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Ekologie strnada rákosního *Emberiza schoeniclus* v rybničních podmínkách

disertační práce

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Prohlášení

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Zuzana MUSILOVÁ

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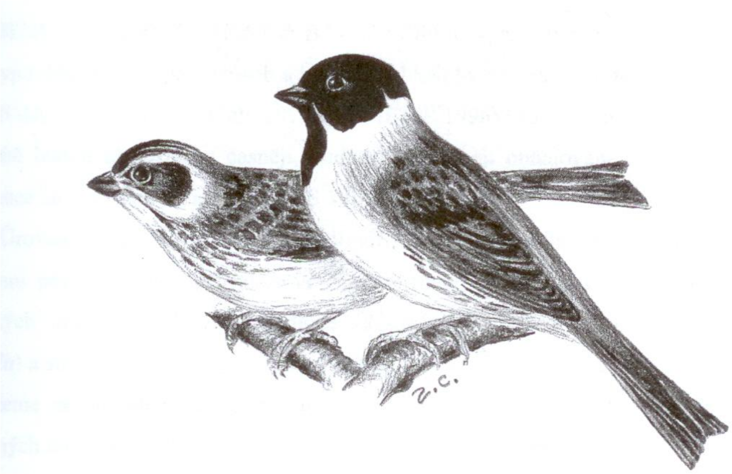
Strnad rákosní *se zdržuje pouze tam, kde na bažinatých místech rostou vysoké vodní rostliny, rákosí, orobinec, ostřice, vrboví, tedy u rybníků, řek, břehů jezerních a na mokrých lukách. Tam také hnízdí. Hnízdo bývá velmi skrytě umístěno na půdě malých ostrovů a jiných vodou nepokrytých místech... Dvakrát za léto, v květnu a počátkem července, nacházíme v něm 4 až 6 úhledných vajíček... Samice sedá na vejcích velmi pevně; samec přilétá jakmile se k hnízdu blížíme, úzkostně a velmi naříká. Podle všeho bývá samice v poledních hodinách na krátkou dobu samcem vystřídána. Mláďata líhnou se po 12 až 14 dnech a bývají obvyklým způsobem vyživována a vychovávána. Strnad rákosní jest čilý, úhledný pták... Jeho vábení jest jasné, protáhlé „cíií“, zpěv pak, jak Neumann velmi příhodně praví, jest koktavý: „strnad rákosní škrtí takřka jednotlivé tóny ze sebe“. Zpívá pilně...*

Alfred Brehm 1928. Brehmův život zvířat. přel. J. Janda, díl III., svazek IV., str. 351–352.



ÚVOD a SHRNUTÍ

> *„It would appear that, in response to a stable and predictable resource, many species have evolved a strategy of returning to the same network of areas throughout their life cycle...When wetland habitat is predictable, this is a good strategy, but increasingly, human disruption to annual cycles makes this a strategy that is less likely to ensure survival and successful reproduction.“*
>
> Tony Fox in Kear 2005: Duck, Geese and Swans, p 134

Studium ptačí „life-history“ počínaje variabilitou ve velikosti a počtu vajec, přes dobu inkubace, počet snůšek za rok, až po přežívání mláďat a dospělců patří mezi již tradičně zkoumané odvětví ornitologie (Lack 1968, Owen & Black 1990, Newton 1998, Kear 2005, Benett & Owens 2005). Takřka ve všech stadiích svého životního cyklu jsou ptáci ohrožováni na životě, ať již z důvodů nedostatku potravy, predace, nepříznivého počasí, nemocí nebo lidskými zásahy (Benett & Owens 2005). V rámci ptačí říše existuje vysoká variabilita, jak se s těmito omezeními vyrovnat. Pomocí přírodní selekce dochází k optimalizaci investic do růstu, přežívání a reprodukce (např. Lack 1954, Lack 1968, Charnov & Krebs 1974). Tyto tři okruhy spolu velice úzce souvisí. Růst je náročný a snižuje energetické zásoby, které by mohly být investovány do reprodukce. Obdobně reprodukce omezuje následné přežívání (Lack 1968, Owen & Black 1990). Přírodní výběr v podstatě neumožňuje maximalizaci růstu a přežívání všech věkových kategorií a zároveň maximalizaci reprodukce. Tento fakt vede k pozitivnímu vztahu mezi věkem v době prvního zahnízdění a následným přežíváním, a také ke vztahu negativnímu mezi počtem snůšek za rok a přežíváním (Partridge & Harvey 1988). Benett & Owens (2005) se pokusili s použitím vícerozměrných korelačních analýz shrnout klíčové vztahy v rámci *life history* u více než 2000 druhů ptáků a zjistili následující pozitivní korelace: váha samice koreluje s váhou vajec a, váha vajec koreluje s dobou inkubace, inkubace ovlivňuje dobu strávenou péčí o mláďata a věk při prvním zahnízdění, který pozitivně koreluje s přežíváním dospělců. Jediný negativní vztah byl zjištěn mezi reprodukčním úsilím (celkový počet snůšek za rok, velikost snůšky) a přežíváním v dospělosti. Při snaze o optimalizaci výše uvedených parametrů vstupují do hry také ekologické faktory, jako např. potravní specializace, reprodukční strategie (altriciální, prekociální druhy) a strategie přežívání (*„fast“ and „slow“ life histories*) (Lack 1968, Owen & Black 1990, Newton 1992, Benett & Owens 2005, Kear 2005).

Zmíněné ekologické faktory se často projevují zejména v rychle se měnících podmínkách různých typů ekosystémů vystavených dlouhodobým antropogenním vlivům (Newton 1998). Mokřady patří k nejvíce ohroženým ekosystémům naší planety (Finlayson & Moser 1991, Boere *et al.* 2006). V podmínkách střední Evropy byly mokřady po staletí ohrožovány vysoušením a přeměnou v zemědělsky využívané plochy či přímo v zastavěné oblasti, čímž došlo k jejich nynější fragmentaci (Chytil *et al.* 1999). Sledování rozsahu těchto změn i jejich dopadu na celá rostlinná i živočišná společenstava je z mnoha metodických důvodů značně problematické (Musil 2005). V této souvislosti bývají využívány určité modelové organismy, mnohdy označované jako indikátory, které změnami své početnosti, distribuce, ekologie i etologie odrážejí celkové změny zmíněných společenstev. Velice často jsou takto využíváni právě ptáci, které upřednostňuje mimo jiné právě jejich relativně snadná zachytitelnost, propracovanost metod výzkumu i jejich terminální či sub-terminální postavení v potravních řetězcích (Bibby *et al.* 1992, Wiens 1992, Perrins *et al.* 1993, Newton 1998, Musil 2005). Tento klíčový význam ptáků byl rozpoznán i v samotných počátcích snah o celosvětovou ochranu mokřadních biotopů. Ne náhodou byla tzv. Ramsarská úmluva v roce 1971 oficiálně nazvána jako *Úmluva o mokřadech majících mezinárodní význam především jako biotopy vodního ptactva* (Chytil et al. 1999, Finlayson & Moser 1991, Boere *et al.* 2006) I mezi vodními a mokřadními druhy ptáků najdeme velké spektrum druhů lišících se mimo jiné potravní specializací, životní strategií, migračním chováním, tělesnou velikostí a v neposlední řadě i vztahem člověka k těmto druhům. Možná právě proto většina vodních a mokřadních druhů ptáků na našem území ubývá nebo přibývá, a to jak v době zimování (Musilová *et al.* 2009, Musil *et al. subm.*), tak v době hnízdění (Musil 2000, Šťastný *et al.* 2006).

Mezi rákosinné druhy pěvců řadíme i strnada rákosního *Emberiza schoeniclus* (např. Blümel 1989, van Vessem & Trucker 1997), který představuje vhodný modelový druh.

Rozšíření rákosinných druhů úzce souvisí s jejich nároky na prostředí (Leisler 1975, Leisler 1981, Leisler *et al.* 1989, Báldi *et al.* 1998, Báldi & Kisbenedek 1999, Martínez-Vilalta *et al.* 2002). V rámci této skupiny se strnad rákosní jeví spíše jako méně specializovaný, je schopen okupovat širší škálu mokřadů a může také inklinovat k sušším biotopům (Martínez-Vilalta *et al.* 2002, Grujbárová *et al.* 2005). Mnohými studiemi bylo zjištěno, že migrující jedinci se snaží navrátit na svá hnízdiště co nejdříve, aby získali výhodu při kompetici o teritoria před ostatními (Hopp *et al.* 1999, Klemp 2003, Sergio & Newton 2003, Tryjanowski *et al.* 2004, Sergio *et al.* 2007). Tyto později přilétající druhy se snaží obsazovat teritoria obývaná v předchozím roce. Naopak druhy, které se navracejí na svá hnízdiště brzy na jaře, v době méně příznivých klimatických podmínek, se po příletu shlukují do potravních hejn. Tato seskupení pravděpodobně slouží k vylepšení jejich tělesné kondice (Newton 2008). Strnad rákosní patří do této druhé skupiny časně přilétajících druhů (*early-arriving species*) (Blümel 1989, Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997). Dále se vyznačuje různými typy zpěvu samců v závislosti na momentálním reprodukčním statutu (Nemeth 1996, Suter *et al.* 2009).

