02	4.7	3	1	3	2	52.83	1	1	1	0	-0.75	1.52	0
<i>Emberiza hortulana</i>	-1	0	-0.60	5.0	2	1	2	2	50.71	1	1	3	0	-0.69	0.29	3
<i>Emberiza schoeniclus</i>	0	0	0.07	6.0	0	3	1	2	54.37	1	1	2	1	-0.70	1.06	0
<i>Erithacus rubecula</i>	0	0	0.03	2.5	3	1	3	2	51.74	1	2	2	1	-0.74	0.61	0
<i>Falco cherrug</i>	0	0	-0.32	3.0	2	1	4	1	44.59	1	3	2	1	1.19	0.41	3
<i>Falco peregrinus</i>	2	2	0.97	4.5	5	1	4	1	45.80	1	3	2	1	1.26	0.68	3
<i>Falco subuteo</i>	1	2	0.35	3.0	2	1	4	1	50.54	1	3	3	0	0.35	-0.60	2
<i>Falco tinnunculus</i>	0	0	0.04	5.0	2	1	4	1	50.68	2	3	2	1	0.30	-0.76	0
<i>Ficedula albicollis</i>	0	0	0.16	2.5	3	1	3	1	49.17	3	3	3	0	-0.43	-0.69	0
<i>Ficedula hypoleuca</i>	0	-1	0.08	2.0	0	1	3	1	56.35	3	3	3	0	-0.50	-1.01	0
<i>Ficedula parva</i>	2	1	0.24	1.0	0	1	3	1	52.99	2	3	3	0	-0.58	-1.05	2
<i>Fringilla coelebs</i>	0	0	0.01	3.7	5	1	2	2	50.40	1	3	2	1	-0.69	1.05	0
<i>Fulica atra</i>	-1	0	0.00	7.0	0	3	2	2	50.07	1	1	2	1	0.24	0.05	0
<i>Galerida cristata</i>	-1	1	-0.89	7.0	0	1	2	2	45.99	1	1	1	0	-0.58	1.45	1
<i>Gallinago gallinago</i>	-2	-1	-0.36	7.0	0	2	3	1	56.16	1	1	2	0	0.12	-0.03	2
<i>Gallinula chloropus</i>	0	1	-0.02	7.0	0	3	3	2	48.74	1	1	2	1	-0.38	-0.21	0
<i>Garrulus glandarius</i>	0	0	0.02	2.5	3	1	2	3	50.55	1	3	1	1	-0.14	-0.85	0
<i>Glaucidium passerinum</i>	0	-1	0.66	1.0	0	1	4	1	59.68	3	3	1	0	0.37	-0.43	2
<i>Haliaeetus albicilla</i>	2	0	1.38	6.0	0	2	4	1	55.54	1	3	1	1	4.15	2.12	3
<i>Hippolais icterina</i>	0	0	0.02	3.5	1	1	3	2	53.42	1	3	3	0	-0.60	-0.93	0
<i>Hirundo rustica</i>	0	1	0.00	5.0	2	1	3	1	50.96	2	3	3	0	-0.62	-0.10	1
<i>Ixobrychus minutus</i>	0	2	0.11	6.0	2	3	4	1	47.14	1	2	3	0	-0.30	-1.15	3
<i>Jynx torquilla</i>	0	1	0.06	3.5	1	1	3	1	52.93	3	3	3	0	-0.85	-1.20	2
<i>Lanius collurio</i>	0	1	0.02	6.0	0	1	4	2	50.94	1	2	3	0	-0.48	-0.78	1
<i>Lanius excubitor</i>	0	1	-0.04	4.5	3	1	4	1	54.32	1	2	2	1	-0.20	-0.45	1
<i>Lanius senator</i>	-1	1	-2.00	4.3	3	1	3	1	41.28	1	2	3	0	-0.49	-0.94	2
<i>Larus canus</i>	-1	-2	0.00	7.0	0	3	2	3	59.30	1	1	2	1	0.51	-0.68	0
<i>Larus ridibundus</i>	-2	0	-0.45	7.0	0	3	2	3	55.37	1	1	2	1	0.54	0.13	0
<i>Limosa limosa</i>	-2	0	-0.98	7.0	0	3	3	1	51.44	1	1	3	0	0.56	0.06	3
<i>Locustella fluviatilis</i>	0	0	0.25	3.5	2	2	3	1	51.44	1	1	3	0	-0.70	-1.10	0
<i>Locustella luscinioides</i>	0	0	0.45	7.0	0	3	3	1	49.09	1	1	3	0	-0.59	-0.07	1
<i>Locustella naevia</i>	0	0	0.24	6.0	0	2	3	1	52.78	1	1	3	0	-0.96	0.20	0
<i>Lullula arborea</i>	0	1	0.26	4.0	4	1	2	2	47.68	1	1	2	0	-0.51	1.87	2
<i>Luscinia megarhynchos</i>	1	0	0.28	4.0	2	2	3	2	45.21	1	1	3	0	-0.53	-0.63	1

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Species	abundance	Change in trend mag.	distribution	position	Habitat breadth	humidity	position	Diet breadth	Latitudinal distribution	Nest type	loc.	distance	Migration flexibility	PC 1	PC 2	Legal protection
<i>Merops apiaster</i>	2	3	0.71	6.0	0	1	3	1	43.67	3	2	3	0	-0.41	-1.79	2
<i>Militaria calandra</i>	2	4	0.64	6.0	0	1	2	2	45.98	1	1	2	1	-0.77	0.89	3
<i>Milvus migrans</i>	-1	-3	0.11	2.0	0	2	4	1	46.73	1	3	3	0	1.27	0.27	3
<i>Milvus milvus</i>	2	0	0.58	3.0	2	1	4	1	47.60	1	3	2	1	1.39	0.31	3
<i>Motacilla alba</i>	0	0	0.02	5.0	2	2	3	1	51.82	2	3	2	0	-0.75	1.05	0
<i>Motacilla cinerea</i>	0	0	0.08	4.0	4	3	3	2	47.52	2	3	2	1	-0.73	1.17	0
<i>Motacilla flava</i>	1	2	0.03	7.0	0	2	3	1	51.63	1	3	3	0	-0.78	0.69	2
<i>Muscicapa striata</i>	0	1	0.02	3.0	2	1	3	1	51.57	2	3	3	0	-0.51	-0.70	1
<i>Netta rutina</i>	1	1	0.71	7.0	0	3	2	1	44.39	1	1	2	0	0.76	-1.92	2
<i>Nucifraga caryocatactes</i>	0	-1	0.03	1.0	0	1	2	2	53.10	1	3	1	0	0.04	0.20	1
<i>Numenius arguta</i>	-2	0	-1.08	7.0	0	3	3	2	57.17	1	1	2	0	1.29	0.21	3
<i>Nycticorax nycticorax</i>	1	-1	0.67	6.0	2	3	4	1	45.09	1	3	3	0	0.41	-0.26	2
<i>Oenanthe oenanthe</i>	-2	-1	-0.65	7.0	0	1	3	2	51.87	2	2	3	0	-0.65	0.95	2
<i>Oriolus oriolus</i>	0	0	0.10	3.0	2	2	3	2	48.16	1	3	3	0	-0.41	-0.67	2
<i>Otis tarda</i>	-2	0	-2.00	7.0	0	1	2	2	44.31	1	1	1	0	2.66	0.01	3
<i>Parus ater</i>	-1	-3	0.14	7.0	0	3	2	2	48.17	1	1	2	1	-0.86	1.64	2
<i>Parus biarmicus</i>	0	1	0.08	2.0	2	1	2	2	51.36	3	3	1	1	-0.51	-0.61	0
<i>Parus caeruleus</i>	0	1	0.01	3.0	2	1	2	2	49.87	3	3	1	1	-0.63	-0.73	0
<i>Parus cristatus</i>	0	1	-0.05	1.0	0	1	2	2	52.32	3	3	1	0	-0.33	0.46	0
<i>Parus major</i>	0	0	0.01	3.0	2	1	2	2	50.87	3	3	1	1	-0.78	-0.32	0
<i>Parus montanus</i>	0	0	0.19	2.0	0	1	2	2	55.55	3	3	1	0	-0.33	-0.92	0
<i>Parus palustris</i>	0	0	0.01	2.0	2	1	2	2	49.95	3	3	1	0	-0.56	-0.37	0
<i>Passer domesticus</i>	0	1	0.00	5.0	2	1	2	2	51.52	2	3	1	0	-1.15	3.09	0
<i>Passer montanus</i>	0	0	-0.02	4.3	3	1	2	2	48.99	3	3	1	0	-0.87	1.71	0
<i>Perdix perdix</i>	1	2	-0.11	7.0	0	1	1	1	50.02	1	1	1	0	0.03	-3.12	1
<i>Pernis apivorus</i>	1	1	0.12	2.0	0	1	3	1	51.88	1	3	3	0	1.10	0.11	2
<i>Phalacrocorax carbo</i>	-2	-4	0.24	6.0	0	3	4	1	51.66	1	3	2	1	1.47	0.81	1
<i>Phoenicurus ochruros</i>	0	-1	0.03	5.0	2	1	3	2	48.10	2	3	2	0	-0.53	0.32	0
<i>Phoenicurus phoenicurus</i>	1	2	0.06	3.0	2	1	3	2	53.25	3	3	3	0	-0.32	0.36	0
<i>Phylloscopus collybita</i>	0	0	0.06	3.5	3	1	3	2	52.08	2	1	2	0	-0.75	0.74	0
<i>Phylloscopus sibilatrix</i>	0	0	0.03	2.0	0	1	3	1	53.40	2	1	3	0	-0.60	-0.83	0
<i>Phylloscopus trochilus</i>	0	0	0.06	3.5	3	1	3	2	54.87	2	1	3	0	-0.44	-0.31	0
<i>Pica pica</i>	1	-1	0.04	5.0	2	1	2	3	52.27	2	3	1	0	0.00	-0.41	0
<i>Picus canus</i>	0	0	-0.04	2.5	3	1	3	1	51.74	3	3	1	0	0.11	0.00	0
<i>Picus viridis</i>	0	1	0.01	2.5	3	1	3	1	48.50	3	3	1	0	-0.17	-0.61	0
<i>Podiceps cristatus</i>	-1	0	-0.04	7.0	0	3	4	1	51.53	1	1	2	0	0.72	-0.44	1
<i>Podiceps nigricollis</i>	-2	-1	-1.14	7.0	0	3	3	2	49.23	1	1	2	0	0.17	-0.21	1

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Species	abundance	Change in trend mag.	distribution	Habitat position	Habitat breadth	humidity	position	Diet breadth	Latitudinal distribution	Nest type	Nest loc.	distance	Migration flexibility	PC 1	PC 2	Legal protection
<i>Porzana parva</i>	2	3	1.38	7.0	0	3	3	3	1	1	1	3	0	-0.65	0.09	3
<i>Porzana porzana</i>	2	3	0.31	7.0	0	3	3	3	2	1	1	3	0	-0.58	-0.60	2
<i>Prunella collaris</i>	0	0	0.22	7.0	0	1	2	2	2	2	2	1	1	-0.63	-0.49	2
<i>Prunella modularis</i>	1	0	0.05	3.0	2	1	3	2	2	1	2	2	1	-0.71	1.11	0
<i>Pyrrhula pyrrhula</i>	0	0	0.01	2.5	3	1	1	2	2	1	3	2	1	-0.57	0.15	0
<i>Rallus aquaticus</i>	2	3	0.37	7.0	0	3	3	3	2	1	2	2	1	-0.49	-0.41	2
<i>Regulus ingicapillus</i>	1	1	0.38	1.0	0	1	3	3	1	2	3	2	1	-0.75	0.11	0
<i>Regulus regulus</i>	0	0	0.07	1.0	0	1	3	3	1	2	3	1	1	-0.64	0.16	0
<i>Remiz pendulinus</i>	0	-1	-0.15	4.5	3	2	3	2	2	2	3	2	0	-0.59	-0.21	1
<i>Riparia riparia</i>	0	0	-0.32	7.0	0	2	3	3	1	3	2	3	0	-0.65	-0.58	1
<i>Saxicola rubetra</i>	1	0	-0.04	6.5	1	1	3	2	2	1	1	3	0	-0.57	-0.93	1
<i>Saxicola torquata</i>	0	0	0.31	6.0	0	1	3	2	2	1	1	2	0	-0.79	1.73	1
<i>Scolopax rusticola</i>	1	1	-0.11	1.5	0	2	3	2	2	1	1	2	0	0.18	1.78	1
<i>Serinus serinus</i>	0	0	0.02	3.0	2	1	1	2	2	1	3	2	0	-0.82	0.87	0
<i>Sitta europea</i>	0	0	0.04	2.5	3	1	2	2	2	3	3	1	0	-0.25	-0.59	0
<i>Sterna hirundo</i>	2	3	0.27	7.0	0	3	4	4	1	1	1	3	0	0.17	-0.02	2
<i>Streptopelia decaocto</i>	0	0	0.01	4.0	0	1	1	1	1	1	3	1	0	-0.65	3.53	0
<i>Streptopelia turtur</i>	0	1	-0.05	4.0	4	1	1	1	1	1	2	3	0	-0.40	0.19	0
<i>Strix aluco</i>	2	2	0.01	2.5	3	1	4	1	1	3	3	1	0	1.16	0.94	0
<i>Strix uralensis</i>	2	1	1.00	1.0	0	1	4	1	1	2	3	1	0	1.39	1.07	3
<i>Sturnus vulgaris</i>	0	1	0.01	4.3	3	1	3	2	2	3	3	2	1	-0.37	0.25	0
<i>Sylvia atricapilla</i>	1	0	0.06	3.3	3	1	3	2	2	1	2	2	0	-0.73	0.03	0
<i>Sylvia borin</i>	0	-1	0.02	2.5	1	1	3	2	2	1	2	3	0	-0.77	0.02	0
<i>Sylvia communis</i>	0	1	0.07	5.5	1	1	3	2	2	1	2	3	0	-0.73	-0.08	0
<i>Sylvia curruca</i>	0	1	0.04	4.5	1	1	3	2	2	1	2	3	0	-0.75	0.01	0
<i>Sylvia nisoria</i>	2	3	0.07	4.0	2	1	3	2	2	1	2	3	0	-0.50	-0.75	2
<i>Tachybaptus ruficollis</i>	-1	0	0.00	7.0	0	3	3	3	1	1	1	2	1	-0.40	0.40	1
<i>Tetrao tetrix</i>	-2	-1	-0.35	4.0	4	1	2	2	2	1	1	1	0	0.52	-1.83	2
<i>Tetrao urogallus</i>	-1	1	-0.38	1.5	1	1	2	2	2	1	1	1	0	1.62	-0.65	3
<i>Tringa totanus</i>	-1	1	-0.02	7.0	0	3	3	3	1	1	1	2	0	0.34	0.04	3
<i>Troglodytes troglodytes</i>	2	2	0.04	3.7	5	2	3	3	1	2	2	1	1	-0.53	0.86	0
<i>Turdus merula</i>	0	0	0.01	2.7	3	1	3	2	2	1	3	1	1	-0.65	2.09	0
<i>Turdus philomelos</i>	0	0	0.02	4.0	4	1	3	2	2	1	3	2	1	-0.81	1.80	0
<i>Turdus pilaris</i>	0	0	0.07	3.5	1	1	3	2	2	1	3	2	1	-0.38	0.47	0
<i>Turdus torquatus</i>	-2	-2	-0.19	3.0	2	1	3	2	2	1	3	2	1	-0.49	-0.41	2
<i>Turdus viscivorus</i>	0	0	0.16	2.7	3	1	2	2	2	1	3	2	1	-0.28	0.88	0
<i>Tyto alba</i>	-2	0	-0.21	6.5	1	1	4	1	1	1	3	1	0	0.28	-0.78	2
<i>Upupa epops</i>	0	1	-0.19	4.0	4	1	3	3	1	3	3	3	0	-0.33	-0.88	2
<i>Vanellus vanellus</i>	-2	-1	-0.16	7.0	0	2	3	3	1	1	1	2	0	0.59	0.47	0

Příspěvek III.