V první části (**Kapitola I.**) byly testovány otázky výběru hnízdního prostředí v souvislosti s načasováním hnízdění, hnízdní úspěšností a věkem samic. Jak již bylo zmíněno, strnad rákosní patří v rámci rákosinných druhů pěvců k méně specializovaným (Blümel 1989, Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997, Báldi & Kisbenedek 1999). V našich podmínkách obývá širokou škálu mokřadních biotopů (litorální a příbřežní porosty rybníků, zbytky vlhkých luk, úhory, pravidelně kosené louky, příbřežní porosty podél drobných vodních toků, rašeliniště ap.) (Hudec 1983, Šťastný *et al.* 2006). Méně specializované druhy (*habitat generalists*) jsou pravděpodobně schopny nejen obývat širší škálu biotopů, ale také lépe využívat dostupné zdroje (Brown 1984) včetně výběru místa k zahnízdění. Při studiu hnízdní biologie strnada rákosního na jihočeských rybníkách nás zajímaly především otázky preference mikrohabitatu pro umístění hnízda během hnízdní sezony, vliv tohoto výběru na hnízdní úspěšnost a vliv zkušenosti samice vyjádřený věkem na preferenci hnízdního mikrohabitatu. Předpokládali jsme, že kvalitnější samice budou schopny okupovat optimální místa k zahnízdění, přičemž kvalita těchto jedinců byla vyjádřena pomocí načasování hnízdění, hnízdní úspěšnosti a zkušenosti resp. věku. Přežívání a pravděpodobnost vyvedení dříve snesených snůšek bývá vyšší než u pozdějších hnízdních pokusů (Lack 1968, Perrins 1970, Benett & Owens 2005), obdobně starší jedinci mají vyšší reprodukční úspěšnost než mladší méně zkušení (Curio 1983, Geslin *et al.* 2004).

Zjistili jsme, že samice jeví tendenci okupovat obdobná místa k zahnízdění během celého hnízdního období (tedy v průběhu vegetační sezony), včetně obdobné výšky vegetace a stejného podílu vegetace loňské v bezprostředním okolí hnízda. Starší a tedy zkušenější samice navíc preferovaly nižší vegetaci. Tyto výsledky naznačují potřebu samice orientovat se v okolí a uniknout před potencionálním predátorem, případně rozhodnout možnou obranu hnízda (Curio 1978, Halupka & Halupka 1997). Vzhledem k tomu, že nebyl potvrzen předpokládaný vztah mezi načasováním hnízdění a hnízdní úspěšností (resp. denní mírou přežívání hnízd), domníváme se, že samice se snaží minimalizovat efekt načasování i pomocí vhodného výběru mikrohabitatu hnízda během dlouhé hnízdní sezony. Kromě toho ptáci otevřené krajiny, jako je strnad rákosní, hnízdící na zemi, jsou vystaveni vysokému predačnímu tlaku, a individuální reprodukční úspěšnost je proto vysoce variabilní (Newton 1992). Zjistili jsme také, že starší samice hnízdí dříve než dvouleté nezkušené samice, jak dokládají mnohé studie (např. Harvay *et al.* 1985, Dhont 1989, Geslin *et al.* 2004), pravděpodobně z důvodů možnosti opětovného zahnízdění. Zajímavé bylo také zjištění, že starší samice narozdíl od dvouletých nepreferovaly ostřicové porosty (*Carex spp.*), které jsou na sledovaných lokalitách původnější než ostatní využívané druhy litorálu, např. třtina křovištní *Calamagrostis epigeios* a chrastice rákosovitá *Phalaris arundinacea* (Janda *et al.* 1996, van Vessem & Trucker 1997). Preference nepůvodních porostů zkušenými samicemi může souviset s poměrně velkou přizpůsobivostí daného druhu při výběru vhodného hnízdního mikrohabitatu.

Výsledky naší studie (Kapitola I.) naznačují vyšší odolnost strnada rákosního vůči vnějším zásahům do mokřadních ekosystémů v podmínkách intenzivně obhospodařovaných jihočeských rybníků v porovnání s více specializovanými rákosinnými druhy (např. rákosník velký *Acrocephalus arundinaceus*, rákosník obecný *Acrocephalus scirpaceus*, cvrčilka slavíková *Locustella luscinioides).* Tuto skutečnost podporuje i stabilní početnost strnada rákosního u nás v porovnání s ubývajícími druhy rákosníků a cvrčilek (Musil 1999, Musil 2000, Šťastný *et al.* 2006). Naopak klesající trend strnada rákosního byl zjištěn ve Velké Británii, Belgii a Francii (BirdLife International 2004), kde tento druh jeví tendenci obsazovat nepůvodní biotopy v kulturní zemědělské krajině (Gregory & Baillie 1998, Siriwardena *et al.* 2000).

Významem fragmentovaných mokřadních biotopů pro strnada rákosního v rybničnaté krajině jižních Čech jsme se zabývali dále při studiu fidelity (návratnosti na hnízdiště) a obsazování teritorií (**Kapitola II.**). Fidelita je u pěvců široce rozšířena, dospělí jedinci se v takovém případě snaží vracet na místo předchozího hnízdění opakovaně (Greenwood & Harvey 1982, Berthold 2001, Klemp 2003, Newton 2008). Většina druhů s vysokou fidelitou má nízkou filopatrii (návratnost na rodiště). Fidelita s sebou nesporně nese řadu výhod, jako např. lokální znalost prostředí (potravní zdroje, úkryty ap.), adaptaci na lokální podmínky nebo znalost místních kompetičních a sociálních vztahů (např. Greenwood 1980, Berthold 2001, Newton 2008). Naopak výhody disperse jsou následující: vyhledání výhodnějšího prostředí (např. v habitatech s probíhající sukcesí, meziročně se měnících potravních zdrojích ap.) a redukce příbuzenského křížení (*inbreeding*) (Verhulst *et al.* 1997, Berthold 2001, Hansson *et al.* 2002a, Hansson *et al.* 2002b, Calabuig *et al.* 2008). Zdá se, že strnad rákosní se přiklání k výhodám fidelity a vykazuje nízkou filopatrii. Tento jev se odráží nejen v podmínkách jihočeských rybníků, ale na celém našem území, jak dokládají údaje ze zpětných hlášení shromážděných Kroužkovací stanicí Národního Muzea v Praze (Musilová 2008). Vzhledem k tomu, že strnad rákosní patří mezi druhy, které přilétají na svá hnízdiště brzy na jaře a poté tvoří potravní hejna (viz výše), zabývali jsme se v Kapitole II. kromě faktorů ovlivňujícími fidelitu také faktory ovlivňujícími obsazování teritorií po rozpadu těchto hejn. Předpokládali jsme nízký vliv tělesné hmotnosti při obsazování teritorií z důvodů intenzivního krmení v předhnízdní době. Dále jsme předpokládali propojení mezi úspěšností při obsazení teritoria a fidelitou v následujících letech. Jedinci, kteří jsou schopni obsadit optimální biotop, se ho budou pravděpodobně snažit získat i v následujících letech. Vliv hnízdní úspěšnosti na fidelitu v následujících letech jsme testovali u jedinců, jejichž hnízda se podařilo nalézt, přičemž jsme očekávali nižší fidelitu v případě neúspěšného hnízdění.

Očekávané propojení mezi úspěšným obsazením teritoria a následující fidelitou se potvrdilo, a to především u samců. Rozdíl mezi pohlavími byl zaznamenán také u návratnosti v následujících letech, kdy častěji kontrolováni byli opět samci, což dokládají i mnohé studie (např. Solonen 1979, Pratt & Peach 1991, Krištín *et al.* 2007, Sedláček & Fuchs 2008, Vadasz C. *et al.* 2008, Schlossberg 2009). Nižší fidelitu samic si vysvětlujeme jejich vyšší mortalitou, jež může být způsobená vyčerpáním během reprodukce zvyšující se s možností opakovaného hnízdění během jednoho roku (Lack 1954, Benett & Owen 2005). Zajímavý výsledek přineslo testování faktorů ovlivňujících úspěšnost při obsazování teritorií. Potvrdil se význam potravních hejn, neboť hmotnost jedinců při obsazování teritorií nehrála roli. Jako úspěšnější se ukázali starší samci. Dvouletí samci jsou tedy pravděpodobně vytlačováni do méně výhodných biotopů (Greenwood & Harvey 1982) a jejich šance na obsazení optimálního teritoria se naskýtá až po získání zkušeností (Pärt 2001). Dále jsme nepotvrdili vztah mezi reprodukční úspěšností a fidelitou, což je v rozporu s obecným předpokladem snížení fidelity po neúspěšném hnízdění (Harvey *et al.* 1979, Howlett *et al.* 2003, Wesołowski 2006, Johnson & Walters 2008, Berkunsky & Reboreda 2009). Domníváme se, že nedostatek hnízdních možností na sledovaných lokalitách, a tedy vysoká kompetice mezi samci, vede k tomu, že na sledovaných lokalitách tento obecný předpoklad neplatí. Podporu pro toto tvrzení lze hledat i mezi dalšími studiemi, které zmíněný vztah nepotvrdily (Gavin & Bollinger 1988, Haig & Oring 1988, Payne & Payne 1993, Pyle *et al.* 2001, Shutler & Clark 2003, Hallworth *et al.* 2008) a předpokládají nižší vliv reprodukčního úspěchu na fidelitu v optimálních biotopech, které jsou okupovány v každém případě (Greenwood 1980, Newton 2008).

Tato studie dokládá propojení mezi obsazováním teritorií v téže sezoně a fidelitou v následujících letech. Oba jevy jsou limitovány nedostatkem vhodných teritorií u samců, u samic pak hraje významnou roli vyšší mortalita. Samci a samice se pravděpodobně liší ve své *life-history* rozdílným věkem při prvním zahnízdění. Velká kompetice a nedostatek hnízdních habitatů, které jsou okupovány převážně víceletými zkušenými samci, odhaluje klíčovou roli fragmentovaných rybničních biotopů pro tento studijní druh.

> *„All those who have attended to the subject, believe that there is severest rivalry between the males of many species to attract by singing the females."*
>
> Charles Darwin 1859. On the Origin of Species. 1st Edition, pp 88–89

Ptačí zpěv má nepochybně dvě hlavní funkce. Intrasexuální funkce se uplatňuje při obraně teritoria před případnými vetřelci stejného pohlaví (*male-male competition*), naopak intersexuální funkce zpěvu slouží k nalákání samic a jejich stimulaci k hnízdění (*mate choice*). Nezbytným předpokladem pro posouzení kvality samce pomocí zpěvu, pokud jej hodnotí soupeř nebo samice, je nutná náročnost a tedy tzv. „čestnost" (*honesty)* tohoto signálu (Zahavi 1975, Grafen 1990). Tyto požadavky zpěv splňuje, neboť je značně energeticky náročný a odráží rozdíly v raném období vývoje samce (Nowicki *et al.* 1998). Zpěv zároveň odráží komplexní obraz reprodukčního chování, který je vysoce variabilní napříč jednotlivými druhy. Při obou funkcích zpěvu se uplatňují specifické parametry (Marler & Slabbekoorn 2004). Lze je rozdělit do čtyř hlavních kategorií: celkový výkon při zpěvu (*song output*), komplexita zpěvu (*song complexity*), konkrétní prvky (*local song structure*) a vlastní provedení zpěvu (*vocal performance*), viz např. Marler & Slabbekoorn 2004, Searcy & Nowicki 2005. Použití konkrétních parametrů se mezi jednotlivými druhy liší, přičemž může vnitrodruhově docházet i k jejich kombinaci (Marler & Slabbekoorn 2004). Intenzita provedení první kategorie, která konkrétně představuje celkové množství vyprodukovaného zpěvu během jednotky času (*song rate*), v naprosté většině případů pozitivně koreluje s úspěšností konkrétního jedince při lákání samic i obhajobě teritoria. Samice při párování jednoduše preferují samce, kteří zpívají s větší intenzitou (např. Radesäter *et al.* 1987, Eens *et al.* 1991, Collins *et al.* 1994). Čestnost tohoto signálu je spojována s energetickou náročností jeho provedení. S*ong rate* může také narůstat s dostupností potravy (Gottlander 1987).

Vhodným modelovým druhem při studiu samčího zpěvu a jeho funkce je strnad rákosní (*Emberiza schoeniclus*). Bylo zjištěno, že samci tohoto druhu používají různé typy zpěvu. Pokud je samec nespárovaný, což znamená, že samici se mu ještě nepodařilo získat nebo o ni přišel, používá tzv. rychlý typ zpěvu (I.). Spárovaný samec zpívá tzv. pomalým typem zpěvu (II.) (Nemeth 1996). Pomalý zpěv může mít kontinuální průběh, kdy vzniká třetí typ zpěvu (III.). Dochází tedy ke zvýšení intenzity zpěvu (*song rate*). S velkou pravděpodobností se v případě třetího typu zpěvu jedná o čestný signál kvality, který se uplatňuje při lákání samic. Tento fakt byl zjištěn při studiu mimopárové paternity (Suter *et al.* 2009). Během inkubace a krmení mláďat byl navíc zkoumán tzv. „all-clear“ signál, který slouží k nesexuální akustické komunikaci mezi zpívajícím samcem a inkubující samicí. Samice, která sedí na vejcích nebo krmí mláďata, se může bezpečně vzdálit, aniž by ohrozila hnízdo prozrazením, neboť samec zpívající poblíž hnízda signalizuje, že nehrozí žádné nebezpečí (Wingelmaier *et al.* 2007). Tři typy zpěvu strnada rákosního, kromě „all-clear“ signálu, byly definovány na základě analýzy hlasových nahrávek (Nemeth 1996, Suter *et al.* 2009).

Zmíněné typy zpěvu tedy s velkou pravděpodobností slouží právě při *mate choice* (Nemeth 1996). Přikláníme se k tomuto tvrzení, neboť podle našich nepublikovaných dat se při samčí kompetici (*male-male competition*) projevuje tzv. *overlapping*. Atakující samec se snaží vlastním zpěvem překrýt současně zpívajícího samce (Dabelsteen *et al.* 1996). Momentální způsob zpěvu určený samicím zřejmě není při překrývání (*overlappingu*) překážkou (nepubl. data), v tomto případě zpěv samců plní svoji duální funkci (Marler & Slabbekoorn 2004, Searcy & Nowicki 2005). Nás ovšem zajímala především intrasexuální funkce zpěvu samců. V **kapitole III.** jsme se zabývali načasováním různých typů zpěvu strnada rákosního v průběhu hnízdní sezony a vztahem mezi těmito typy zpěvu a různými fázemi hnízdění (předhnízdní období, týden před snesením prvního vejce, období snášení vajec, inkubace, krmení mláďat v hnízdě, krmení vylétlých mláďat, více než dva týdny po vyvedení mláďat, predace nebo opuštění snůšky) a počtem obsazených teritorií na lokalitě. Předpokládali jsme nárůst III. typu zpěvu (čestného signálu kvality) ve fertilní fázi samice (týden před snesením prvního vejce a období snášení vajec) a naopak pokles tohoto typu v době inkubace a krmení mláďat v hnízdě a naopak nárůst typu II. Předpovídali jsme tedy, že „all-clear“ nesexuální signál samici v době inkubace a krmení mláďat bude náležet zpěvu typu II (spárovaný samec).

Při analýze nahrávek jsme zjistili, že v průběhu hnízdní sezony není žádný výrazný trend v použití třech typů zpěvu. Toto zjištění patrně souvisí s neobvyklou délkou hnízdní sezony (březen až červenec) a poměrně zanedbatelnou synchronizací hnízdících párů v důsledku možnosti náhradního hnízdění (viz kapitola I). Naopak v průběhu jednotlivých hnízdních fází se typy zpěvu významně lišily. Potvrdili jsme funkci rychlého a pomalého zpěvu podle Nemetha (1996), přičemž zpěv nespárovaných samců se vyskytoval v předhnízdním období, ve stadiu samostatných mláďat a v případě predace nebo opuštění snůšky. Ve všech těchto případech lze spekulovat o absenci samice v teritoriu samce. Při predaci nebo opuštění snůšky se mohlo dokonce jednat o její uhynutí. V ostatních fázích, kdy bylo možné prokázat hnízdění a tedy přítomnost samice, nebyl zjištěn jediný záznam rychlého zpěvu samce. Kontinuální zpěv třetího typu (signál kvality) převažoval v období před snesením prvního vejce, kdy dochází ke kopulacím (Marthinsen et al. 2005). Překvapivé ovšem bylo zjištění, když jsme porovnali podíl typu zpěvu II. a III. ve fertilní fázi samice a poté při inkubaci a krmení mláďat. V obou obdobích byl tento podíl vyrovnaný. Nedošlo tedy k poklesu zpěvu třetího typu, který slouží k lákání samic a nárůstu zpěvu druhého typu, který měl plynule přecházet směrem ke komunikační nesexuální funkci „all-clear“ signálu (Wingelmaier *et al.* 2007). Vzhledem k tomu, že u strnada rákosního byl zjištěn v rámci pěvců poměrně vysoký podíl mimopárové paternity (Dixon et al. 1994, Bowmann & Komdeur 2005, Bowmann & Komdeur 2006, Kleven & Lifjeld 2005), domníváme se, že zpěv třetího typu v době inkubace slouží především k nalákání samic z okolí k mimopárovým kopulacím. Tuto domněnku potvrzuje i nárůst typu zpěvu III. na lokalitách s vyšším počtem obsazených teritorií, a tedy lepší podmínky pro zvýšení fitness samce pomocí mimopárové paternity.

LITERATURA

Báldi, A. & Kisbenedek, T. 1999. Species-specific distribution of reed-nesting passerine birds across reed-bed edges: effect of spatial scale and edge type. *Acta Zoologica Academiae Scientarum Hungaricae* **45 /2/**: 97–114.

Báldi, A., Moskát, C. & Zágon, A. 1998. Faunal mapping of birds in a riparian area of River Danube after construction of a hydroelectric power station. *Folia Zoologica* **47**:173–180.

Benett, P.M. & Owens, P.F. 2005. *Evolutionary Ecology of Birds.* Oxford University Press, New York.

Bensch, S. & Hasselquist, D. 1991. Territory infidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *J. Anim. Ecol.* **60**: 857–871.

Berkunsky, I. & Reboreda, J.C. 2009. Nest-site fidelity and cavity reoccupation by Blue-fronted Parrots Amazona aestiva in the dry Chaco of Argentina. *Ibis* **151**: 145–150.

Berthold, P. 2001. *Bird Migration: A General Survey,* English edn. Oxford University Press, New York.

Bibby, C.J., Burness, N.D. & Hill, A.D. 1992. *Bird Census Techniques*. Academic Press, London.

BirdLife International 2004. *Birds in Europe: populations, estimates, trends and conservation status*. BirdLife Conservation Series No. 12, Cambridge, UK.

Blümel, H. 1982. *Die Rohrammer.* Die Neue Brehm-Bucherei. Nr. 544. A. Ziemsen, Wittenberg Lutherstadt.

Bouwman, K.M. & Komdeur, J. 2005. Old female Reed Buntings (*Emberiza schoeniclus*) increase extra-pair paternity in their broods when mated to young males. *Behaviour* **142**: 1449–1463.

Bouwman, K.M. & Komdeur, J. 2006. Weather conditions affect levels of extra-pair paternity in the Reed Bunting *Emberiza schoeniclus*. *J. Avian Biol.* **37**: 238–244.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124: 255–279.

Calabuig, G., Ortego, J. Cordero, P.J., & Aparicio, J.M. 2008. Causes, consequences and mechanism of breeding dispersal in the colonial lesser kestrel, *Falco neumanni*. *Anim. Behav.* **76**: 1989–1996.