Koleček J., Schleuning M., Burfield I. J., Báldi A., Böhning-Gaese K., Devictor V., García J. M. F., Hořák D., van Turnhout C. A. M., Hnatyna O. & Reif J. (rukopis): Species protection by national legislation improves bird population trends in Eastern European countries.

Species protection by national legislation improves bird population trends in Eastern European countries

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Abstract

Establishing lists of protected species is a major legal conservation tool, which is widely used over the globe. However, large scale assessments of the effects of species protection on animal populations are rare. While legal protection was shown to deliver benefits to birds in the Western European countries and in the United States, such evaluation has never been performed in Eastern Europe, where modern environmental legislation was just established in early 1990s after political changes. To test the effect of species protection on species' long-term population trends, we compared population trends of protected and non-protected bird species between 1970–1990 and 1990–2000 in ten Eastern European countries, controlling for effects of phylogeny and species traits. Within Eastern Europe, population trends of protected species were more positive than those of non-protected species. This suggests that species protection at the national scale contributed to prevent the population declines of the focal species. The positive effect of protection status was mostly driven by a great improvement of population trends of protected species in countries that protected smaller actual proportions of species. Population trends of the protected species remained nearly unchanged in countries where a large majority of local bird fauna is listed as protected, but the unprotected species had more declining population trends here. Our results show that the two conservation strategies applied in Eastern European countries affected bird population trends differently. We conclude that combining both approaches would be most efficient in preventing further population declines of the majority of species and in improving population trends of the most threatened species.

Keywords: Abundance, Birds, Conservation effectiveness, Eastern Europe, Environmental changes, Legal protection, Political changes, Traits

1. Introduction

Many animal species underwent dramatic population declines or even local extirpations in the last century (Bonebrake et al., 2010) caused by exploitation, land-use change, climate change and biological invasions (Ebbinge, 1991; Rolland et al., 2010; Williams et al., 2012). In response to these adverse changes, policy makers established lists of protected species supported by legislation, to limit their exploitation and direct habitat destruction (e.g. Anonymous, 1973; Anonymous, 1981). Since applying legal protection has financial consequences, it is important to learn whether the protection of the listed species performs effectively or whether one must consider alternative management options (Williams et al., 2012). Although the benefit of various management applications have been assessed on many species (e.g. Donazar, 1990; Ausden and Hirons, 2002; Bradbury and Allen, 2003; Wilson et al., 2007), general assessments of environmental legislation at national or international level are far less common (Voříšek et al., 2008). This can be done by a comparison of long-term population trends between protected and non-protected species. For this purpose, birds are a useful model group because we have good knowledge about long-term changes in their distribution and abundance (e.g. BirdLife International/European Bird Census Council, 2000; BirdLife International, 2004).

Effective legal protection should prevent population declines of protected species or result in more positive population trends in protected species in comparison to non-protected ones. For instance, a gradual improvement of the population status of bird species protected under the Endangered Species Act was found in the United States (Male and Bean, 2005). In Europe, populations of bird species that have received special protection under the Annex I of EU Birds Directive since 1981 have increased more than other species in the Western European EU-15 Member States (Donald et al., 2007). These results indicate that sophisticated systems of conservation policies applied over large regions for sufficiently long time appear to perform effectively.

Whether and how this legislation has positive effects also in Eastern European countries has never been investigated, although this region is of high importance for biodiversity conservation in Europe. Lower intensity of land use resulted here in richer biodiversity than in Western European countries (Galewski et al., 2011). It is thus of eminent importance to evaluate whether or not species protection affects population trends also in this region (Pullin et al., 2009; Stoate et al., 2009). In addition, Eastern European countries offer an interesting context to test the effectiveness of species protection, because modern

environmental legislation was just established after political changes in the early 1990s. Eastern European countries express two basic models of conservation policies protecting (i) only the rare, most endangered and/or charismatic species or (ii) most of the species including unthreatened or common species leaving only a few (mostly game) species unprotected. The first approach will be probably more successful in terms of facilitating population growth of target species if the appropriate species have been selected for listing as protected. In contrast, the second approach can hardly provide targeted protection for all species listed but secures a basic level of protection for all species and thus is likely to prevent severe population declines and extirpation.

Besides the species legal protection, many environmental and life history factors affect bird population growth rates (e.g. Gregory et al., 2007). They are related to species' susceptibility to adverse conditions and therefore affect the effectiveness of species protection (Böhning-Gaese and Oberrath, 2003; Jiguet et al., 2007; Van Turnhout et al., 2010; Webb et al., 2010). Accordingly, together with the species' legal protection status, we also tested the effects of species' ecological traits and life histories on avian population trends and accounted for these effects in analyses of the effectiveness of legal species protection.

Here, we perform an assessment of the effects of legal species protection on population trends of birds in Eastern Europe, controlling for the effects of species traits. If species protection is efficient, we predict that (i) population trends of protected species will improve over time in countries protecting only small proportion of species, and (ii) population trends of non-protected species will deteriorate in countries protecting most of their bird fauna.

We report the effects of species protection for two different levels: (i) for the regional level across all countries and (ii) for two groups of countries defined by their model of conservation policy, i.e., distinguishing between countries protecting only the most endangered species or protecting most of the species including common species.

2. Methods

2.1. Protected species lists

To obtain protected bird species lists as specified by national acts on nature conservation in Eastern European countries, we requested information from experts involved in bird species protection in a given country, working both for governmental and non-governmental

organizations. We received feedback from 14 countries (among the 15 countries contacted) and species lists suitable for our study were supplied for the following ten countries: Belarus, Croatia, Czech Republic, Estonia, Hungary, Latvia, Moldova, Poland, Slovakia and Ukraine (Table A1). We considered the legislation which came into effect between 1990 and 1995, i.e. shortly after fall of communism and corresponding to the time period for which the population change data have been available (see below). The only exception was Latvia where the protected species lists used in this study dated back to 1987. We recognized two groups of countries according to the proportion of species listed for legal bird protection relative to the total number of bird species breeding in a given country (Table A1). The proportion of protected species was not evenly distributed among countries: some countries are protecting a targeted subset of species, while others are protecting most bird species. It is likely that this difference reflects different protection intensities for the listed species and one can expect more targeted protection of few species to result in more positive effects on population trends of protected species than a conservation strategy including the majority of species. The first group included five countries which listed less than 55% of bird species as protected: Belarus, Czech Republic, Latvia, Moldova and Ukraine. The second group included five countries with more than 80% protected bird species: Croatia, Estonia, Hungary, Poland and Slovakia. We used a simple two-level coding of bird protection: protected species were coded as 1, species non-protected at least in certain periods of the year were coded as 0.

2.2. Population trends

We used population trends for 1970–1990 (BiE1) provided by BirdLife International/European Bird Census Council (2000) and population trends for 1990–2000 (BiE2) by BirdLife International (2004). For the purposes of our analysis, trends in the first time period described population status of species prior to being listed as protected in a given country, whereas trends in the second time period described population status after listing. BiE1 and BiE2 are the best long-term data available for comparisons of bird population trends among European countries in different time periods and have been widely used (e.g. Donald et al., 2001; 2007; Sanderson et al., 2006; Jones and Cresswell, 2010). They are the only sources covering all breeding species in the focal countries. However, BiE1 and BiE2 slightly differ in the scales used to express the population trends. Therefore, we standardized the population trends in the period 1990–2000 to the same values as used in 1970–1990. As a result, we obtained three trend categories: -1 = species' populations showed $>20\%$ decrease

or species went extinct, 0 = species' populations were stable with a change of 0–20% in any direction, 1 = species' population showed >20% increase. For further analyses we did not consider species with the trends specified as “unknown” or “fluctuating” in BiE1 or BiE2. In addition, we excluded new breeders that colonized a given country during the period of 1990–2000 and species which went extinct in a given country during 1970–1990, because the trends of such species could not be affected by their protection status. As a result, we used data on 306 bird species with population trends in 1970–1990 and 1990–2000 (Table A2).

2.3. Species traits

We defined 16 species' traits which have been demonstrated to influence population trends in previous studies (e.g. Gregory et al., 2007; Jiguet et al., 2007; Van Turnhout et al., 2010) and included them as explanatory variables in statistical analyses. These traits characterized species' breeding habitat and dietary niche, nest type and location, migration strategy, life history (for all these traits we used data from Cramp, 1977–1994; Böhning-Gaese et al., 2000; Böhning-Gaese and Oberrath, 2003 and Koleček and Reif, 2011) and climatic niche (calculated using data from Hagemeijer and Blair, 1997 and Haylock et al., 2008).

For habitat, dietary and climatic niche, we distinguished between niche position (i.e. mean value of the respective variable) and niche breadth (i.e. range of the respective variable). Habitat niche was based on a classification of species' habitat requirements along a gradient of decreasing complexity of vegetation structure and density from (1) closed forest to (7) open country without solitary trees or shrubs. Species were given up to three different values and habitat niche position was calculated as the mean of these values. Habitat niche breadth was determined as the difference between the extreme values. In addition, we used another expression of habitat requirements along a gradient of increasing habitat humidity from (1) non-humid and (2) wetland to (3) aquatic habitats. Dietary niche position was based on a classification of species into four different trophic levels as either (1) herbivorous, (2) herbivorous and insectivorous, or omnivorous, (3) insectivorous or (4) carnivorous. Dietary niche breadth was based on a classification of species into (1) obligatory herbivorous (i.e. plant sources only, e.g. *Loxia curvirostra*) or obligatory insectivorous/carnivorous (i.e. animal sources only, e.g. *Buteo buteo* or *Apus apus*), (2) herbivorous and insectivorous/carnivorous (i.e. plant and animal sources, e.g. *Parus major*), or (3) omnivorous (i.e. plant, animal and other sources, e.g. *Corvus corax*). Nest type was scored along the gradient of the three levels of increasing nest concealment. Nest location described the height of the nest above the

ground: from (1) the ground or close to the ground and (2) middle high – i.e. shrubs and lower trees to (3) high trees. Migration distance was defined as the distance to the wintering grounds distinguishing between (1) residents, (2) short-distance migrants (the major part of the population wintering north of the Sahara Desert), and (3) long-distance migrants (the major part of the population wintering south of the Sahara Desert). Moreover, we defined migration flexibility as the variation in migration behaviour within a species. Thus, we recognized (0) obligatory migrants and obligatory residents, and (1) facultative migrants. Climatic niche was calculated from maps of mean temperatures in the main three-month species-specific breeding season (mostly April, May and June) for the period 1961–1990 based on temperature data obtained from Haylock et al. (2008) following Jiguet et al. (2007). Climatic niche position was defined as the mean breeding season temperature over the European breeding range of a species within Europe (taken from Hagemeyer and Blair, 1997). Climatic niche range was classified as the difference between maximum and minimum temperature across the European breeding range.

Furthermore, we chose five life history traits, i.e., body mass, egg mass, incubation length, clutch size and number of broods per season as mean values from published data (Cramp, 1977–1994). As these traits are correlated, we reduced their number by principal component analysis (PCA) into two independent gradients (see also Reif et al., 2010). Each species was positioned along the two most important ordination axes, and these scores were used for further analyses (Fig. A1). The first ordination axis (PC1, explaining 55.6% of the variability among species, eigenvalue = 2.78) expressed a gradient from ‘fast strategy’ (r-selected) species (i.e. those having small eggs, small body mass, multiple broods and large clutch sizes) to ‘slow strategy’ (K-selected) species (hereafter the ‘first life history axis’). The second axis (PC2, explaining 19.5% of variability, eigenvalue = 0.98) depicted an independent gradient from species allocating most of their energy to just one breeding attempt per season – i.e. having a single brood and larger clutch sizes – to species spreading their investments to multiple breeding attempts per season – i.e. having multiple broods and smaller clutch sizes (Fig. A1).

2.4. Data analysis

We tested the effect of species protection by comparing population trends between protected and non-protected species with linear mixed effect models (library nlme, R Development Core Team, 2005). The response variable was population trend, the explanatory variables with

fixed effects were: time period (i.e. 1970–1990 and 1990–2000), protection status (i.e. protected and non-protected), species' traits (defined in section 2.3.) and country. The interaction of a given explanatory variable with the time period quantified the effect of this variable on the change in population trends between the two time periods across species and countries. In the case of protection status, we included a three-way interaction between time period, protection status and country to test country-specific effects of species protection on species trends. However, we did not estimate country-specific effects for trait variables since models would be too complex and since we did not expect interactions between species traits, time period and country. To control for a potential impact of common evolutionary history on the observed relationships, we accounted for phylogenetic relatedness among species, expressed as species nested in genus nested in family as random effects in all models (see Lockwood et al., 2002; Jiguet et al., 2010). We also fitted the linear models without the random effects of bird taxonomy and compared model fit between the two models with a likelihood ratio test.

In order to select the best subset among the trait variables, we performed model simplification using the information theoretic approach (Burnham and Anderson, 2002) in a two-step procedure. In step one, we selected the variables with the highest explanatory power within each of six groups consisting of related traits: (i) habitat niche, (ii) dietary niche, (iii) climatic niche, (iv) migration strategy, (v) nest type and location and (vi) life history axes, respectively (Table 2). Within each group, all trait variables and their twofold interactions were assessed. We performed model averaging across all candidate models within each group obtaining model averaged coefficients with their confidence intervals (Johnson and Omland, 2004). The terms whose confidence limits did not include zero were taken for the next step (see below). In step two, we combined selected terms from the different groups of species traits into a full model, which was further reduced by the same assessment procedure. Once again, we dropped the variables whose confidence limits included zero and thus obtained a final set of the trait variables. This final model thus contained the remaining set of species traits, as well as the variables time period, protection status and country. Significance of fixed effects in the final model was assessed with a type-II analysis of deviance using Wald χ^2 -tests that is independent of the sequence of factors in the final model.

For visualizing effects predicted by the final model, we calculated predicted values of population trends estimated by the final model to quantify country- and period-specific effects of species' conservation status. We thus calculated predicted population trends for each

species in each country and calculated means and standard errors across species' population trends for protected and non-protected species, respectively. We plotted these values (i) across all countries, (ii) for the two groups of countries defined by protection strategy, and (iii) for every individual country.

3. Results

The final model showed large differences in population trends between the time periods 1970–1990 and 1990–2000, between countries, as well as between species differing in their protection status and in species traits (Table 1).

3.1. Effects of species protection

Species protection showed a significant effect on changes in species population trends in Eastern Europe between the two time periods, as indicated by the significance of the interaction between protection status and time period (Table 1). At the regional level in 1970–1990, protected species had more negative population trends than non-protected species, but mean trends of both groups became similar in 1990–2000. That is, population trends of protected species improved in the second time period, while this was not the case for non-protected species (Table 1, Fig. 1). Nevertheless, mean population trends remained negative irrespective of species' protection status in 1990–2000 (Fig. 1).

The positive effect of protection status on changes in population trends was driven mainly by countries where less than 55% of the bird species were protected (Fig. 2). In these countries, population trends of protected species improved markedly after protection was legally enforced in the 1990s. The population trends of non-protected species were more positive than those of protected species between 1970 and 1990, but trends of non-protected species improved only slightly during 1990–2000 (Fig. 2a). In the group of five countries with more than 80% protected bird species, population trends of protected species were the same in both periods. At the same time, population trends of non-protected species deteriorated in these countries. Positive population trends from 1970–1990 turned to negative trends from 1990–2000 (Fig. 2b).

At the country level, the effect of species protection status was generally positive corresponding to the regional-scale pattern, but it varied considerably among individual countries (Fig. A2; 3-way interaction term in Table 1).

3.2. Effects of species traits

Population trends were significantly affected by four trait variables and three of these relationships changed between the two time periods. Testing the effect of migration flexibility showed that facultative migrants had more positive population trends than obligatory migrants or residents in 1970–1990, but this relationship disappeared in 1990–2000 (Table 2). An interesting pattern was observed in the case of nest location. In addition, ground nesting species had more negative population trends than the above ground nesting species in 1970–1990, but this difference in population trends was significantly weaker in 1990–2000 (Table 2). The effect of the first life history axis (PC1) did not differ between the two time periods; r-selected species showed more negative population trends in both periods than K-selected species (Table 2). An effect was also detectable for the second life history axis (PC2). Species allocating energy into fewer breeding attempts had more negative population trends than species spreading their investments into multiple breeding attempts (Table 2). This relationship was observed in 1970–1990, but was not detectable in 1990–2000 (Table 2).

3.3. Effects of phylogenetic relatedness

The model containing taxonomic information as additional random effects explained a significantly larger proportion of the variability in bird population trends than the linear model without this random effect (Likelihood ratio = 438.4, $P < 0.001$). This suggests that phylogenetic relatedness played a significant role and justifies our effort to control for its effects. However, variance partitioning among random effects showed that the residual variance was by far the most important component of overall variance (accounting for 76.9% of variability, variance = 0.32). Family explained 4.7% (variance = 0.02) and genus explained less than 0.1% of variability in population trends (variance < 0.01). Species had the most notable effect explaining 18.4% of variability (variance = 0.07).

4. Discussion

Our results clearly show that the species protection guaranteed by national legislation was positively related to changes in bird populations in Eastern Europe. After controlling for the effects of species' ecology, life history and phylogenetic relatedness, population trends of protected bird species showed greater improvement from 1970–1990 to 1990–2000 than the trends of non-protected species.

This pattern suggests that the modern conservation legislation adopted in early 1990s in Eastern European countries was generally effective in protecting bird species listed in national laws. This agrees with the positive influence of species protection already found in Western Europe (Donald et al., 2007) and North America (Male and Bean, 2005). On the other hand, improvement of population trends found in the present study was not as strong as the positive effect of listing the species into Annex I of the Birds Directive found by Donald et al. (2007) using population trend data obtained in the same time intervals. This difference can be caused either by a higher effectiveness of the species protection under Birds Directive which applied the protection conditions at the international level or by longer time elapsed since it came into effect in individual countries. In the future, it would be interesting to test whether the implementation of the Birds Directive into the national legislation provided benefits for Annex I species in some Eastern European countries after accession to the EU in 2004, and whether the generally good performance of national species protection continued.

Although generally positive, the effect of species protection showed a great variability across Eastern European countries. This fact was probably caused by various country-specific factors which are difficult to uncover without expert knowledge of local conditions.

It is interesting that the results confirmed both predictions about the efficiency of protection in countries differing in the proportion of species being listed as protected. Thus in countries that listed only a small proportion of species, the targeted protection resulted in a better improvement of the protected species' trends. This pattern was indeed evident in the respective countries suggesting a selection of appropriate species for protection efforts and an effective enforcement of legal protection. At the same time, in the countries listing more than 80% of species as protected (including common species such as *Sylvia atricapilla* or *Parus major* – see Table A2) the effective protection prevented further population decline of the protected species while the trends of non-protected species markedly deteriorated here: from the positive trends in 1970–1990 to negative trends in 1990–2000. It is thus possible that these species were subject to exploitation and disturbance such as hunting and habitat destruction in these countries in 1990s (Chiron and Julliard, 2013). Therefore, both approaches to species protection can deliver positive outcomes for conservation practice. As a perspective, we suggest that a combination of the two conservation models can achieve the best outcomes for species protection: a basic level of protection for most (or even all) species will successfully prevent population declines, whereas a selected subset of threatened species shall be protected

under more stringent conditions, including active support if feasible (Garnett et al., 2003), facilitating positive effects on population trends.

We must take into account that the effect of population improvements by establishing new legislation could be masked by temporal coincidence with other factors. Among them, an improvement of the environmental conditions after 1990, that was observed at least in some post-communist countries (Goławski, 2006; Koleček et al., 2010), is an obvious candidate. For example, several studies provide evidence that land abandonment after collapse of communism improved population trends of many farmland bird species (Stoate et al., 2009; Kamp et al., 2011). A similar population increase was found in forest birds due to lower impacts of acid emissions on forest stands (Flousek, 1989) achieved by improvement of air cleaning technologies in coal power stations (Hůnová et al., 2004). However, such factors should affect the species irrespective of their protection status and they thus cannot explain the observed difference in improvement of population trends between the protected and non-protected species. Therefore, we suggest that, in addition to these factors, the species protection status might have played a significant role.

Consistent with earlier studies (Böhning-Gaese and Oberrath, 2003; Jiguet et al., 2007; Van Turnhout et al., 2010; Webb et al., 2010), species' traits also influenced bird population trends in Eastern Europe. Declines of obligatory long-distance migrants in 1970–1990 and, in turn, the same trends of species of all migration strategies in 1990–2000, correspond with pan-European analysis of Sanderson et al. (2006) who observed a significant decline of trans-Saharan migrants in 1970–1990, but not in 1990–2000. Negative population trends of ground nesting species are most likely driven by the decline of farmland birds frequently reported in European countries (Donald et al., 2001; 2006). The reduction of the rate of their decline observed in our study may be related to reduced agricultural intensity in Eastern Europe after the fall of communism (Donald et al., 2001; Stoate et al., 2009), which resulted in temporal farmland bird recovery in some countries (Reif et al., 2008 but see Báldi and Batáry, 2011). For non-farmland birds, breeding in semi-natural terrestrial habitats, encroachment by nitrophilic grasses and shrubs might be a cause for the decline of ground-nesters (Van Turnhout et al., 2010). A decline in nitrogen and phosphate emissions might have ameliorated the situation for these species. In addition, we found that K-selected species, as well as species spreading their breeding investment into multiple breeding attempts, had more positive population trends than r-selected species and species allocating their energy to just one breeding attempt, respectively. Similar relationships were observed in France (Jiguet et

al., 2007) and in the Czech Republic (Reif et al., 2010). The traits identified above are also found in invasive bird species (Sol et al., 2012). Sol et al. (2012) suggest that successful invaders are species that are able to wait longer until environmental conditions are suitable for reproduction (i.e. K-selected species) and, more importantly, those having multiple breeding attempts. It seems possible that the life histories identified above could be generally advantageous for survival under adverse environmental conditions, at least for birds.

In conclusion, we found positive effects of species protection delivered by national legislation in Eastern Europe. National legal protection plays an important role in preventing population declines at a regional scale. At the same time, direction and magnitude of its effects showed considerable variation among the countries. In future studies, it would be interesting to explain this variation by a more detailed analysis focused on the level of implementation and enforcement of the bird conservation legislation, as well as on other local factors like the history and tradition of nature conservation or socio-economic factors. Such an assessment can supply important lessons for further development of the national and international bird protection policies formulating widely applicable rules to achieve the highest effectiveness. Our study is a first step on this research avenue.

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Table 1. Analysis of deviance of the final linear mixed effects model including effects of species' traits and legal protection status on population trends of 306 bird species in two time periods (first: 1970–1990, second: 1990–2000). Mixed effects models accounted for avian phylogenetic relatedness by including family, genus and species as nested random effects. Significance of effects was assessed with a Type II analysis that is independent of the sequence of factors in the model using a Wald chi²-test. The residuals of the final model traced normal distribution.

Explanatory variable	Df	Chi ²	P
Protection status	1	6.18	0.013
Country	9	144.61	< 0.001
Time period	1	7.67	0.006
PC1	1	5.92	0.015
PC2	1	2.79	0.095
Nest location	1	9.74	0.002
Migration flexibility	1	3.07	0.080
Protection × country	9	31.94	< 0.001
Protection × time period	1	32.06	< 0.001
Country × time period	9	73.90	< 0.001
PC2 × time period	1	10.73	0.001
Nest location × time period	1	6.97	0.008
Migration flexibility × time period	1	11.82	0.001
Protection × country × time period	9	18.52	0.030

Table 2. Effects of species' traits on population trends of 306 bird species in two time periods (first: 1970–1990, second: 1990–2000) in 10 Eastern European countries as revealed by the final linear mixed effects model. The main effect refers to the relationship between a given trait and the population trend in the first time period, the interaction term refers to the change in trends between the first and second time period.

Trait variable	Estimate	SE	df	t	P
Migration flexibility	0.15	0.05	139	2.96	0.004
Migration flexibility × time period	−0.14	0.04	3366	−3.42	0.001
Nest location	0.11	0.03	139	3.84	< 0.001
Nest location × time period	−0.05	0.02	3366	−2.62	0.009
PC1	−0.04	0.02	139	−2.42	0.017
PC2	0.07	0.03	139	2.70	0.008
PC2 × time period	−0.06	0.02	3366	−3.25	0.001

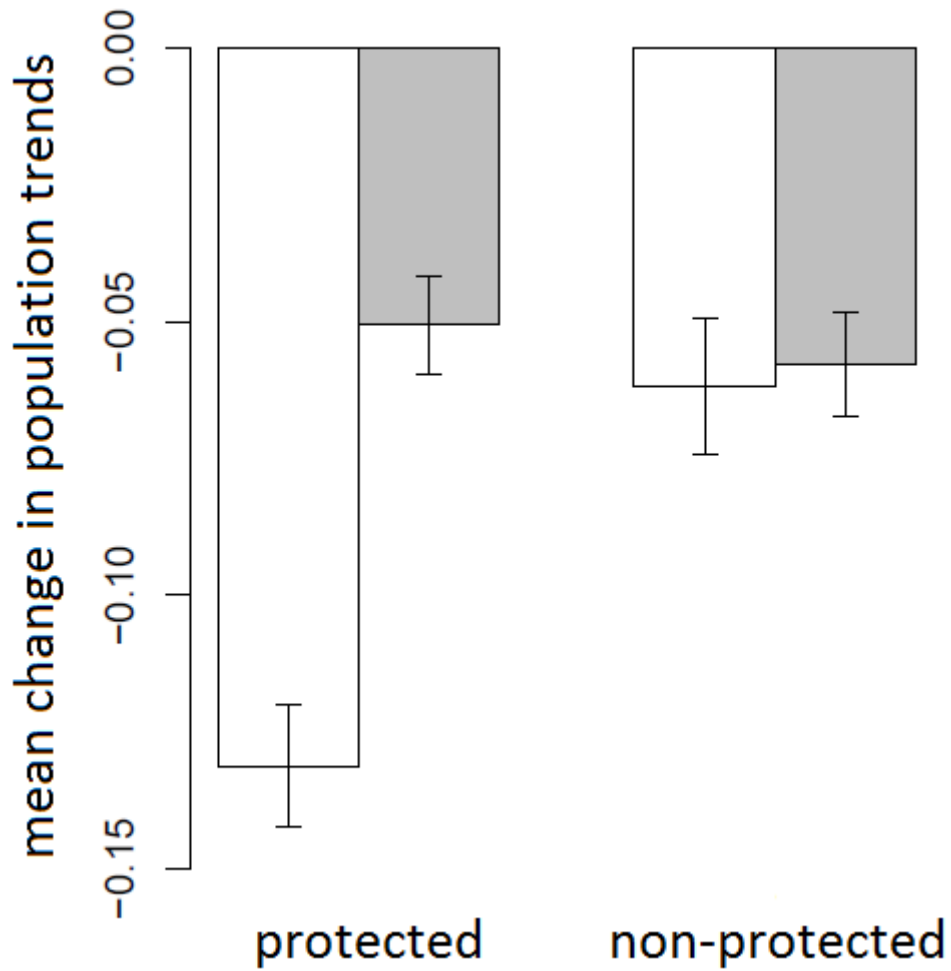


Figure 1. Predicted values of population trends (\pm SE) of 306 protected and non-protected species in 10 Eastern European countries in 1970–1990 (white bars) and 1990–2000 (grey bars) as estimated by the final model (see Table 1). Population trends range between -1 and 1 . See section 2. for more details.