Collins, S.A., Hubbard, C. & Houtman A.M. 1994. Female mate choice in the zebra finch: The effect of male choice beak colour and male song. *Behav. Ecol. and Sociol.* **35**: 21–25.

Cramp, S. & Perrins, C.M. 1994. *The birds of the Western Palearctic. Vol. IX.: Buntings and New World Warblers.* Oxford UniversityPress, Oxford and New York.

Curio, E. 1978. The Adaptive Significance of Avian Mobbing. I. Teleonomic hypothesis and predictions. *Zeitschrift für Tierpsychologie* **48**: 175–183.

Curio, E. 1983. Why do young birds reproduce less well? *Ibis* **125**: 400–404.

Dabelsteen, T., McGregor, P.K., Sheppard, M., Whittaker, X. & Pedersen, S.B. 1996. Is the signal of overlapping different from that of alternating duringmatched singing in great tits? *J. Avian Biol.* **27**: 189–194.

Dhont, A.A. 1989. The effect of old age on reproduction of Great Tits *Parus major* and Blue Tits *P.caeruleus*. *Ibis* **131**: 268–280.

Dixon A., Ross D., Omalley S. L. C. & Burke T. 1994. Parental investment inversely related to degree of extra-pair paternity in the Reed Bunting. *Nature* **371**: 698–700.

Eens, M., Pinxten, R. & Verheyen, R.F. 1991. Male song as a cue for mate choice in the European Starling. *Behav.* **116**: 210–238.

Finlayson, M. & Moser, M. (eds) 1991. Wetlands. *IWRB, Slimbridge UK.*

Boere, G.C., Galbraith, C.A. & Stroud, D.A. (eds) 2006. *Waterbirds around the world.* TSO Scotland Ltd, Edinburgh, UK.

Gavin, T. A. & Bollinger, E.K. 1988. Reproductive correlates of site fidelity in Bobolinks (*Dolichonyx oryzivorus*). *Ecology* **69**: 96–103.

Geslin, T., Questiau, S. & Eybert, M.C. 2004. Age-related improvement in reproductive success in Bluethroats *Luscinia svecica*. *Bird Study* **51**: 178–184.

Gjerdrum, C., Elphick, C.S. & Rubega, M. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: the importance of nest habitat, timing and study site differences. *Condor* **107**: 849–862.

Glutz von Blotzheim, U. & Bauer, K. (eds) 1997. *Hand buch der Vogel Mitteleuropas.* Ba 14; Anea Verlag, Wiesbaden.

Gottlander, K. 1987. Variation in the song rate of the male pied flycatcher (Ficedula hypoleuca): Causes and consequences. *Anim. Behav.* **35**: 1037–1043.

Grafen , A 1990. Biological sygnals as handicaps. *J. Theor. Biol.* **144**: 517–546.

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematic* 13: 1–21.

Greenwood, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim.Behav.* **28**: 1140–1162.

Gregory, R.D.&Baillie, S.R. 1998. Larg-scale habitat use of a group of declining British birds. *J.Appl.Ecol.* **35**: 785–799.

Grujbárová, Z., Kocian, L. & Némethová, D. 2005. Habitat selection in the sedge warbler (*Acrocephalus schoenobaenus*) and the Reed Bunting (*Emberiza schoeniclus*). *Biologia* **60**: 571–577.

Haig, S.M. & Oring, L.W. 1988. Mate, site and territory fidelity in Piping Plovers. *Auk* **105**: 268–277.

Hallworth, M., Ueland, A., Anderson, E., Lambert, J.D. & Reitsma, L. 2008. Habitat selection and site fidelity of Canada Warblers (*Wilsonia canadensis*) in Central New Hampshire. *Auk* **125**: 880–888.

Halupka, K. & Halupka, L. 1996. The influence of reproductive season stage on nest defence by Meadow Pipits (*Anthus pratensis*). *Ethology Ecology & Evolution* **9**: 89–98.

Hansson, B., Bensch, S. & Hasselquist, D. 2002a. Restricted dispersal in a long-distance migrant bird with patchy distribution, the Great Reed Warbler. *Oecologia* **130**: 536–542.

Hansson, B., Bensch, S. & Hasselquist, D. 2002b. Predictors of natal dispersal in Great Reed Warblers: results from small and large census areas. *J. Avian Biol.* **33**: 311–314.

Harvey, P.H., Stenning, M. J. & Campbell, B. 1985. Individual variation in seasonal breeding success in Pied Fycatchers (*Ficedula hypoleuca*). *J.Anim.Ecol.* **54**: 391–398.

Harvey, P.H., Greenwood, P.J. & Perrins, C.M. 1979. Breeding area fidelity to Great Tits (*Parus major*). *J. Anim. Ecol.* **48**: 305–313.

Highsmith, R.T. 1989. The singing behaviour of golden-winged warblers. *Wils. Bull.* **101**: 36–50.

Hopp, S.L., Kirby, A. & Boone, C.A. 1999. Banding returns, arrival pattern and site fidelity of White Eyed Viros. *Wilson Bull.* **111**: 46–55.

Howlett, J.S. & Stutchbury, B.J. 2003. Determinants of between-season site, territory, and mate fidelity in hooded warblers (*Wilsonia citrina*). *Auk* **120**: 457–465.

Hudec, K. (ed.) 1983. *Fauna of ČSSR. Birds III (2).* Academia, Praha.

Charnov, E.L. & Krebs, J.R. 1974. On clutch-size and fitness. *Ibis* **116**: 217–219.

Chytil, J., Hakrová, P., Hudec, K., Husák, Š., Jandová, J., Pellantová, J. 1999: *Mokřady České republiky – přehled vodních a mokřadních lokalit ČR*. Český ramsarský výbor, Mikulov.

Janda, J. & Pechar, L. et al. 1996. *Sustainable use of fishponds in the Třeboňsko protected landscape area and biosphere reserve.* České koordinační středisko IUCN - Světového svazu ochrany přírody Praha a IUCN Gland, Švýcarsko a Cambridge, Velká Británie, 189 pp.

Johnson, M. & Walters, J.R. 2008. Effects of mate and site fidelity on nest survival of Western Sandpipers (*Calidris mauri*). *Auk* **125**: 76–86.

Kear, J. (ed.) 2005. *Duck, Geese and Swans.* Oxford University Press, New York.

Klemp, S. 2003. Altitudinal dispersal within the breeding season in the Grey Wagtail *Motacilla cinerea. Ibis* **145**. 509–511.

Kleven, O. & Lifjeld, J.T. 2005. No evidence for increased offspring heterozygosity from extrapair mating in the Reed Bunting (*Emberiza schoeniclus*). *Behav.Ecol.* **16**: 561–565.

Krištín, A., Hoi, H., Valera, F. & Hoi, C. 2007. Philopatry, dispersal pattern and nest-site reuse in Leader Grey Shrikes (*Lanius minor*). *Biodivers. Conserv.* **16**. 987–995.

Lack D. 1968. *Ecological adaptations for breeding in birds*. Methuen and Co., London.

Lack, D. 1954. *The natural regulation of animal numbers.* Clarendon Press, Oxford.

Leisler, B. 1975. The significance of foot morphology in the habitat separation of Central European *Acrocephalus* and *Locustella* species. *J.Orn.* **119**: 117–153.

Leisler, B. 1981. Die ökologische Einnischung mitteleuropäischer Rohrsänger (*Acrocephalus*, Sylviinae), I. Habitattrennung. *Vogelvarte* **31**: 45–74.

Leisler, B., Ley, H. W. & Winkler, H. 1989. Habitat, behaviour and morphology of *Acrocephalus* warblers: an integrated analysis. *Ornis Scand.* **20**: 181–186.

Martínez-Vilalta, J., Bertolero, A., Bigas, D., Paquet, J.Y. & Martínez-Vilalta, A. 2002. Habitat selection of passerine birds nesting in the Ebro delta reedbeds (NE Spain): management implications. *Wetlands* **22**: 318–325.

Musil, P., Musilová, Z., Fuchs, R.& Poláková, S. Long-term changes in numbers and distribution of wintering waterbirds in the Czech Republic (1966–2008). *Submitted to Bird Study.*

Musil, P. 1999. Monitoring of Water Bird Breeding Populations in the Czech Republic (1988–1997). Vogelwelt 119: 253–256.

Musil, P., Pykal, J. & Janda, J. 1996. *Birds of fishponds in the Třeboň Biosphere Reserve and effect of the most important factors.* In: IUCN (eds): Sustainable use of fishponds in the Třeboňsko protected landscape area and biosphere reserve*:* České koordinační středisko IUCN - Světového svazu ochrany přírody Praha a IUCN Gland, Švýcarsko a Cambridge, Velká Británie: 111–128.

Musil, P. 2000. Monitoring hnízdních populací vodních ptáků. *Sylvia* 36: 6–11.

Musil, P. 2005. Monitoring populací vodních ptáků: 208-223. In: Vačkář, D. (ed.) *Ukazatelé změn Biodiversity*, Academia, Praha, *300 pp.*

Musilová, Z., Musil, P., Poláková, S. & Fuchs, R. 2009. Wintering ducks in the Czech Republic: population size, changes in population trends and distribution. *Wildfowl. Special Issue:* 73–85.

Musilová, Z. 2008. Reed Bunting *Emberiza schoeniclus.* In: Cepák, J., Klvaňa P., Škopek, J., Schröpfer, L., Jelínek, M., Hořák, D., Formánek, J. & Zárybnický J., (eds.) 2008. *Czech and Slovak Bird Migration Atlas.* Aventinum. Praha, Czech Republic. [In Czech with English summary.]

Nemeth, E. 1996. Different singing styles in mated and unmated Reed Buntings Emberiza schoeniclus. Ibis **138**: 172–176.

Newton, I. 1992. *Life time reproduction in Birds.* Academic Press, London.