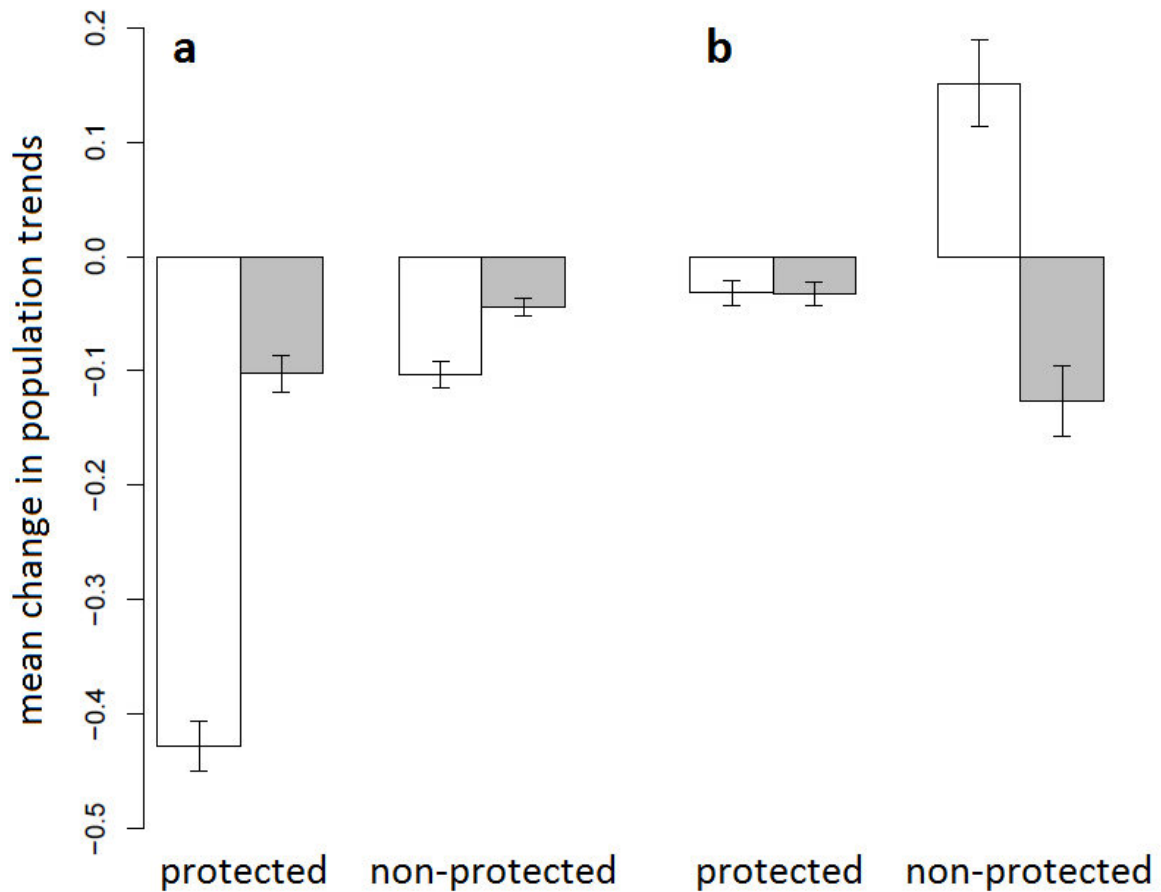


Figure 2. Predicted values of population trends (\pm SE) of 306 protected and non-protected species in Eastern European countries protecting (a) less than 55% species (five countries) and (b) more than 80% species (five countries) in 1970–1990 (white bars) and 1990–2000 (grey bars) as estimated by the final model (see Table 1). Population trends range between -1 and 1 . See section 2.4. for more details.

Table A1. Temporal validity, national legislation regarding protected species, and the proportion of protected species (%) using the full national lists of protected species in 10 Eastern European countries.

Country	Country code	Legislation tool	Valid since	% protected
Belarus	BY	Act no. 201	1993	27
Croatia	HR	Act no. 30/94 and 72/94	1995	92
Czech Rep.	CZ	Act no. 114/92 and 395/92	1992	52
Estonia	EST	Act no. RT Part I 1994, No. 46. Art. 773	1994	81
Hungary	H	Statute no. 12/1993	1993	91
Latvia	LV	Act no. 107	1987	25
Moldova	MD	Act no. 439	1995	32
Poland	PL	Act no. Dz.U.91.114.492 and Dz.U.95.13.61	1995	92
Slovakia	SK	Act no. 287/94 and 192/93	1993	81
Ukraine	UA	Act no. 1264-XII	1994	21

Table A2. List of the 306 bird species and their protection status in 10 Eastern European countries in 1990–2000 used in the analyses. Dashes (–) denote where the species does not occur in that country, 0 – game / non-protected bird species, 1 – legally protected species. See sections 2.1. and 2.2. for more details. See the Table A1 for the country codes.

Species	BY	CZ	EST	H	HR	LV	MD	PL	SK	UA
<i>Accipiter brevipes</i>	–	–	–	1	1	–	–	–	–	1
<i>Accipiter gentilis</i>	0	1	1	1	1	1	1	1	0	0
<i>Accipiter nisus</i>	0	1	1	1	1	1	1	1	0	0
<i>Acrocephalus arundinaceus</i>	0	1	1	1	1	0	0	1	1	0
<i>Acrocephalus dumetorum</i>	–	–	1	–	–	0	–	–	–	–
<i>Acrocephalus melanopogon</i>	–	–	–	1	1	–	–	–	1	–
<i>Acrocephalus paludicola</i>	–	–	–	1	–	0	–	1	–	–
<i>Acrocephalus palustris</i>	0	0	1	1	1	0	0	1	1	0
<i>Acrocephalus schoenobaenus</i>	0	0	1	1	1	0	0	–	1	0
<i>Acrocephalus scirpaceus</i>	–	0	1	1	1	0	0	1	1	0
<i>Actitis hypoleucos</i>	0	1	1	1	1	0	0	1	0	0
<i>Aegithalos caudatus</i>	–	0	1	1	1	0	1	1	1	0
<i>Aegolius funereus</i>	–	1	1	–	1	1	–	1	1	–
<i>Aegyptius monachus</i>	–	–	–	–	–	–	–	–	–	1
<i>Alauda arvensis</i>	0	0	1	1	1	0	0	1	0	0
<i>Alca torda</i>	–	–	1	–	–	–	–	–	–	–
<i>Alcedo atthis</i>	1	–	–	1	1	–	1	–	1	0
<i>Alectoris graeca</i>	–	–	–	–	1	–	–	–	–	–
<i>Anas acuta</i>	–	–	0	0	–	0	–	1	–	–
<i>Anas clypeata</i>	–	1	0	1	–	0	–	1	1	0
<i>Anas crecca</i>	0	1	0	–	0	0	–	0	0	0
<i>Anas penelope</i>	–	–	0	–	–	–	–	1	–	0
<i>Anas platyrhynchos</i>	0	0	0	0	0	0	0	0	0	0
<i>Anas querquedula</i>	0	1	0	0	0	0	0	1	0	0
<i>Anas strepera</i>	0	1	0	1	0	0	0	1	–	0
<i>Anser anser</i>	–	0	0	1	1	1	0	0	0	0
<i>Anthus campestris</i>	–	1	1	1	1	0	0	1	1	0
<i>Anthus pratensis</i>	0	0	1	–	–	0	0	1	1	0
<i>Anthus spinoletta</i>	–	1	–	–	1	–	–	1	1	0
<i>Anthus trivialis</i>	0	0	1	1	1	0	0	1	1	0
<i>Apus apus</i>	–	1	1	1	1	0	0	1	1	0
<i>Apus melba</i>	–	–	–	–	1	–	–	–	–	0
<i>Apus pallidus</i>	–	–	–	–	1	–	–	–	–	–
<i>Aquila chrysaetos</i>	1	–	1	–	1	1	–	1	1	1
<i>Aquila clanga</i>	–	–	–	–	–	–	–	1	–	1
<i>Aquila heliaca</i>	–	–	–	1	1	–	–	–	1	1

<i>Aquila pomarina</i>	1	–	1	1	1	1	1	1	1	
<i>Ardea cinerea</i>	0	0	0	1	1	1	0	0	1	0
<i>Ardea purpurea</i>	–	1	–	1	1	–	1	–	1	0
<i>Ardeola ralloides</i>	–	–	–	1	1	–	1	–	–	1
<i>Arenaria interpres</i>	–	–	1	–	–	–	–	–	–	–
<i>Asio flammeus</i>	1	–	1	–	1	1	–	–	–	–
<i>Asio otus</i>	–	0	–	1	1	–	1	–	1	0
<i>Athene noctua</i>	1	1	–	1	1	–	1	1	1	0
<i>Aythya ferina</i>	0	0	0	0	0	0	0	0	1	0
<i>Aythya fuligula</i>	0	0	0	1	0	0	–	0	1	0
<i>Aythya marila</i>	–	–	1	–	–	–	–	–	–	–
<i>Aythya nyroca</i>	1	–	–	1	1	–	0	1	1	1
<i>Bonasa bonasia</i>	0	1	0	1	1	0	–	0	0	0
<i>Botaurus stellaris</i>	–	1	1	1	1	1	1	1	1	0
<i>Branta leucopsis</i>	–	–	1	–	–	–	–	–	–	–
<i>Bubo bubo</i>	1	1	1	1	1	1	1	1	1	1
<i>Bucephala clangula</i>	1	1	0	–	–	0	–	1	–	–
<i>Burhinus oedicnemus</i>	1	1	–	1	1	–	–	–	1	1
<i>Buteo buteo</i>	0	0	1	1	1	1	1	1	1	0
<i>Buteo rufinus</i>	–	–	–	–	–	–	–	–	–	1
<i>Calandrella brachydactyla</i>	–	–	–	1	1	–	–	–	–	0
<i>Calandrella rufescens</i>	–	–	–	–	–	–	–	–	–	0
<i>Calidris alpina</i>	–	–	1	–	–	1	–	1	–	–
<i>Calonectris diomedea</i>	–	–	–	–	1	–	–	–	–	–
<i>Caprimulgus europaeus</i>	0	1	1	1	1	0	1	1	1	0
<i>Carduelis cannabina</i>	–	0	1	1	1	0	0	1	1	0
<i>Carduelis carduelis</i>	0	0	1	1	1	0	0	1	1	0
<i>Carduelis chloris</i>	0	0	1	1	1	0	0	1	1	0
<i>Carduelis flammea</i>	–	0	–	–	–	–	–	1	1	–
<i>Carduelis spinus</i>	–	–	–	1	1	0	–	1	1	–
<i>Carpodacus erythrinus</i>	0	1	1	–	–	0	–	1	1	0
<i>Cephus grylle</i>	–	–	1	–	–	–	–	–	–	–
<i>Certhia brachydactyla</i>	–	0	–	1	1	–	–	1	1	0
<i>Certhia familiaris</i>	0	0	1	1	1	0	0	1	1	0
<i>Cettia cetti</i>	–	–	–	–	1	–	–	–	–	–
<i>Charadrius alexandrinus</i>	–	–	–	1	1	–	–	–	–	1
<i>Charadrius dubius</i>	0	0	1	–	1	0	0	1	1	0
<i>Charadrius hiaticula</i>	–	–	1	–	–	0	–	1	–	–
<i>Chlidonias hybridus</i>	–	–	–	–	1	–	0	1	–	0
<i>Chlidonias leucopterus</i>	–	–	1	–	–	–	–	–	–	–
<i>Chlidonias niger</i>	–	1	1	–	1	–	0	–	1	–
<i>Ciconia ciconia</i>	0	1	1	1	1	0	1	1	1	0
<i>Ciconia nigra</i>	1	1	1	1	1	1	1	1	1	1
<i>Cinclus cinclus</i>	–	0	1	–	1	–	–	1	1	0
<i>Circaetus gallicus</i>	1	–	1	1	1	–	–	1	1	1