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

Newton, I. 2008. *The migration ecology of birds.* Academic Press, London.

Nowicki, S., Peters, S. & Podos, J. 1998. Song learning, early nutrition and sexual selectionin songbirds. *Amer. Zoologist* **38**: 179–190.

Okulewicz, J. 1989. Breeding biology and ecology of the Reed Bunting (*Emberiza schoeniclus*) in the region of the Milicz fishpond area. *Ptaki Slaska* **7**:1–39.

Owen, M. & Black, J.M. 1990. *Waterfowl Ecology.* Chapman and Hall, New York.

Pärt, T. 2001. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe. Anim. Behav.* **62**: 379–388.

Partridge, L. & Harvey, P.H. 1988. The ecological context of life history evolution. *Science* **241**. 1449–1455.

Payne, R.B. & Payne, L.L. 1993. Breeding dispersal in Indigo Buntings: Circumstances and consequences for breeding success and population structure. *Condor* **95**: 1–24.

Perrins, C.M. 1970. The timing of birds´ breeding season. *Ibis* **112**: 242–255.

Perrins, C.M., Lebreton, J.D. & Hirons, G.J.M. (eds) 1993. *Bird population studies; relevance to conservation and management.* Oxford University Press.

Pyle, P., Sydeman, W.J. & Hester M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin´s auklets. *J. Anim. Ecol.* **70**: 1088–1097.

Radesäter, T., Jakobsson, S., Andbjer, N., Bylin, A. & Nyström, K. 1987. Song rate and pair formation in the willow warbler, Phylloscopus trochilus. *Anim. Behav.* **35**: 1645–1651.

Searcy, W.A. & Nowicki, S. 2005. *The evolution of animal communication.* Princeton University Press. New Jersey.

Sedláček, O. & Fuchs, R. 2008. Breeding site fidelity in urban Common Redstarts *Phoenicurus phoenicurus. Ardea* **96**: 261–269.

Sergio, F. & Newton, I. 2003. Occupancy as a measure of territory quality. *J. Anim. Ecol.* **72**: 857–865.

Sergio, F., Blas, J., Forero, M.G., Donázar, J.A. & Hiraldo, F. 2007. Sequential settlement and site dependence in a migratory raptor. *Behav.Ecol.* **9**: 811–821.

Schlossberg, S. 2009. Site fidelity of shrubland and forest birds. *Condor* **111**: 238–246.

Siriwardena G. M., Crick H. Q. P., Baillie S. R. & Wilson J. D. 2000. Agricultural habitat-type and the breedimg farmland birds in Britain. *Bird Study* **47**: 66–81.

Solonen, T. 1979. Population dynamics of the Garden Warbler *Sylvia borin* in southern Finland. *Ornis Fenn.* **56**: 3–12.

Suter, S.M., Ermacora, D., Rielle, N. & Meyer, D.R. 2009. A distinct reed bunting dawn song and its relation to extrapair paternity. *Anim. Behav.* **77**: 473–480.

Šťastný K., Bejček V. & Hudec K. 2006. *Atlas of breeding birds in the Czech Republic 2001–2003*. Aventinum, Praha.

Tryjanowski, P., Sparks, T.H., Ptaszyk, J. &Kosicki, J. 2004. Do White Storks Ciconia ciconia always profit from an early return to their breeding grounds? *Bird Study* **51**: 222–227.

Vadász, C., Német, Á., Karcza, Z., Loránt, M., Biró, C. & Csörgő, T. 2008. Study of site fidelity of Acrocephalus Warblers in Central Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae* **54**: 167–175.

van Vessem, J. & Trucker, G.M. 1997. *Inland wetlands.* In: Tucker G. M. & Evans M. I. (eds.). Habitats for birds in Europe: a conservation strategy for the wider environment. Cambridge, U.K.: BirdLife International (BirdLife Conservation Series no. 6).

Verhulst, S., Perrins, C.M. & Riddington, R. 1997. Natal dispersal of Great Tits in a patchy environment. *Ecology* **78**: 864–872.

Wesołowski, T. 2006. Nest-site re-use: March Tit *Poecile palustris* decision in a primeval forest. *Bird Study* **53**: 199–204.

Wiens, J.A. 1989. *The Ecology of Bird Communities.* Cambridge University Press

Wingelmaier, K., Winkler, H. & Nemeth, E. 2007. Reed Bunting (*Emberiza schoeniclus*) males sing an "all-clear" signal to their incubating females. *Behav.* **144**: 195–206.

Zahavi, A. 1975. Mate selection - a selection for a handicap. *J. Theor. Biol.* **53**: 205–214.

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Souhlasím, aby společně dosažené výsledky byly použity v její disertační práci.

RNDr. Petr Musil, PhD.

KAPITOLA I.

Musilová, Z. & Musil, P. Nest site selection in the Reed Bunting *Emberiza schoeniclus* in fishpond habitats. *submitted*

Nest site selection in the Reed Bunting *Emberiza schoeniclus* in fishpond habitats

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Abstract

Nest site selection was analysed using variation in timing of breeding, nesting success and age of females in the Reed Bunting in fishpond habitats in mosaic Central European landscape. In total, we monitored 130 nests with 38 known females on five fishponds in South Bohemia, the Czech Republic, in 2000-2009. In order to determine the effects of breeding parameters on nest site selection, we formulated generalized linear models and estimated daily nest survival using program MARK. First-egg laying date was significantly associated only with type of vegetation and maximal height of vegetation. Moreover, mean height of vegetation and proportion of previous year vegetation seem to be constant during the whole breeding season. Nest fate was explained by proportion of previous year vegetation. The effect of laying date on nesting success or daily nest survival was not confirmed. We found out that older females laid eggs earlier and located the nests in lower vegetation than young ones. In addition, young females prefer sedge, while older females prefer Wood Small-reed *Camagrostis epigeios* and Reed Canary Grass *Phalaris arundinacea* for a nest location.

Key words: the Reed Bunting, daily nest survival, nesting success, timing of breeding, age of females

Running title: Nest site selection in the Reed Bunting

Introduction

Littoral stands of fishponds and lakes are occupied by a limited number of passerine species in Western Palearctic. Individual species inhabiting fishpond landscape can use various littoral vegetation differing in height, density and other structural parameters of wetland plant communities (Musil et al. 1996, van Vessem et al. 1997, Báldi & Kisbenedek 1999).

The spatial distribution of bird species is closely related to the habitat requirements of the species (Báldi et al. 1998) and reed-nesting passerines respond individually to the spatial structure of reedbeds (Leisler 1981, Báldi & Kisbenedek 1999). The pattern of the dispersion of these species across reedbeds is in accordance with their ecomorphology (Leisler 1975, Leisler et al. 1989). Among Reed Warblers *Acrocephalus* spp., individual species differ in preference of various height of vegetation and various water level (Leisler 1981, Martínez-Vilalta et al. 2002).

An example of habitat generalist using variable types of littoral vegetation is the Reed Bunting *Emberiza schoeniclus*, which occupies a wide scale of wetlands habitats (Blümel 1989, Cramp & Perrins 1994, Glutz von Blotzheim and Bauer 1997, Báldi & Kisbenedek 1999). Moreover, this species is able to expand to agricultural country (Siriwardena et al. 2000), probably due to inclination to drier wetland habitats (Martínez-Vilalta et al. 2002, Grujbárová et al. 2005). Nest site selection may be similar throughout a species range or it could reflect habitat availability or constraints on nesting success among regions (Gjerdrum et al. 2005). Nevertheless, habitats generalists are supposed to be capable of not only occupying a wider range of habitats, but also exploring a wider range of resources (Brown 1984) including nest sites. The determinants of nest site selection and their subsequent consequences for nesting success are not straightforward and this information could be important for guiding management activities (Gjerdrum et al. 2005).

We predicted that individuals with higher fitness are able to occupy optimal nest sites (Benett & Owens 2005). We can identify individual fitness using the following parameters: timing of breeding, nesting success and age of individuals. Survival and probability of recruitment are usually higher for early-hatched fledglings than for those hatched later (Lack 1968, Perrins 1970, Benett & Owens 2005). Reproductive success of older birds is generally higher than of the young ones (Curio 1983, Geslin et al. 2004). Poorer performance of young breeders could be explained by age-related enhancement of reproductive success, which can be a consequence of long-term optimisation of reproduction with minimisation of first-time investment. Moreover, lower reproductive success of young breeders is often related to a lack of breeding skill (Curio 1983).

The main aim of this study is to assess the effect of nest-site selection on variation in breeding performance (timing of breeding, nesting success and age of females) in the Reed Bunting *Emberiza schoeniclus*. We evaluate habitat preference and optimal breeding habitat using differences in timing of breeding, nesting success and experience of breeding females. Moreover, we try to assess the possible impact of habitat degradation on occurrence of the Reed Bunting in South Bohemian fishpond area.

Methods

The Reed Bunting is a small, short-distance migratory, sexual dimorphic, granivorous passerine that breeds on the ground in open wetland habitats (Hudec 1983, Blümel 1989, Cramp & Perrins 1994). Therefore, it shows highly fragmented (patched) distribution in Central European Landscape. Males arrive in the Czech Republic at the end of February or the beginning of March, a few days before females. Even though socially monogamous species, Reed Buntings show a high level of extra-pair paternity (Dixon et al. 1994, Bowmann & Komdeur 2005, Bowmann &

Komdeur 2006, Kleven & Lifjeld 2005). They are able to breed usually twice during one breeding season (e.g. Blümel 1989, Glütz von Blotzheim & Bauer 1997). According to our observation, re-nesting usually follows an unsuccessful breeding attempt.