<i>Circus aeruginosus</i>	-	1	1	1	1	1	1	1	1	0
<i>Circus cyaneus</i>	-	1	1	-	-	1	-	1	-	1
<i>Circus macrourus</i>	-	-	-	-	-	-	1	-	-	1
<i>Circus pygargus</i>	-	1	1	1	1	1	1	1	-	0
<i>Cisticola junicidis</i>	-	-	-	-	1	-	-	-	-	-
<i>Clamator glandarius</i>	-	-	-	-	1	-	-	-	-	-
<i>Coccoth. coccothraustes</i>	-	0	1	1	1	0	0	1	1	0
<i>Columba livia f.domestica</i>	0	-	0	-	0	0	0	-	-	0
<i>Columba oenas</i>	0	1	1	1	1	1	1	1	1	0
<i>Columba palumbus</i>	0	0	0	0	0	0	1	0	0	0
<i>Coracias garrulus</i>	1	1	1	1	1	1	1	1	1	0
<i>Corvus corax</i>	0	1	0	1	1	0	1	1	1	0
<i>Corvus corone</i>	0	0	0	1	0	0	0	0	0	0
<i>Corvus frugilegus</i>	0	0	0	0	0	0	0	0	0	0
<i>Corvus monedula</i>	0	1	0	1	0	0	0	1	0	0
<i>Coturnix coturnix</i>	-	-	1	1	1	-	0	-	1	0
<i>Crex crex</i>	0	1	1	-	1	1	1	1	0	0
<i>Cuculus canorus</i>	0	0	1	1	1	0	0	1	1	0
<i>Cygnus cygnus</i>	-	-	1	-	-	1	-	-	-	-
<i>Cygnus olor</i>	1	0	1	-	-	0	1	1	1	0
<i>Delichon urbica</i>	0	0	1	1	1	0	0	1	1	0
<i>Dendrocopos leucotos</i>	0	1	1	1	1	1	-	1	1	0
<i>Dendrocopos major</i>	0	0	1	1	1	0	0	1	1	0
<i>Dendrocopos medius</i>	0	1	-	1	1	-	0	1	1	0
<i>Dendrocopos minor</i>	0	0	1	1	1	0	0	1	1	0
<i>Dendrocopos syriacus</i>	-	1	-	1	1	-	0	1	1	0
<i>Dryocopus martius</i>	0	0	1	1	1	0	-	1	1	0
<i>Egretta alba</i>	-	-	-	1	1	-	1	-	-	0
<i>Egretta garzetta</i>	-	-	-	1	1	-	0	-	-	0
<i>Emberiza cia</i>	-	-	-	1	1	-	-	-	1	0
<i>Emberiza circlus</i>	-	-	-	-	1	-	-	-	-	-
<i>Emberiza citrinella</i>	0	0	1	1	1	0	0	1	1	0
<i>Emberiza hortulana</i>	-	1	1	1	1	0	0	1	1	0
<i>Emberiza melanocephala</i>	-	-	-	-	1	-	-	-	-	0
<i>Emberiza schoeniclus</i>	0	0	1	1	1	0	0	1	1	0
<i>Eremophila alpestris</i>	-	-	-	-	1	-	-	-	-	-
<i>Erithacus rubecula</i>	0	0	1	1	1	0	0	1	1	0
<i>Falco biarmicus</i>	-	-	-	-	1	-	-	-	-	-
<i>Falco cherrug</i>	-	1	-	1	1	-	1	-	1	1
<i>Falco columbarius</i>	1	-	1	-	-	1	-	-	-	-
<i>Falco elenora</i>	-	-	-	-	1	-	-	-	-	-
<i>Falco naumanni</i>	-	-	-	-	-	-	1	-	-	1
<i>Falco peregrinus</i>	-	1	-	-	1	-	-	-	1	1
<i>Falco subbuteo</i>	1	1	1	-	1	1	1	1	1	0
<i>Falco tinnunculus</i>	-	0	1	1	1	1	1	1	1	0

<i>Falco vespertinus</i>	1	-	-	1	1	-	1	-	-	0
<i>Ficedula albicollis</i>	0	0	-	1	1	-	0	1	1	0
<i>Ficedula hypoleuca</i>	0	0	1	-	-	0	0	1	-	0
<i>Ficedula parva</i>	0	1	1	1	1	0	0	1	1	0
<i>Fringilla coelebs</i>	0	0	1	1	1	0	0	1	1	0
<i>Fringilla montifringilla</i>	-	-	-	-	-	0	-	-	-	-
<i>Fulica atra</i>	0	0	0	0	0	0	0	0	0	-
<i>Galerida cristata</i>	-	1	1	1	1	1	0	1	0	0
<i>Gallinago gallinago</i>	0	1	0	-	0	0	-	1	0	0
<i>Gallinago media</i>	0	-	1	-	-	0	-	1	-	0
<i>Gallinula chloropus</i>	0	0	1	1	1	0	0	1	0	0
<i>Garrulus glandarius</i>	0	0	0	0	0	0	0	1	0	0
<i>Gavia arctica</i>	-	-	1	-	-	1	-	-	-	-
<i>Geochelidon nilotica</i>	-	-	-	-	-	-	-	-	-	0
<i>Glareola nordmanni</i>	-	-	-	-	-	-	-	-	-	1
<i>Glaucidium passerinum</i>	1	1	1	-	-	1	-	1	1	-
<i>Grus grus</i>	1	-	1	-	-	1	-	1	-	1
<i>Gyps fulvus</i>	-	-	-	-	-	-	-	-	-	1
<i>Haematopus ostralegus</i>	1	-	1	-	-	1	-	1	-	1
<i>Haliaeetus albicilla</i>	1	1	1	1	1	1	-	1	-	1
<i>Hieraaetus fasciatus</i>	-	-	-	-	1	-	-	-	-	-
<i>Hieraaetus pennatus</i>	1	-	-	1	-	-	1	-	1	1
<i>Himantopus himantopus</i>	-	-	-	-	-	-	0	-	-	1
<i>Hippolais icterina</i>	0	0	1	1	1	0	0	1	1	0
<i>Hippolais olivetorum</i>	-	-	-	-	1	-	-	-	-	-
<i>Hippolais pallida</i>	-	-	-	1	1	-	-	-	-	-
<i>Hippolais polyglotta</i>	-	-	-	-	1	-	-	-	-	-
<i>Hirundo daurica</i>	-	-	-	-	1	-	-	-	-	-
<i>Hirundo rupestris</i>	-	-	-	-	1	-	-	-	-	-
<i>Hirundo rustica</i>	0	1	1	1	-	0	0	1	1	0
<i>Ixobrychus minutus</i>	1	1	-	1	1	1	0	1	1	0
<i>Jynx torquilla</i>	0	1	1	1	1	0	0	1	1	0
<i>Lagopus lagopus</i>	1	-	1	-	-	1	-	-	-	-
<i>Lanius collurio</i>	0	1	1	1	1	0	0	1	1	0
<i>Lanius excubitor</i>	1	1	1	-	-	1	-	-	1	1
<i>Lanius minor</i>	1	-	-	1	1	-	0	1	1	0
<i>Lanius senator</i>	-	1	-	-	1	-	-	1	-	-
<i>Larus argentatus</i>	1	-	0	-	-	0	-	1	-	0
<i>Larus cachinnans</i>	-	-	-	-	1	-	-	-	-	-
<i>Larus canus</i>	0	0	0	-	-	-	-	1	-	-
<i>Larus fuscus</i>	-	-	1	-	-	-	-	-	-	-
<i>Larus marinus</i>	-	-	0	-	-	-	-	-	-	-
<i>Larus melanocephalus</i>	-	-	-	1	-	-	-	-	-	-
<i>Larus minutus</i>	-	-	1	-	-	-	-	1	-	-
<i>Larus ridibundus</i>	0	0	0	1	1	0	0	1	1	-

<i>Limosa limosa</i>	0	1	1	–	–	0	–	1	1	0
<i>Locustella fluviatilis</i>	0	0	1	1	1	0	0	1	1	–
<i>Locustella luscinioides</i>	1	1	1	1	1	0	0	1	1	0
<i>Locustella naevia</i>	0	0	1	1	1	0	0	1	1	0
<i>Loxia curvirostra</i>	–	–	–	–	1	–	–	–	–	–
<i>Lullula arborea</i>	0	1	1	1	1	0	0	1	1	0
<i>Luscinia luscinia</i>	0	–	1	1	–	0	0	1	1	0
<i>Luscinia megarhynchos</i>	–	1	–	1	1	–	–	1	1	0
<i>Luscinia svecica</i>	1	–	1	1	1	0	–	1	–	0
<i>Lymnocyptes minimus</i>	–	–	1	–	–	0	–	–	–	–
<i>Melanitta fusca</i>	–	–	1	–	–	–	–	–	–	–
<i>Melanocorypha calandra</i>	–	–	–	–	1	–	0	–	–	0
<i>Mergus merganser</i>	1	–	0	–	–	0	–	1	–	0
<i>Mergus serrator</i>	1	–	0	–	–	0	–	1	–	1
<i>Merops apiaster</i>	–	1	–	1	1	–	0	–	1	0
<i>Miliaria calandra</i>	–	1	–	1	1	–	0	1	1	0
<i>Milvus migrans</i>	0	1	1	1	1	1	1	1	1	0
<i>Milvus milvus</i>	1	1	–	–	1	–	–	1	1	–
<i>Monticola saxatilis</i>	–	–	–	1	1	–	1	–	1	1
<i>Monticola solitarius</i>	–	–	–	–	1	–	–	–	–	–
<i>Motacilla alba</i>	0	0	1	1	1	0	0	1	1	0
<i>Motacilla cinerea</i>	–	0	1	1	1	–	–	1	1	0
<i>Motacilla citreola</i>	–	–	–	–	–	–	–	–	–	0
<i>Motacilla flava</i>	0	1	1	1	1	0	0	1	1	0
<i>Muscicapa striata</i>	0	1	1	1	1	0	0	1	1	–
<i>Neophron percnopterus</i>	–	–	–	–	–	–	1	–	–	–
<i>Netta rufina</i>	–	1	–	–	–	–	–	–	1	0
<i>Nucifraga caryocatactes</i>	–	1	1	–	1	0	–	1	1	0
<i>Numenius arquata</i>	1	1	1	1	–	1	–	1	1	1
<i>Numenius phaeopus</i>	1	–	1	–	–	–	–	–	–	–
<i>Nycticorax nycticorax</i>	–	1	–	1	1	–	0	1	1	–
<i>Oenanthe hispanica</i>	–	–	–	–	1	–	–	–	–	–
<i>Oenanthe isabellina</i>	–	–	–	–	–	–	–	–	–	0
<i>Oenanthe oenanthe</i>	0	1	1	1	1	0	0	1	1	0
<i>Oenanthe pleshanka</i>	–	–	–	–	–	–	–	–	–	0
<i>Oriolus oriolus</i>	0	1	1	1	1	0	0	1	1	0
<i>Otis tarda</i>	–	1	–	1	–	–	–	–	1	1
<i>Otus scops</i>	–	–	–	1	1	–	1	–	–	1
<i>Pandion haliaetus</i>	1	–	1	–	–	1	1	1	–	1
<i>Panurus biarmicus</i>	–	1	1	1	1	–	1	1	–	0
<i>Parus ater</i>	–	0	–	1	1	–	–	1	1	0
<i>Parus caeruleus</i>	0	0	1	1	1	0	0	1	1	0
<i>Parus cristatus</i>	0	0	1	–	1	0	–	1	1	0
<i>Parus lugubris</i>	–	–	–	–	1	–	–	–	–	–
<i>Parus major</i>	0	0	1	1	1	0	0	1	1	0

<i>Parus montanus</i>	0	0	1	0	1	0	–	1	1	0
<i>Parus palustris</i>	0	0	1	1	1	0	0	1	1	0
<i>Passer domesticus</i>	–	0	0	0	1	0	0	1	0	0
<i>Passer hispaniolensis</i>	–	–	–	–	1	–	–	–	–	–
<i>Passer montanus</i>	0	0	0	1	1	0	0	1	0	0
<i>Perdix perdix</i>	–	1	–	0	1	1	0	0	0	–
<i>Pernis apivorus</i>	0	1	1	1	1	1	1	1	1	0
<i>Phalacrocorax aristotelis</i>	–	–	–	–	1	–	–	–	–	1
<i>Phalacrocorax carbo</i>	–	1	0	0	0	–	–	0	1	0
<i>Phalacrocorax pygmaeus</i>	–	–	–	–	–	–	–	–	–	1
<i>Phasianus colchicus</i>	–	–	–	0	1	–	1	–	–	0
<i>Philomachus pugnax</i>	–	–	1	–	–	0	–	1	–	0
<i>Phoenicurus ochruros</i>	0	0	1	1	1	0	0	1	1	0
<i>Phoenicurus phoenicurus</i>	0	0	1	1	1	0	0	1	1	0
<i>Phylloscopus collybita</i>	0	0	1	1	1	0	0	1	1	0
<i>Phylloscopus sibilatrix</i>	0	0	1	1	1	0	0	1	1	0
<i>Phylloscopus trochiloides</i>	–	–	–	–	–	0	–	–	–	–
<i>Phylloscopus trochilus</i>	0	0	1	–	–	0	0	1	1	0
<i>Pica pica</i>	0	0	0	0	0	0	0	0	0	0
<i>Picoides tridactylus</i>	0	–	1	–	1	–	–	1	1	0
<i>Picus canus</i>	0	0	1	1	1	1	0	1	1	0
<i>Picus viridis</i>	1	0	1	1	1	0	1	1	1	0
<i>Platalea leucorodia</i>	–	–	–	1	1	–	1	–	–	1
<i>Plegadis falcinellus</i>	–	–	–	–	–	–	1	–	–	–
<i>Pluvialis apricaria</i>	1	–	1	–	–	1	–	–	–	–
<i>Podiceps auritus</i>	–	–	1	–	–	0	–	–	–	–
<i>Podiceps cristatus</i>	0	1	0	1	1	0	0	1	0	0
<i>Podiceps grisegena</i>	1	–	1	1	–	0	–	–	–	0
<i>Podiceps nigricollis</i>	–	1	1	1	1	0	1	–	–	–
<i>Porzana parva</i>	–	1	–	1	1	1	0	1	1	0
<i>Porzana porzana</i>	0	1	–	1	–	0	0	1	1	0
<i>Porzana pusilla</i>	–	–	–	–	–	–	0	–	–	–
<i>Prunella collaris</i>	–	1	–	–	1	–	–	1	1	1
<i>Prunella modularis</i>	0	0	1	1	1	0	–	1	0	0
<i>Puffinus yelkouan</i>	–	–	–	–	1	–	–	–	–	–
<i>Pyrrhocorax graculus</i>	–	–	–	–	1	–	–	–	–	–
<i>Pyrrhula pyrrhula</i>	0	0	1	–	1	0	–	1	1	–
<i>Rallus aquaticus</i>	0	1	1	1	1	–	0	1	0	0
<i>Recurvirostra avosetta</i>	–	–	1	–	–	–	–	–	–	–
<i>Regulus ignicapillus</i>	–	0	–	–	1	–	–	1	1	1
<i>Regulus regulus</i>	–	0	–	1	1	–	–	1	1	0
<i>Remiz pendulinus</i>	1	1	1	1	1	1	1	1	1	0
<i>Riparia riparia</i>	0	1	1	1	1	0	1	1	1	0
<i>Saxicola rubetra</i>	0	1	1	1	1	0	0	1	1	0
<i>Saxicola torquata</i>	–	1	–	1	1	–	0	1	1	0