The study was carried out on fishponds in South Bohemia (Jindřichův Hradec district, the Czech Republic) located close to Kardašova Řečice town (49˚11'– 49˚13' E, 14˚51'-14˚ 54' N, 443-480 m a.s.l.) (four fishponds: Hejtmánků – 1.6 ha, Špitálský – 5.9 ha, Obecní – 10.3 ha, and Šlechtův ponds – 5.6 ha) and close to Lužnice village (Černičný fishpond - 49˚05' E, 14˚45' N, 42.6 ha, 425 m a.s.l.). Reed Buntings occupy the edge of fishponds dominated by *Phragmites australis*, *Typha angustifolia*, *Phalaris arundinacea*, *Glyceria sp.* and *Calamagrostis epigeios*. Trees and bushes are mainly composed of *Salix alba* and *Alnus glutinosa* in the study area (for more details of the habitat see Janda et al. 1996). Particular fishponds were isolated without wetlands corridors, surrounded by mixture of forest patches, fields and villages. The number of occupied territories varied between 2 and 9 breeding pairs on individual fishponds.

In total, we monitored 130 nests of the study species in 2000 – 2009. Nests were found with the use of a systematic searching of the focal area or monitoring of feeding parents. Nests were discovered at various stages of development, including nest building, incubation and brood rearing and were repeatedly controlled. The following components of each brood were recorded: a) date of first egg laying (assuming one egg laid per day), b) the day of the nesting season on which the nest was found, c) the last day the nest was checked when alive, d) the last day the nest was checked, e) the fate of the nest (success vs. failure) (Cooch & White 2009). The date of failure was estimated as mid-point between the date when the nest was last controlled to be active and the date on which was found the nestlings to have left the nest or to have failed. When nestling age was not known accurately from observation of hatching, it could be estimated by comparing the degree of development (feather, weight, body measurement) with known-age broods. Age estimates allowed back-calculation of first egg date for the nest, assuming 13-day incubation period and 2-day hatching period, depending on clutch size (Blümel 1982, Hudec 1983, Okulewicz 1989, Cramp &Perrins 1994, Glütz von Blotzheim & Bauer 1997).

The following environmental parameters were recorded close to the nest: vegetation structure, maximal and mean height of vegetation, proportion of last year vegetation (in %), distance from open water an the nearest tree, height of the nest above ground, proportion of trees (in distance of 10m around the nest) and finally, estimation of visibility of the nest. Vegetation was separated in four types using dominance species (Reed Canary Grass *Phalaris arundinacea*, sedges *Carex spp.*, Wood Small-reed *Calamagrostis epigeios* and Common Reed *Phragmites australis*).

Our research activities were carried out during the breeding season from March to the beginning of July of 2000 to 2009. Adult caught Reed Buntings were marked using unique individual combination of colour rings (Ecotone). Moreover, all birds were ringed with aluminium rings of the National Museum Prague. Age was categorised as 2 years or older (2K and +2K in the Euring system) (Bub 1985, Svensson 1992). Accuracy of the age determination was verified by long-term ringing and recovery of individually marked birds.

In order to analyse first-egg laying date and nest fates, we formulated generalised linear models (GLZ, binominal distribution, logit-link function), in which laying date and breeding outcome was included as the response variable. Parameters of nest site (see above) were considered as potential explanatory variables. Differences in timing of breeding in particular years were significant (ANOVA: F (7, 118) = 2.2029, $p < 0.05$). We use relative first-egg laying date (i.e. first-egg laying date of individual clutch – median of first-egg laying date in particular year) in aim to eliminate the effect of variable climatic condition of particular years on timing of breeding.

In order to determine whether age of females was associated with nesting success, laying date and nest site parameters (see above), we formulated generalised linear models (GLZ, binominal distribution, logit-link function), with the age of females as the response variable. Nesting success, laying date and nest site parameters were considered as potential explanatory variables.

We used program MARK 2.1 (White & Burnham 1999) to model daily survival rate (DSR) across the 25-day nesting period and across the 92-day breeding season (Dinsmore et al. 2002, Cooch & White 2009). We used all nest-site variables (see above) and first-egg laying date as additive covariates in the models of daily nest survival. We use logit-link function to force all estimates of DSR to the interval (0, 1) (Lebreton *et al.* 1992). Akaike's Information Criterion (AICc) was used to select the best approximating model and differences in AICc between models were also calculated (ΔAICc). A total of 7 candidate models were based on questions of interest (Cooch & White 2009). The model with the lowest value of AICc was considered the most parsimonious explanation for the data. Models were equally parsimonious if the difference in AICc from the best fit model was ≤2 (Burnham & Anderson 2002). Currently, there is no goodness-of-fit test for nest survival data in MARK (Cooch & White 2009).

Results

First-egg laying date was significantly associated with type of vegetation and maximal height of vegetation using the GLZ model (Table 1). Laying date was later for nests located in Reed Canary Grass (25th May±22 days) than in sedges (12th May±15 days), Wood Small-reed (13th May±17 days) or Common Reed (4th May±8 days). Similarly, maximal height of vegetation was positively related to laying date. No significant interaction was found between first-egg date and mean height of vegetation, proportion of previous year vegetation, distance of open water and the nearest tree, proportion of trees in 10m circle, height of the nest above ground and the visibility of the nest (Table 1).

Nest fate of individual nests was explained significantly only by proportion of previous year vegetation surrounding the nest using the GLZ model (Table 2), while the effect of the remaining environmental variables was not significantly correlated. Nests with equal proportion of previous year and current year vegetation were more successful than nests with majority of previous year vegetation (Fig. 1). The effect of the laying date on individual breeding success was not confirmed.

Daily nest survival for Reed Bunting, calculated as constant over the 25-day nesting cycle and over the 92-day breeding season, was 0.97±0.01 (95% CI 0.95–0.98). The best model for daily nest survival with the lowest AICc included only an intercept for DSR (Table 3.). Models that included variation in vegetation type, distance from edges (open water, nearest tree) and proportion of trees, proportion of previous vegetation, mean height of vegetation and nest height, first-egg laying date and nest visibility had low support (Table 3).

When isolating nests with females of known age, we analysed the effect of female age on laying date, breeding success and parameters concerning location of the nest (see above for details), using the GLZ model. Age of females was significantly associated with first-egg date, type of vegetation and mean height of vegetation surrounding the nest, while the relationship between female age and breeding success was not confirmed (Table 4). The remaining parameters of nest location were not related to female age. Older females laid eggs earlier than young ones (age 2 year: 17th May± 13 days, age > 2 year: 9th May±17 days, n = 38), see figure 3. Young females prefer sedge, while older females prefer Wood Small-reed and Reed Canary Grass for a nest location. Older females locate the nests in lower vegetation than young females (Fig. 3).

Discussion

According to our study, Reed Bunting females tend to occupy nest sites with similar environmental parameters (except maximal height of vegetation) during the whole breeding season. Moreover, we can emphasise the importance of unchanging proportion of previous year vegetation and mean height of vegetation despite quick grow up of wetland plants. This fact could confirm a necessity of female's view from the nest and her possible escape from potential predator or potential nest defence decision (Curio 1978, Halupka & Halupka 1997). The effect of vegetation type on laying date and preference of Reed Canary Grass later in breeding season supports female's tendency to occupy an even height of vegetation during the whole breeding season. Reed Canary Grass is the lowest among investigated vegetation types and it is usually destructed after winter season. In addition, we can assume that females attempt to minimise the effect of timing on breeding performance using unchanging microhabitat of the nest site.

Generally, in migrant birds arrival date to the breeding ground affects the start of egg-laying (Sandberg & Moore 1996, Wesołowski &Maziarz 2009). In this case, we can exclude the effect of arrival date on timing of breeding. Reed Bunting represents an early-arriving species (Newton 2008), forming flocks after the arrival due to an intensive feeding and an improvement of body condition after migration (Musilová et al. 2010). On the contrary, food availability could positively affect timing of breeding (Barlein 1996, Thibault & Villard 2005, Newton 2008).

We did not confirm any significant effect of nest site parameters on individual nesting success except a negative effect of higher proportion of previous year vegetation. An important parameter affecting nesting success could be nest visibility, which is related to vegetation density (Martin 1995, Clark & Shutler 1999). Moreover, Brickle & Peach (2004) showed that survival of nests at the egg stage was positively related to the extent of nest concealment. Lesser density of previous year vegetation could facilitate movement of mammalian predators (Martin 1993).

Gjerdrum et al. (2005) explain the lack of strong relationship between habitat and nest success by claiming that nest site selection is sufficiently effective and most birds simply avoid building nests in an unsuitable habitat. Correspondingly, Bradbury et al. (2000) did not confirm differences in breeding success between two farm types in the Yellowhammer in Britain. On the contrary, Arriero et al. (2006) showed the effect of habitat structure on Blue Tit reproductive success in Mediterranean forest type. Also Knutson et al. (2004) showed a significant effect of environmental variables on daily nest survival of forest passerines in fragmented forests in Minnesota.

Moreover, we did not confirm any significant effect of timing of breeding on breeding success as well as on daily nest survival. This is in contrast with the general expectation that timing of breeding is a critical parameter for reproductive success due to food supply, re-nesting or prompt development of nestlings (e.g. Perrins 1969, Perrins 1970, Owen & Black 1990, Gjerdrum et al. 2005). Nevertheless, no effect of timing on reproduction success as well as daily nest survival support the finding of female's effort to minimise this impact (see above) due to extended breeding season. Yom-Tov (1992) showed that Reed Bunting is the earliest breeder, followed by the Yellowhammer and the Corn Bunting. Moreover, short-lived open nesting passerines like Reed Bunting can usually produce several breeding attempts in a year, but predation on the eggs and chicks is often heavy and many nests fail. Individual breeding outcome is therefore highly variable (Newton 1992). Therefore, we assume that reproduction success is unpredictable in this study habitat.

For the Reed Buntings in our study, older females laid their eggs earlier than young ones and preferred lower vegetation while young females preferred sedge. Earlier breeding outset of experienced passerine females was confirmed in several studies (Harvay et al. 1985, Dhont 1989, Geslin at al. 2004) and our findings seem to follow this general pattern. On the other hand, Garamszegi et al. (2004) showed that late-breeding older females of Collared Flycatcher are able to realise similar reproductive success to that of early breeding young females. We expected that older Reed Bunting females tend to breed earlier due to the higher possibility of re-nesting. This species, open nesting on the ground, could be associated with ´fast´ life-histories, which mean fast development, high fecundity and following low survivorship of the birds (Lack 1968, Rowe et al. 1994, Benett & Owens 2002). Moreover, life history theory predicts that the cost of reproduction has important effects on subsequent performance reducing female fitness.

Older females locate their nests in lower vegetation, which could indicate higher importance of lower vegetation due to previous experiences of older birds. Older females also avoided sedge, as a native vegetation species more frequently flooded, probably due to protecting nest against flooding. Okulewicz (1989) showed that sedges were the most preferred vegetation types in Southwest Poland. The same finding confirms also Hudec (1983) in Czechoslovakia. In our study area, management practices such as dredging, manuring and summer draining have caused marked changes in the composition of wetland plant species. Both the area and species richness decreased for reed vegetation (represented by stands of the common reed and tall sedges) and some types of soft littoral vegetation have expanded. Moreover, the majority of sedge species are retreating and e.g. Reed Canary Grass quickly invades free niches (Janda et al. 1996, van Vessem 1997). Preference of less native vegetation species in experienced females could indicate better sense of direction across suitable microhabitat of the nest site.

Females use unchanging microhabitat of the nest site despite the relative wide range of habitat requirements. It could be in accordance with findings of Passineli et al. (2008) that small wetland fragments are equally suited as breeding grounds for the Reed Bunting as large ones. Our study indicate that Reed Bunting could be less sensitive to habitat changes and degradation in contrast to more specialised reed-nesting passerines due to plasticity of female’s nest site selection across various vegetation type. Moreover, we can find connection with trend in numbers of this wetland species. There is a stable population trend in the Czech Republic in contrast to decreasing Warblers (*Acrocephalus* and *Locustella*) (Musil 1999, Musil 2000, Šťastný et al. 2006). On the contrary, decreasing trend of this species was recorded in some Western European countries, e.g. Great Britain, Belgium and France (Birdlife International 2004), where Reed Buntings are apparently related to agricultural landscape more then to natural wetland habitats (Gregory & Baillie 1998, Siriwardena et al. 2000).

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References

Arriero E., Sanz J. J. & Romero-Pujante M. 2006. Habitat structure in Mediterranean deciduous oak forests in relation to reproductive success in the Blue Tit *Parus caeruleus*. Bird Study 53: 12-19.

Bairlein F. 1996: Ökologie der Vögel. Gustav Fisher Verlag, Stuttgart.

Báldi A. & Kisbenedek T. 1999. Species-specific distribution of reed-nesting passerine birds across reed-bed edges: effect of spatial scale and edge type. Acta Zoologica Academiae Scientarum Hungaricae 45 /2/: 97-114.

Báldi A., Moskát C. & Zágon A. 1998. Faunal mapping of birds in a riparian area of River Danube after construction of a hydroelectric power station. Folia Zoologica 47:173-180.

Benett P. M. & Owens P. F. 2005. Evolutionary Ecology of Birds. Oxford University Press, New York.

BirdLife International 2004. Birds in Europe: populations, estimates, trends and conservation status. BirdLife Conservation Series No. 12, Cambridge, UK.

Blümel H. 1982. Die Rohrammer. Die Neue Brehm-Bucherei. Die Neue Brehm-Bucherei. Nr. 544. A. Ziemsen, Wittenberg Lutherstadt.

Bouwman K. M. & Komdeur J. 2005. Old female Reed Buntings (*Emberiza schoeniclus*) increase extra-pair paternity in their broods when mated to young males. Behaviour 142: 1449-1463.

Bouwman K. M. & Komdeur J. 2006. Weather conditions affect levels of extra-pair paternity in the Reed Bunting *Emberiza schoeniclus*. J. Avian Biol. 37: 238-244.

Bradbury B. B., Kyrkos A., Morris A. J., Clark S. C., Perkins A. J. & Wilson J. D. 2000. Habitat association and breeding success of Yellowhammers on lowland farmland. J.Appl.Ecol. 37: 789-805.

Brown J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124: 255-279.

Bub H. 1985. Kennzeichen und Mauser europäischer Singvögel. Die Neue Brehm-Bucherei. Nr. 570. A. Ziemsen, Wittenberg Lutherstadt.

Burnham K. P. & Anderson D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Clark R. G. & Shutler D. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80: 272-287.

Cooch E. & White G. 2009. Program MARK. A Gentle Introduction. 8th edition. Department of fish, Wildlife, and Cons. Biol. Colorado State University, Fort Collins.

Cramp S. & Perrins C. M. 1994. The birds of the Western Palearctic. Vol. IX.: Buntings and New World Warblers. Oxford UniversityPress, Oxford and New York.

Curio E. 1978: The Adaptive Significance of Avian Mobbing. I. Teleonomic hypothesis and predictions. Zeitschrift für Tierpsychologie 48: 175-183.

Curio E. 1983. Why do young birds reproduce less well? Ibis 125: 400-404.

Dhont A. A. 1989. The effect of old age on reproduction of Great Tits *Parus major* and Blue Tits *P.caeruleus*. Ibis 131: 268-280.

Dinsmore S. J., White G. C. & Knopf F. L. 2002. Advanced techniques for modeling avian nest survival. Ecology 83: 3476-3488.

Dixon A., Ross D., Omalley S. L. C. & Burke T. 1994. Parental investment inversely related to degree of extra-pair paternity in the Reed Bunting. Nature 371: 698-700.

Garamszegi L. Z., Török J., Tóth L. & Michl G. 2004. Effect of timing and female quality on clutch size in the Collared Flycatcher *Ficedulla albicollis*. Bird Study 51: 270-277.

Geslin T., Questiau S. & Eybert M. C. 2004. Age-related improvement in reproductive success in Bluethroats *Luscinia svecica*. Bird Study 51: 178-184.

Gjerdrum C., Elphick C. S. & Rubega M. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: the importance of nest habitat, timing and study site differences. Condor 107: 849-862.

Glutz von Blotzheim, U. & Bauer, K. (eds.) 1997. Hand buch der Vogel Mitteleuropas. Ba 14; Anea Verlag, Wiesbaden.

Gregory R. D.&Baillie S. R. 1998. Larg-scale habitat use of a group of declining British birds. J.Appl.Ecol. 35: 785-799.

Grujbárová Z., Kocian L. & Némethová D. 2005. Habitat selection in the sedge warbler (*Acrocephalus schoenobaenus*) and the Reed Bunting (*Emberiza schoeniclus*). Biologia 60: 571-577.

Halupka K. & Halupka L. 1996: The influence of reproductive season stage on nest defence by Meadow Pipits (*Anthus pratensis*). Ethology Ecology & Evolution 9: 89-98.

Harvey P. H., Stenning M. J. & Campbell B. 1985. Individual variation in seasonal breeding success in Pied Fycatchers (*Ficedula hypoleuca*). J.Anim.Ecol. 54: 391-398.

Hudec K. (ed.) 1983: Fauna of ČSSR. Birds III (2). Academia, Praha.

Janda J. & Pechar L. et al. 1996. Sustainable use of fishponds in the Třeboňsko protected landscape area and biosphere reserve. České koordinační středisko IUCN - Světového svazu ochrany přírody Praha a IUCN Gland, Švýcarsko a Cambridge, Velká Británie, 189 pp.

Kleven O. & Lifjeld J. T. 2005. No evidence for increased offspring heterozygosity from extrapair mating in the Reed Bunting (*Emberiza schoeniclus*). Behav.Ecol. 16: 561-565.

Knutson M. G., Niemi G. J., Newton W. E. & Friberg M. A. 2004. Avian nest success in Midwestern forests fragmented by agriculture. Condor 106: 116-130.

Lack D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London.

Lebreton J. D., Pradel R. & Clobert J. 1993. The statistical analysis of survival in animal populations. Trend. Ecol. Evol. 8: 91-95.

Leisler B. 1975. The significance of foot morphology in the habitat separation of Central European *Acrocephalus* and *Locustella* species. J.Orn. 119: 117-153.

Leisler B. 1981. Die ökologische Einnischung mitteleuropäischer Rohrsänger (*Acrocephalus*, Sylviinae), I. Habitattrennung. Vogelvarte 31: 45-74.

Leisler B., Ley H. W. & Winkler H. 1989. Habitat, behaviour and morphology of *Acrocephalus* warblers: an integrated analysis. Ornis Scand. 20: 181-186.

Martin T. E. 1993. Nest predation and nest sites. Bioscience 43: 523-532.

Martin T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101-127.

Martínez-Vilalta J., Bertolero A., Bigas D., Paquet J. Y. & Martínez-Vilalta A. 2002. Habitat selection of passerine birds nesting in the Ebro delta reedbeds (NE Spain): management implications. Wetlands 22: 318-325.

Musil P. 1999. Monitoring of Water Bird Breeding Populations in the Czech Republic (1988-1997). Vogelwelt 119: 253-256.

Musil P., Pykal J. & Janda J. 1996. Birds of fishponds in the Třeboň Biosphere Reserve and effect of the most important factors. In: IUCN (eds): Sustainable use of fishponds in the Třeboňsko protected landscape area and biosphere reserve*:* České koordinační středisko IUCN - Světového svazu ochrany přírody Praha a IUCN Gland, Švýcarsko a Cambridge, Velká Británie: 111-128.