<i>Scolopax rusticola</i>	0	1	0	–	–	0	–	0	0	0
<i>Serinus serinus</i>	–	0	1	1	1	0	–	1	0	0
<i>Sitta europaea</i>	0	0	1	1	1	0	0	1	1	0
<i>Sitta neumayer</i>	–	–	–	–	1	–	–	–	–	–
<i>Somateria mollissima</i>	–	–	0	–	–	–	–	–	–	1
<i>Sterna albifrons</i>	–	–	1	–	1	–	–	–	–	0
<i>Sterna caspia</i>	–	–	1	–	–	–	–	–	–	1
<i>Sterna hirundo</i>	0	1	1	1	1	0	0	1	1	–
<i>Sterna paradisaea</i>	–	–	1	–	–	–	–	–	–	–
<i>Sterna sandvicensis</i>	–	–	1	–	–	–	–	–	–	–
<i>Streptopelia decaocto</i>	0	0	1	0	1	0	0	–	0	0
<i>Streptopelia turtur</i>	0	0	1	1	1	0	0	1	0	0
<i>Strix aluco</i>	0	0	1	1	1	0	1	1	1	0
<i>Strix uralensis</i>	1	1	1	–	1	–	–	1	1	1
<i>Sturnus vulgaris</i>	0	0	1	0	0	0	0	1	0	–
<i>Sylvia atricapilla</i>	0	0	1	1	1	0	0	1	1	0
<i>Sylvia borin</i>	0	0	1	1	1	0	0	1	1	0
<i>Sylvia cantillans</i>	–	–	–	–	1	–	–	–	–	–
<i>Sylvia communis</i>	0	0	1	1	1	0	0	1	1	–
<i>Sylvia curruca</i>	0	0	1	1	1	0	0	1	1	0
<i>Sylvia hortensis</i>	–	–	–	–	1	–	–	–	–	–
<i>Sylvia melanocephala</i>	–	–	–	–	1	–	–	–	–	–
<i>Sylvia nisoria</i>	–	1	1	1	1	0	0	1	1	0
<i>Tachybaptus ruficollis</i>	1	1	1	1	1	0	1	1	0	–
<i>Tadorna ferruginea</i>	–	–	–	–	–	–	–	–	–	1
<i>Tadorna tadorna</i>	–	–	1	–	–	–	–	1	–	0
<i>Tetrao tetrix</i>	0	1	1	–	–	0	–	1	1	0
<i>Tetrao urogallus</i>	0	1	1	–	1	0	–	1	0	1
<i>Tetrax tetrax</i>	–	–	–	–	–	–	–	–	–	1
<i>Tichodroma muraria</i>	–	–	–	–	1	–	–	1	1	–
<i>Tringa glareola</i>	0	–	1	–	–	0	–	–	–	0
<i>Tringa nebularia</i>	–	–	1	–	–	–	–	–	–	–
<i>Tringa ochropus</i>	0	–	1	–	–	0	–	1	–	0
<i>Tringa totanus</i>	0	1	1	1	1	0	–	1	1	0
<i>Troglodytes troglodytes</i>	0	0	1	1	1	0	0	1	1	0
<i>Turdus iliacus</i>	0	–	1	–	–	0	–	1	–	0
<i>Turdus merula</i>	0	0	0	1	1	0	0	1	0	0
<i>Turdus philomelos</i>	0	0	1	1	1	0	0	1	1	0
<i>Turdus pilaris</i>	0	0	0	1	–	0	–	1	1	0
<i>Turdus torquatus</i>	–	1	–	–	1	–	–	1	1	0
<i>Turdus viscivorus</i>	–	0	1	1	1	0	–	1	1	0
<i>Tyto alba</i>	1	1	–	1	1	–	1	1	1	1
<i>Upupa epops</i>	0	1	–	1	1	1	1	1	1	0
<i>Vanellus vanellus</i>	0	0	1	1	1	0	0	1	1	0
<i>Xenus cinereus</i>	1	–	–	–	–	–	–	–	–	–

Table A3. The fixed effects of species' traits on population trends of 306 bird species in 10 Eastern European countries in two time periods (first: 1970–1990, second: 1990–2000) as revealed by averaging of linear mixed effects models providing estimates and their 95% confidence limits (CI) controlling for the fixed effect of species' legal protection (see Table 1) and random effects of phylogenetic relatedness (see section 3.3. and Appendix A). In the Step 1, we run the model averaging within the groups of related variables; in the Step 2, we combined the best performing terms into one model (see section 2.4. for details). The main effect refers to the relationship between a given trait and the population trend in the first time period, the interaction term refers to the change in trends between the first and second period. The terms whose confidence limits did not include zero are in bold.

Trait variable	Estimate	Lower CI	Upper CI
<i>Step 1</i>			
<i>Climatic niche</i>			
Climatic niche position	-0.001	-0.016	0.013
Climatic niche range	0.001	-0.007	0.009
Climatic niche position × time period	< 0.001	-0.008	0.008
Climatic niche range × time period	-0.002	-0.010	0.006
<i>Dietary niche</i>			
Dietary niche breadth	0.059	-0.045	0.162
Dietary niche position	-0.025	-0.096	0.045
Dietary niche breadth × time period	-0.093	-0.187	0.001
Dietary niche position × time period	0.011	-0.033	0.055
<i>Habitat niche</i>			
Habitat niche breadth	0.011	-0.019	0.041
Habitat niche position	-0.011	-0.041	0.020
Habitat humidity	0.029	-0.047	0.104
Habitat niche breadth × time period	-0.004	-0.024	0.015
Habitat niche position × time period	0.001	-0.008	0.010
Habitat humidity × time period	-0.003	-0.026	0.021
<i>Migration strategy</i>			
Migration distance	-0.090	-0.169	-0.011
Migration flexibility	0.108	-0.012	0.227
Migration distance × time period	0.028	-0.030	0.086
Migration flexibility × time period	-0.105	-0.208	-0.001
<i>Nest type and location</i>			

Nest location	0.122	0.061	0.183
Nest type	-0.010	-0.062	0.041
Nest location × time period	-0.063	-0.107	-0.018
Nest type × time period	0.002	-0.019	0.023
<i>Life-history axes</i>			
PC1	-0.059	-0.097	-0.022
PC2	0.082	0.022	0.141
PC1 × time period	0.035	0.004	0.064
PC2 × time period	-0.067	-0.107	-0.027
<i>Step 2</i>			
Migration distance	-0.047	-0.116	0.021
Migration flexibility	0.119	0.014	0.223
Migration flexibility × time period	-0.119	-0.199	-0.039
Nest location	0.099	0.041	0.157
Nest location × time period	-0.050	-0.091	-0.009
PC1	-0.052	-0.087	-0.017
PC2	0.075	0.020	0.130
PC1 × time period	0.027	-0.001	0.054
PC2 × time period	-0.064	-0.103	-0.026

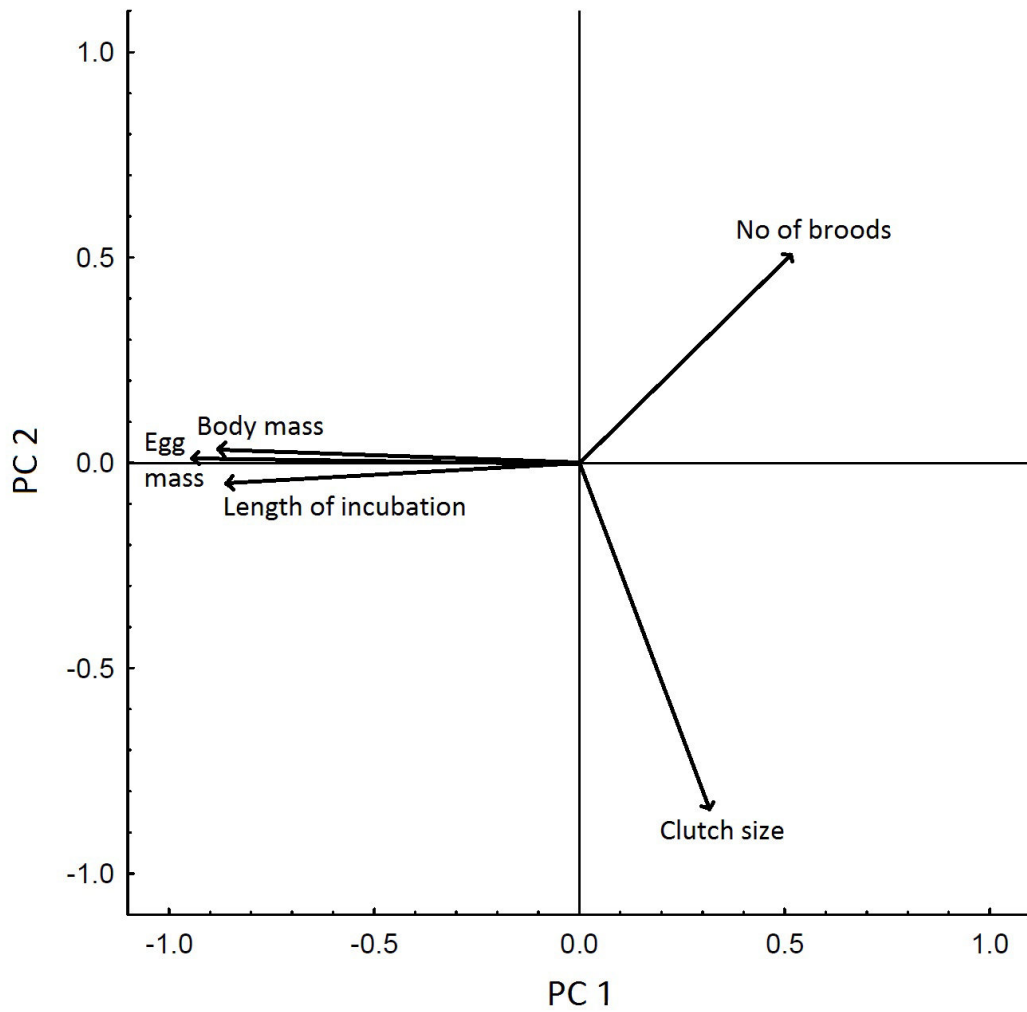


Fig. A1. The two most important ordination axes revealed by a principal component analysis, explaining the largest proportion of variability among five life history traits (i.e. body mass, egg mass, number of broods per year, clutch size and length of incubation) in 306 bird species breeding in 10 Eastern European countries.

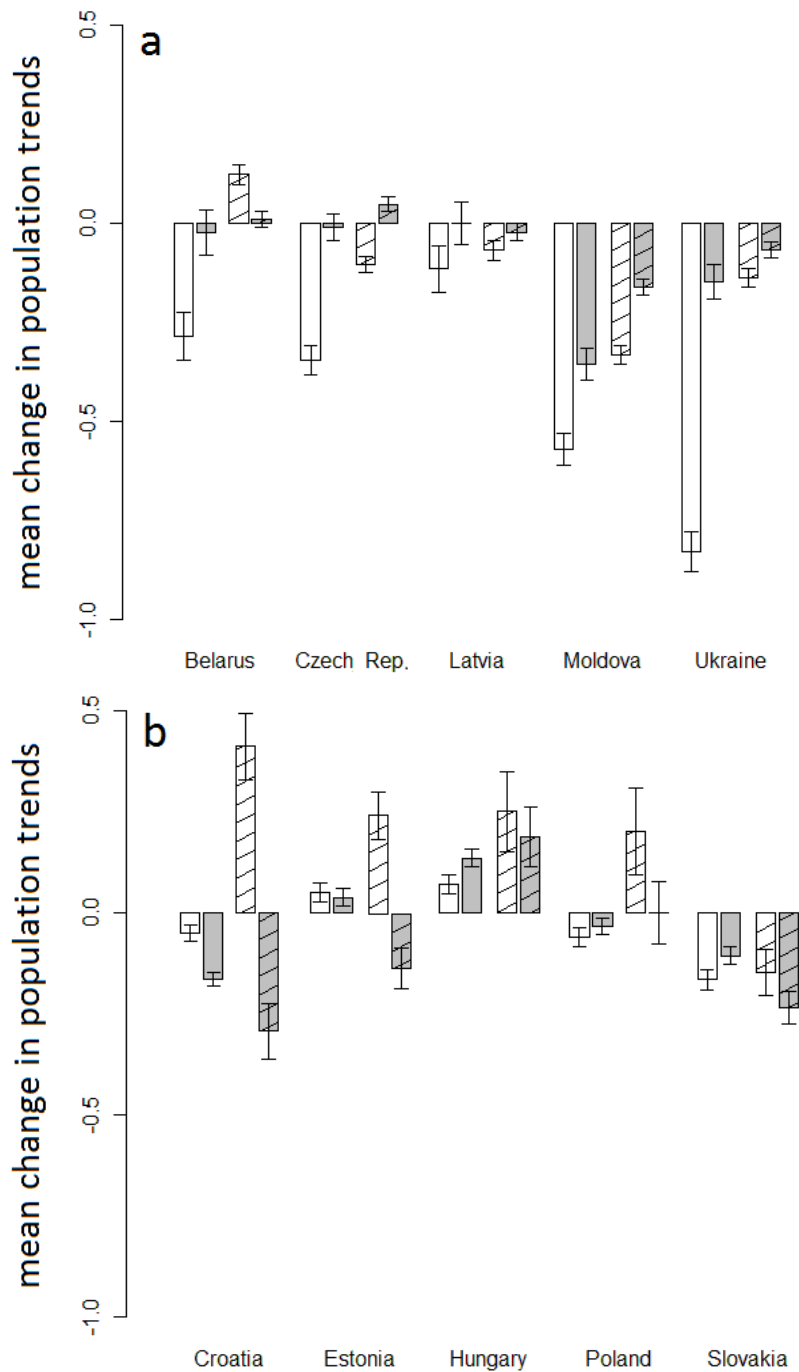


Fig. A2. Predicted values of population trends (\pm SE) of 306 protected (not shadowed) and non-protected (shaded) species in Eastern European countries protecting (a) less than 55% species and (b) more than 80% species in 1970–1990 (white bars) and 1990–2000 (grey bars) as estimated by the final model (see Table 1). The population trends range between -1 and 1 . See section 2.4. for more details.

Appendix A. Results of the two-step selection process of trait variables

We applied information-theoretic approach based on averaging of all candidate models to identify relevant traits that could be included into the final model. In the first step, we assessed all combinations of respective trait variables within groups of related traits. In the second step, we combined the best performing terms (i.e. those whose confidence limits did not include zero) from the previous step into one model and repeated the model averaging to obtain the final set of trait variables.

In the step one, we found following effects on population trends in the focal time periods (1970–1990 and 1990–2000; Table A3): the main effect of migration distance showing more negative population trends of long-distance migrants than the trends of short-distance migrants or residents irrespective to time period; the interaction effect of migration flexibility showing change in difference in the trends between the facultative migrants and obligatory migrants or residents between the time periods; both main and interaction effects of nest location showing more negative population trends of ground nesting species than the trends of above ground nesting species in 1970–1990, but improvement of the trends in the former species in 1990–2000; both main and interaction effects of first (PC1) and second (PC2) life history axis showing more negative population trends of r-selected species than the trends of K-selected species, as well as more negative population trends of species allocating energy into less breeding attempts than the trends of species spreading their investments into multiple breeding attempts; these two relationships applied in 1970–1990 but got weaker in 1990–2000. In contrast, the trait variables describing the effects of habitat, dietary and climatic niche were dropped in the step one.

In the step two, the main effect of migration distance and the time period \times PC1 interaction were dropped. At the same time, the main effect of migration flexibility turned to significance showing that the facultative migrants had more positive population trends than short-distance migrants or residents in 1970–1990, but this difference in trends nearly disappeared in 1990–2000. The other relationships described in the step one held for the step two.

Příspěvek IV.

Koleček J. & Reif J. (rukopis): Interaction between habitat specialization and life history predicts extinction risk in passerine birds.

Interaction between habitat specialization and life history predicts extinction risk in passerine birds

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Abstract

For development of effective conservation measures, it is crucial to know how the ecological traits relate to the risk of species' extinction. This study aims to assess the relative importance of species' habitat specialization and life history as predictors of species' national threat level. Analysing threat level of 87 central European passerine bird species we found that habitat specialists are always more threatened than the habitat generalists. However, this relationship was affected by species' life history. While the slow life history increases the risk of extinction in habitat specialist species, it reduces such risk in habitat generalists. These results suggest that the habitat deterioration is most likely a principle cause of elevated extinction risk, but abilities of species to cope with largely depend on their life histories. It should be taken into account during guiding conservation management targeted on improving population status of the threatened species.

Keywords: birds, red lists, slow-fast continuum, specialization, threatened species

Introduction

Red lists of threatened species express species' extinction risk and thus belong to the fundamental tools in nature conservation (Hamblen 2004). At the national level, red lists help to form and update the lists of protected species and to target the conservation effort on the most threatened ones (Brito *et al.* 2010). Species listing follows a formal assessment of their population status using specified scientific criteria focusing mainly on population development (Mace *et al.* 2008). National red lists may also reflect cultural importance, conservation value and priorities, international responsibility for protection, or a combination of several of these factors (Miller *et al.* 2007). Yet, to apply the red lists into conservation practice more effectively, it is important to have good knowledge of the ecological characteristics of the species being listed in contrast to those being not recognized as threatened.

Birds show huge diversity of life histories and ecological roles (Bennett and Owens 2002) and current knowledge of their ecology enables to formulate predictions concerning traits correlating with the level of their threat. Thus, (i) habitat specialists should show higher levels of threat because they are more susceptible to the recent global changes such as climate and land use change due to their limited ability to switch among different environments (Jiguet *et al.* 2007; Shultz *et al.* 2005). Moreover, habitat specialists often live in more natural habitats that are being destroyed at increasing rate (Owens and Bennett 2000). (ii) Extinction risk could be determined by a position of species' life history along the slow-fast continuum. Species at the slower end of the life history continuum ('K-selected' species) are characterized by smaller clutches, larger eggs, lower fecundity and longer parental care (Stearns 1992). These traits had been shown to limit species' population growth rates (Sæther *et al.* 2005). Under the conditions of recent environmental perturbations, the K-selected species should be more threatened than the species with faster life histories ('r-selected' species). (iii) Recent climatic changes negatively impact on reproduction of species breeding later in breeding season and having smaller number of breeding attempts per year (Salido *et al.* 2012). These species are probably more affected by phenological mismatch between timing of breeding and the amount of food supply than the species starting their breeding earlier and investing energy into more attempts (Both *et al.* 2010). Therefore, we predict the threat level will be higher for the former species and lower for the latter species.

In this study, we test the proposed predictions using data based on 87 passerine bird species breeding in a central European country, the Czech Republic.

Materials and methods

We focused on 87 passerine species breeding in the Czech Republic for which the data on all focal traits were available. Values for threat level were extracted from the current version of the national Red List (Št'astný and Bejček 2003; Table S1) classifying species into the respective standard IUCN categories using the framework outlined by Gärdenfors *et al.* (2001) for development of IUCN Red List at the national level: least concern (0), near threatened (1), vulnerable (2), endangered (3) and critically endangered (4). Threat level was used as a response variable in further analysis.

The degree of habitat specialization was quantified using the habitat species specialization index (SSI) introduced by Julliard *et al.* (2006). The indices of particular species (Table S1) were calculated by Reif *et al.* (2013) using data from a large scale breeding bird monitoring scheme in the Czech Republic. This monitoring scheme is based on standardized point counts conducted by skilled volunteers along hundreds of census transects. These transects are scattered throughout the country and habitat composition in the areas where transects are presented corresponds well to the habitat composition of the whole Czech Republic (Reif *et al.* 2008). We further improved representativeness of bird census data by random selection of transects within higher administrative units (these being of approximately same size) and thus achieved relatively even coverage of all parts of the country. See Reif *et al.* (2013) for more details on data collection.

The index was calculated as a coefficient of variation of species' density over five habitats, assuming that the density is more variable in the specialist species, which are confined to just a few habitats, than in the generalist species, which are distributed more evenly over habitats (Devictor *et al.* 2008). SSI of breeding bird species in the Czech Republic corresponded well to breadth of species' habitat niche calculated by other measures, as well as to the expert-based classification (Reif *et al.* 2010).

Species' life-history was expressed using six traits – body mass, egg mass, number of broods per year, laying date (julian date of the beginning of laying in the first breeding), clutch size and length of incubation expressed as mean values from published data (Št'astný and Hudec 2011). As these traits were closely correlated (e.g. Sæther 1988; Stearns 1992), we used principal component analysis (PCA) to reduce many correlated variables into a smaller number of independent axes (see Koleček and Reif 2011). PCA identified two clear patterns within the assemblage of analyzed species (Fig. 1). The first ordination axis (PC 1, explaining 41.8% of the variability among species) expressed a gradient from 'r-selected' species with fast life histories (i.e. those having small eggs, small body mass, multiple broods and large

clutch sizes) to ‘K-selected’ species with slow life histories. The second axis (PC 2, explaining 23.0% of variability) depicted an independent gradient from species allocating most of their energy to just one breeding attempt per season – i.e. late breeding species with single broods and smaller clutch sizes to species spreading their investments to multiple breeding attempts per season – i.e. earlier breeding species with multiple broods and larger clutch sizes.

We related the threat level to the focal explanatory variables, i.e. SSI, PC1 and PC2, using linear mixed effect models (library nlme, R Development Core Team 2005). The models included all possible combinations of particular variables and their twofold interactions as fixed effects. Model performance was assessed using Akaike Information Criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002). Across all component models, we applied model averaging to reveal the parameter estimates for the explanatory variables with their 95% confidence intervals (Bartoń 2009). We centered the predictors at the mean which is necessary for correct interpretation of interaction effects between continuous explanatory variables (Schielezeth 2010). Moreover, such centering enables comparison of explained variability among variables using their regression coefficients (Schielezeth 2010).

To control for a potential impact of common evolutionary history on the observed relationships, we included bird phylogenetic relatedness expressed as genus nested in family as random effects in all models (see Lockwood *et al.* 2002).

Results

According to the AIC_c -based assessment of all possible combinations of the explanatory variables, species’ threat level was related to both species’ habitat specialization and position along r-K continuum (as expressed by PC1; Table 1, Table 2). The species’ position along the gradient of energy allocation into breeding attempts (PC2) was not present in the best model (Table 1) and its model averaged confidence interval overlapped zero (Table 2). Increasing habitat specialization and slower life history were associated with higher threat levels of passerine bird species (Table 2). The values of the model averaged coefficients of these variables indicate that the habitat specialization is a stronger predictor than life history. Interestingly, these variables also show a negative interaction effect with confidence limits not overlapping zero (Table 2). The model containing this interaction was ranked highest among all candidate models with a weight of 0.48 and AIC_c being by 2.80 smaller than the best ranking model without this interaction. This interaction signifies that the threat level is

higher in the habitat specialists with slow life histories than in the specialists with fast life histories, but the reverse is true for habitat generalists. In other words, while the slow life history increases the risk of extinction in habitat specialist species, it reduces such risk in habitat generalists.

According to the random part of the linear mixed effect models, phylogenetic relatedness did not play a significant role. Family and genus level comprised each only less than 0.01% of variability (overall variance less than 0.01). Residual variance accounted for more than > 99.9% of variability in random effects (variance = 0.72).

Discussion

Species' national threat level is strongly positively related to increasing habitat specialization and species position along slow-fast continuum, whereas the timing of breeding and the number of breeding attempts do not affect the level of threat. Thus, the results met our first two expectations. Interestingly, the significant interaction suggests that the effect of species' habitat specialization differs with respect to life history. While the slow life history increases the risk of extinction in habitat specialist species, it reduces such risk in habitat generalists.

The habitat specialization makes the species at higher risk of regional extinction, probably due to their sensitivity to human-induced environmental perturbations which are more frequent in recent years (Devictor *et al.* 2008). Our results from Central Europe also correspond with the study of Owens and Bennett (2000) showing that the habitat specialists are at the highest risk of extinction due to habitat loss at the global scale. We have confirmed that this effect probably matters at smaller spatial scales too. This is in accordance with widely reported population declines of specialist species across Europe (Le Viol *et al.* 2012). Despite a clear pattern of higher threat for specialist species (but see Dapporto and Dennis 2013), it is less clear which mechanisms make the specialists at a higher extinction risk than the habitat generalists. For specialists, we can speculate that if all local populations of a given species utilize the same resources, then simultaneous resource depletion over a larger region should result in immediate extinction risk of the whole species. By contrast, populations of habitat generalists are often composed of several subpopulations living in different habitats (Hernandez *et al.* 2006) and these habitats rarely would be depleted together. Moreover, individuals of the generalist species can be more flexible in terms of habitat use than the individuals of the habitat specialists and this individual ability could buffer deterioration of certain habitats. Finally, habitat generalists often occupy new environments like urban or

exotic habitats (Devictor *et al.* 2007) that spread over the globe, while habitat specialists are more associated with more natural habitats (Ricklefs 2011) undergoing destruction.

The interaction effect of species' life history shed a new light on the relationship between habitat specialization and threat level. The most threatened habitat specialists are those with slow life histories, whereas the specialists with faster life histories are under lower extinction risk. Species with fast life histories typically express high fecundity (Sæther *et al.* 2005) and we can thus speculate that higher recruitment in their populations can compensate the influence of factors connected to high habitat specialization to some degree. Alternatively, the fast life history species have a small body size, which is negatively correlated with total population size (Nee *et al.* 1991). Therefore, the specialist species with fast life histories can have a higher regional abundance than the specialists with slow life histories and this can result in a lower threat level for the former and higher for the latter ones.

An opposite pattern we found in habitat generalists. This is in accord with the finding of Sol *et al.* (2012), who observed a higher success of slow-strategy species in avian invasions. These species are able to allocate more energy to the future reproduction, can wait for optimal environmental conditions and then enjoy their positive effects leading to more favorable population status in the long-term (Sol *et al.* 2012). We suggest this mechanism is possible for habitat generalists that are not so heavily affected by habitat destruction as habitat specialists. Alternatively, advantages of slow life histories for habitat generalists can be also connected with body size. Because generalist species often dwell in urbanized landscapes with a high abundance of potential nest predators such as domestic cats (Beckerman *et al.* 2007), a large body size will be advantageous during nest defence (Götmark and Post 1996) and can thus lower nest predation resulting in lower extinction risk in species with slower life histories than in the species with faster life histories. Moreover, large passerine species such as corvids also have relatively larger brains than small passerines showing better cognitive ability and higher behavioural plasticity (Sol *et al.* 2005). These characteristics widen an array of opportunities available for bird species in disturbed landscapes and under conditions of environmental changes (Reif *et al.* 2011).

From a conservation perspective, our results indicate that the negative impact of habitat deterioration is a dominant factor for elevating the species' extinction risk, as suggested by a strong effect of species' habitat specialization. However, abilities of species to cope with these adverse environmental changes largely depend on their life history strategy, at least for central European passerine birds. We suggest this finding should be taken into account during guiding conservation planning and management targeted on improving

population status of the threatened species. Clearly, specialist species with fast life histories will need different approaches than the specialists with slower life strategies.

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Table 1. Characteristics of multipredictor linear mixed effect models assessing the relationships between the threat level and habitat specialization (SSI) and life history traits (expressed as two independent principal component axes, PC1, PC2) in 87 passerine species breeding in the Czech Republic. The models are ordered according to their explanatory power as revealed by Akaike information criterion (AICc).

Model	No. of params	AICc	Δ AICc	AICc weight
PC1 + PC2 + PC1 \times SSI	4	233.71	0.00	0.48
PC1 + PC2 + SSI + PC1 \times SSI	5	236.00	2.29	0.15
PC1 + SSI	3	236.51	2.80	0.12
SSI	2	236.96	3.25	0.09
PC1 + PC2 + SSI + PC1 \times SSI + PC2 \times SSI	6	238.28	4.57	0.05
PC1 + PC2 + SSI	4	238.49	4.78	0.04
PC2 + SSI	3	238.89	5.18	0.04
PC1 + PC2 + SSI + PC2 \times SSI	5	240.92	7.21	0.01
PC2 + SSI + PC2 \times SSI	4	241.25	7.54	0.01
Null	1	279.91	46.20	< 0.01
PC2	2	281.19	47.48	< 0.01
PC1	2	281.34	47.63	< 0.01
PC1 + PC2	3	282.67	48.96	< 0.01

Table 2. The model averaged coefficients based on the Akaike Information Criteria (AIC_c) of all multipredictor linear mixed effect models assessing the relationships between the threat level and habitat specialization and life history traits in 87 passerine species breeding in the Czech Republic. The species-specific explanatory variables (centered at mean) are: habitat specialization index (SSI) and two life-history axes as revealed by PCA (PC1, PC2). See the Materials and methods section for definition of particular variables. The terms whose 95% confidence intervals (CI) did not overlap zero are printed in bold.

Trait variable	Estimate	Lower CI	Upper CI
PC1	-0.15	-0.29	-0.01
PC2	-0.04	-0.21	0.13
SSI	2.21	1.63	2.78
PC1 × SSI	-0.59	-1.12	-0.05
PC2 × SSI	0.08	-0.48	0.64

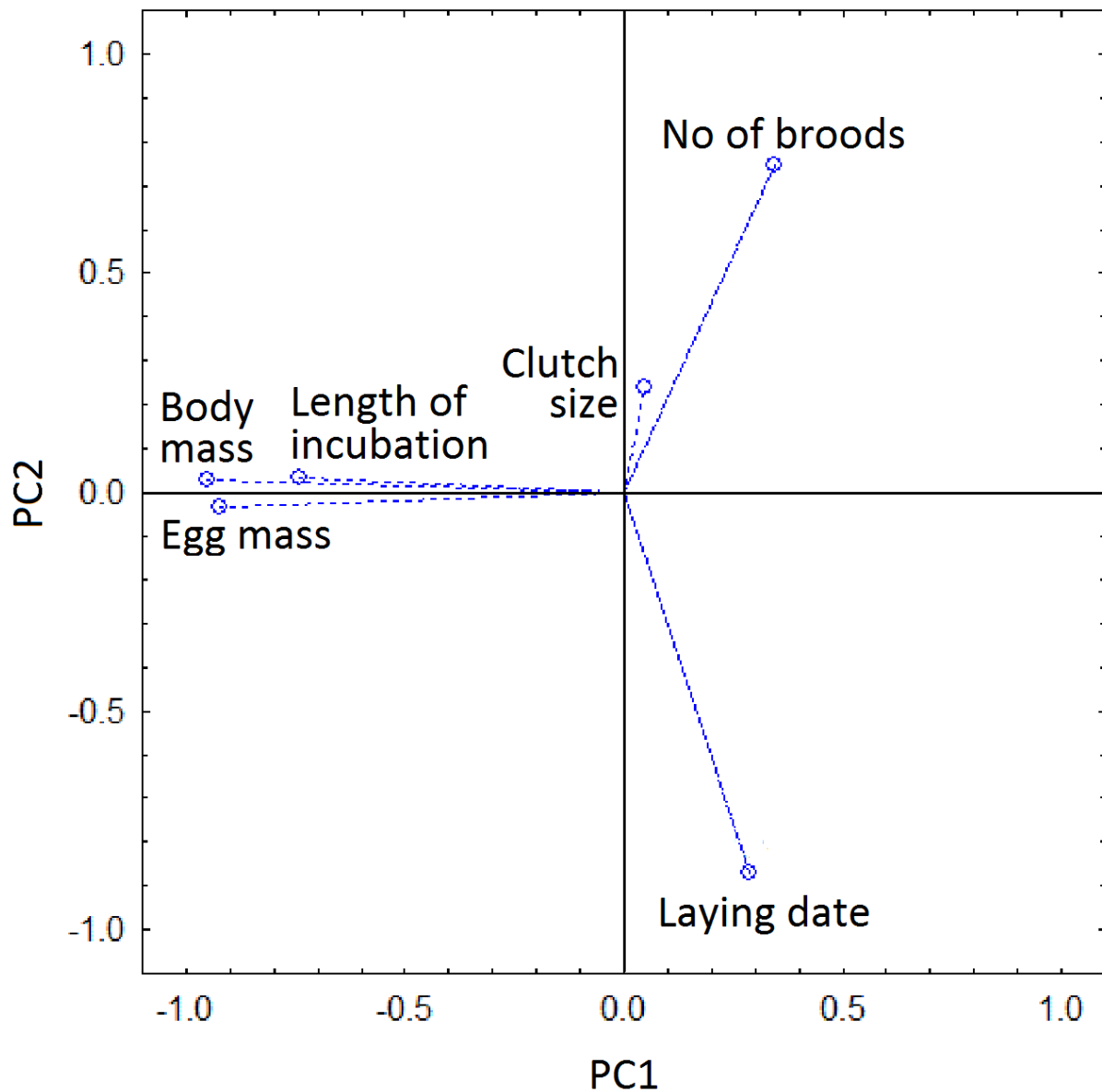


Figure 1. The two most important ordination axes, revealed by a principal component analysis, explaining the largest proportion of variability among six life history traits (i.e. body mass, egg mass, number of broods per year, clutch size, laying date and length of incubation) in 87 passerine bird species breeding in the Czech Republic.

Table S1. The traits of 87 bird species used in the analyses: threat level according to the national IUCN Red List (threat; Šťastný and Bejček 2003), habitat specialization index (SSI) and two most important life history axes as revealed by PCA (PC1, PC2). See the Materials and methods section for definition of particular variables.

Species	Threat	SSI	PC1	PC2
<i>Acrocephalus arundinaceus</i>	2	1.75	-0.21	-1.56
<i>Acrocephalus palustris</i>	0	1.39	0.88	-1.83
<i>Acrocephalus schoenobaenus</i>	0	1.62	0.95	-1.24
<i>Acrocephalus scirpaceus</i>	0	1.49	1.15	-2.29
<i>Aegithalos caudatus</i>	0	0.99	0.91	0.62
<i>Alauda arvensis</i>	0	1.76	0.65	0.98
<i>Anthus pratensis</i>	0	1.94	0.73	0.52
<i>Anthus spinoletta</i>	4	2.45	0.18	0.05
<i>Anthus trivialis</i>	0	1.05	0.71	-0.15
<i>Carduelis cannabina</i>	0	1.21	1.60	0.24
<i>Carduelis carduelis</i>	0	1.07	1.04	-0.02
<i>Carduelis chloris</i>	0	0.97	0.44	0.46
<i>Carduelis flammea</i>	1	0.96	1.78	0.25
<i>Carduelis spinus</i>	0	1.25	1.07	0.27
<i>Carpodacus erythrinus</i>	2	1.03	1.05	-2.51
<i>Certhia brachydactyla</i>	0	1.06	0.25	1.41
<i>Certhia familiaris</i>	0	1.10	0.69	0.99
<i>Cinclus cinclus</i>	0	0.76	-1.96	0.22
<i>Coccothraustes coccothraustes</i>	0	1.01	-0.45	-0.79
<i>Corvus monedula</i>	1	1.02	-6.63	-0.04
<i>Cyanistes caeruleus</i>	0	0.89	0.66	1.19
<i>Emberiza citrinella</i>	0	1.26	0.56	0.77
<i>Emberiza hortulana</i>	4	1.75	0.67	-0.52
<i>Emberiza schoeniclus</i>	0	1.69	0.68	0.55
<i>Erithacus rubecula</i>	0	0.99	0.54	0.60
<i>Ficedula albicollis</i>	1	1.57	0.27	-0.83
<i>Ficedula hypoleuca</i>	1	0.99	0.20	-1.17
<i>Ficedula parva</i>	2	1.64	0.39	-1.78
<i>Fringilla coelebs</i>	0	0.89	0.66	0.66
<i>Galerida cristata</i>	3	1.54	-0.05	0.85
<i>Garrulus glandarius</i>	0	0.94	-4.80	-0.17
<i>Hippolais icterina</i>	0	0.97	0.58	-1.80
<i>Hirundo rustica</i>	0	1.19	0.01	-0.78
<i>Lanius collurio</i>	1	1.46	-0.51	-1.52
<i>Lanius excubitor</i>	2	1.52	-2.03	0.02
<i>Lanius minor</i>	4	1.82	-1.75	-1.21
<i>Locustella fluviatilis</i>	0	1.25	0.63	-2.30
<i>Locustella luscinioides</i>	3	1.92	0.77	-0.79

<i>Locustella naevia</i>	0	1.43	1.22	-0.42
<i>Lophophanes cristatus</i>	0	1.46	-0.18	0.86
<i>Loxia curvirostra</i>	0	1.47	-0.70	3.61
<i>Lullula arborea</i>	3	1.44	0.13	1.59
<i>Luscinia megarhynchos</i>	0	1.50	0.24	-1.52
<i>Luscinia svecica cyanecula</i>	3	1.53	0.27	0.79
<i>Miliaria calandra</i>	2	1.59	-0.02	0.02
<i>Motacilla alba</i>	0	1.14	0.80	0.85
<i>Motacilla cinerea</i>	0	0.75	1.09	1.09
<i>Motacilla flava</i>	2	1.25	0.69	0.19
<i>Muscicapa striata</i>	0	0.99	0.26	-1.51
<i>Nucifraga caryocatactes</i>	2	1.32	-5.33	-0.12
<i>Oenanthe oenanthe</i>	3	2.10	0.31	0.93
<i>Oriolus oriolus</i>	0	1.17	-2.27	-1.86
<i>Panurus biarmicus</i>	3	2.19	1.35	1.70
<i>Parus major</i>	0	0.85	0.70	1.12
<i>Passer domesticus</i>	0	1.35	0.89	2.55
<i>Passer montanus</i>	0	1.15	1.03	1.25
<i>Periparus ater</i>	0	1.30	0.37	0.60
<i>Phoenicurus ochruros</i>	0	1.17	0.32	-0.04
<i>Phoenicurus phoenicurus</i>	0	0.79	0.35	0.81
<i>Phylloscopus collybita</i>	0	0.91	1.00	0.54
<i>Phylloscopus sibilatrix</i>	0	1.14	0.88	-1.09
<i>Phylloscopus trochiloides</i>	1	1.22	1.34	-2.29
<i>Phylloscopus trochilus</i>	0	0.96	0.75	-0.39
<i>Pica pica</i>	0	1.28	-5.77	0.27
<i>Poecile montanus</i>	0	0.98	0.11	0.26
<i>Poecile palustris</i>	0	0.93	0.69	0.79
<i>Prunella modularis</i>	0	0.94	0.98	0.72
<i>Pyrrhula pyrrhula</i>	0	1.05	0.06	-0.41
<i>Regulus ignicapilla</i>	0	1.33	0.67	0.92
<i>Regulus regulus</i>	0	1.44	0.52	1.79
<i>Remiz pendulinus</i>	1	1.69	0.65	0.13
<i>Saxicola rubetra</i>	0	1.80	0.57	-1.34
<i>Saxicola torquata</i>	2	1.47	0.75	1.61
<i>Serinus serinus</i>	0	0.93	1.16	-0.12
<i>Sitta europaea</i>	0	1.00	-0.66	0.02
<i>Sturnus vulgaris</i>	0	1.11	-1.69	0.06
<i>Sylvia atricapilla</i>	0	0.93	1.11	-0.68
<i>Sylvia borin</i>	0	0.97	1.18	-0.94
<i>Sylvia communis</i>	0	1.30	0.93	-0.92
<i>Sylvia curruca</i>	0	1.01	1.37	-0.82
<i>Sylvia nisoria</i>	2	1.90	-0.05	-1.49
<i>Troglodytes troglodytes</i>	0	0.98	-0.07	1.34
<i>Turdus merula</i>	0	0.82	-1.91	1.55
<i>Turdus philomelos</i>	0	0.88	-0.68	1.23

<i>Turdus pilaris</i>	0	1.29	-2.12	0.40
<i>Turdus torquatus</i>	3	1.42	-2.55	-1.38
<i>Turdus viscivorus</i>	0	1.09	-3.08	0.41

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Vzdělání

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2010: RNDr. v oboru Zoologie, Katedra zoologie a Ornitologická laboratoř, PřF UP v Olomouci (rigorózní práce: Rozšíření, biotopická vazba a fenologie vážek okresu Vsetín)

2007–2009: Mgr. v oborech Učitelství geografie pro střední školy – Učitelství biologie v ochraně životního prostředí pro střední školy, Katedra geografie, PřF UP, Olomouc (diplomová práce: Početnost ptáků v lužních lesích střední Moravy)

2004–2007: Bc. v oborech Geografie – Biologie v ochraně životního prostředí (uč.), Katedra geografie, PřF UP v Olomouci (bakalářská práce: Vážky [Odonata] okresu Vsetín)

1996–2004: Gymnázium v Rožnově pod Radhoštěm

Zahraniční vědecko-výzkumné pobyty

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Seznam publikovaných prací

Publikace v odborných časopisech

Mezinárodní impaktované (včetně připravovaných)

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- Koleček J.** 2011: Výzdoba hnízda jako výstraha. *Vesmír* 90: 132–133.
- Koleček J.** 2011: Být slyšen, nebo být milován. *Vesmír* 90: 613–614.
- Koleček J.** 2011: Nebojte se mapovat doupné stromy! *Krása našeho domova* 2/11(53): 6–7.
- Koleček J.** 2012: Za ptačím putováním. *Zpravodaj CHKO Beskydy* 3/2012: 10.
- Koleček J. & Hošek J.** 2012: Poznáte pěnkavy? *Ptačí svět* 2/2012: 3–5.
- Koleček J.** 2012: Využití UV záření při určování stáří sov. *Kroužkovatel* 13: 8.
- Koleček J. & Cepák J.** 2012: Kroužkování ptáků a ekologická výchova. *Kroužkovatel* 13: 13–14.
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Recenzní činnost

- Sylvia (1×), Panurus (1×), Zprávy MOS (1×), Acrocephalus
- oponentské posudky na bakalářské (3×) a diplomové práce (1×)

Další odborná činnost

- vedení a konzultace středoškolských odborných (3×), bakalářských (3×) a diplomových prací (1×)
- předseda Moravského ornitologického spolku – středomoravské pobočky ČSO
- člen redakční rady časopisu *Kroužkovatel*
- správa webových stránek časopisu Sylvia
- projektová činnost, pořádání přírodovědných přednášek a exkurzí
- mediální prezentace