Musil P: 2000. Monitoring hnízdních populací vodních ptáků. Sylvia 36: 6-11.

Musilová Z., Musil P., Fuchs R. & Poláková S. 2010. Territory settlement and site fidelity in the Reed Bunting *Emberiza schoeniclus* in a patchy environment of fishponds. submitted to Bird Study.

Newton I. 1992. Life time reproduction in Birds. Academic Press, London.

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

Newton I. 2008. The migration ecology of birds. Academic Press, London.

Okulewicz, J. 1989. Breeding biology and ecology of the Reed Bunting (*Emberiza schoeniclus*) in the region of the Milicz fishpond area. Ptaki Slaska 7:1-39.

Owen M. & Black J. M. 1990. Waterfowl Ecology. Chapman and Hall, New York.

Pasinelli G., Mayer Ch., Gouskov A. & Schiegg K. 2008. Small and large wetland fragments are equally suited breeding sites for a ground-nesting passerine. Oecologia 156: 703-714.

Perrins C. M. 1969. Eggs, egg formation and timing of breeding. Ibis 138: 2-15.

Perrins C. M. 1970. The timing of birds´ breeding season. Ibis 112: 242-255.

Rowe L., Ludwig D. & Schluter D. 1994. Time, condition and the seasonal decline of avian clutch size. Am.Natur. 143: 698-722.

Sandberg R. and F. R. Moore. 1996. Migratory orientation of Red-eyed Vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. Behavioral Ecology and Sociobiology 39:1-10.

Siriwardena G. M., Crick H. Q. P., Baillie S. R. & Wilson J. D. 2000. Agricultural habitat-type and the breedimg farmland birds in Britain. Bird Study 47: 66-81.

Šťastný K., Bejček V. & Hudec K. 2006. Atlas of breeding birds in the Czech Republic 2001-2003. Aventinum, Praha.

Svensson, L. 1992. Identification guide to European passerines. Fourth edition. Stockholm.

Thibault J. C. & Villard P. 2005. Reproductive ecology of the Corsican Nuthatch *Sitta whiteheadi*. Bird Study 52: 282-288.

van Vessem J. & Trucker G. M. 1997. Inland wetlands. In: Tucker G. M. & Evans M. I. (eds.). Habitats for birds in Europe: a conservation strategy for the wider environment. Cambridge, U.K.: BirdLife International (BirdLife Conservation Series no. 6).

Wesołowski T. & Maziarz M. 2009. Changes in breeding phenology and performance of Wood Warblers *Phylloscopus sibilatrix* in a primeval forest: a thirty-year perspective. Acta Ornithol. 44: 69-80.

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

Yom-Tov Y. 1992. Cluth size and laying dates of three species of buntings *Emberiza* in England. Bird Study 39:111-114.

Table 1. Result of the GLZ model to explain the variation in relative first-egg laying date depending on nest site parameters (type of vegetation, maximal and mean height of vegetation, proportion of previous year vegetation, distance from open water and the nearest tree, height of the nest above ground, proportion of trees in circle 10m around the nest and visibility of the nest (n=109).

Effect	CHi-square	df	P-value
Type of vegetation	15.29	3	< 0.01
Mean height of vegetation	1.26	1	0.26
Maximal height of vegetation	4.06	1	< 0.05
Previous year vegetation (%)	0.36	1	0.55
Distance of open water	0.91	1	0.34
Distance of the nearest tree	0.09	1	0.77
Proportion of trees (%)	0.55	1	0.46
Height of nest above ground	2.43	1	0.12
Visibility (%)	0.17	1	0.68

Table 2. Result of the GLZ model to explain the variation in nesting success depending on relative first-egg laying date and nest site parameters (type of vegetation, maximal and mean height of vegetation, proportion of previous year vegetation, distance from open water and the nearest tree, height of the nest above ground, proportion of trees in circle 10m around the nest and visibility of the nest (n=107).

Effect	CHi-square	df	P-value
Timing of breeding	0.02	1	0.90
Type of vegetation	3.72	3	0.29
Mean height of vegetation	0.05	1	0.83
Maximal height of vegetation	2.54	1	0.11
Previous year vegetation (%)	4.75	1	< 0.05
Distance of open water	0.49	1	0.48
Distance of the nearest tree	0.13	1	0.72
Proportion of trees (%)	0.002	1	0.96
Height of nest above ground	0.08	1	0.77
Visibility (%)	0.67	1	0.41

Table 3. Summary of model selection results for the daily survival rate of Reed Bunting (n=38).

Model	np	AICc	ΔAICc	AICc weight	Deviance
S.	14	170.43	0.00	0.86	141.91
$S_{\text{veget. type}}$	4	175.55	5.12	0.07	167.50
S_{edge}	4	177.74	7.31	0.02	169.69
$S_{\text{previous veget.}}$	2	177.78	7.35	0.01	173.77
$S_{\text{veg.height + nest height}}$	3	179.90	9.47	0.01	173.87
$S_{\text{lay. date}}$	2	181.69	11.27	0.00	177.68
$S_{\text{visibility}}$	2	181.77	11.36	0.00	177.77

AICc = Akaike´s information criterion, ΔAICc = differences between that model and the model with the lowest AICc, np = number of parameters.

Table 4. Result of the GLZ model to explain the relationship between female age and nesting success, relative laying date and nest site parameters (type of vegetation, maximal and mean height of vegetation, proportion of previous year vegetation, distance from open water and the nearest tree, height of the nest above ground, proportion of trees in circle 10m around the nest and visibility of the nest) n = 38.

Effect	CHi-square	df	P-value
Timing of breeding	7.03	1	< 0.01
Breeding success	0.01	1	0.91
Type of vegetation	13.22	3	< 0.01
Breeding success*Type of vegetation	1.26	2	0.53
Mean height of vegetation	7.29	1	< 0.01
Maximal height of vegetation	0.06	1	0.81
Previous year vegetation (%)	0.10	1	0.76
Distance of open water	0.01	1	0.91
Distance of the nearest tree	0.004	1	0.95
Proportion of trees (%)	0.50	1	0.48
Height of nest above ground	0.54	1	0.46
Visibility (%)	0.21	1	0.65

Figure 1. Nesting outcome in relation to proportion of previous year vegetation.

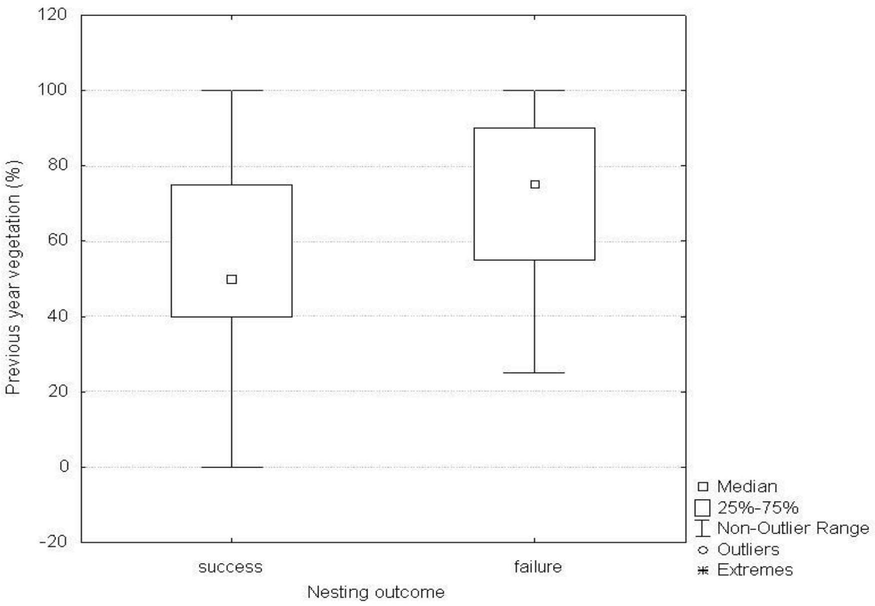


Figure 2. Relative first-egg laying date of young and older females.

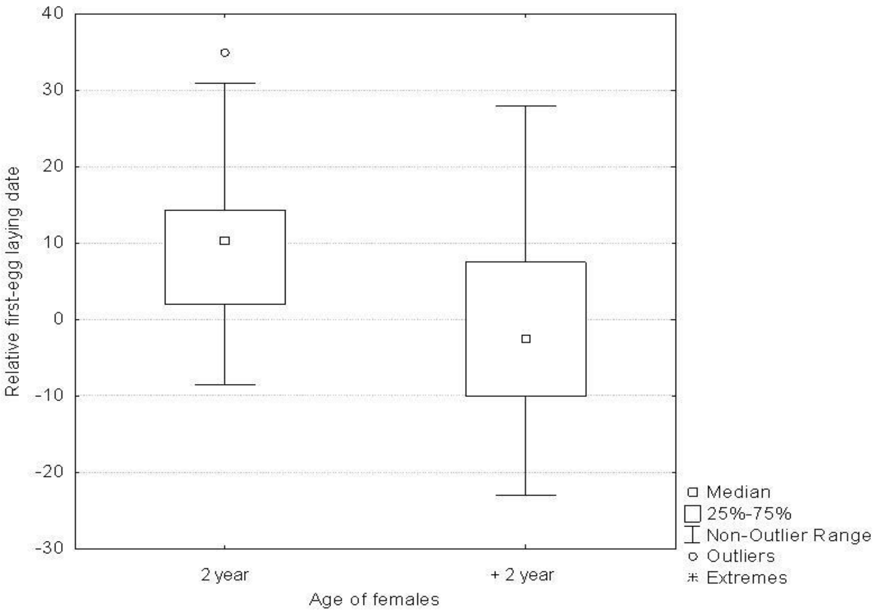
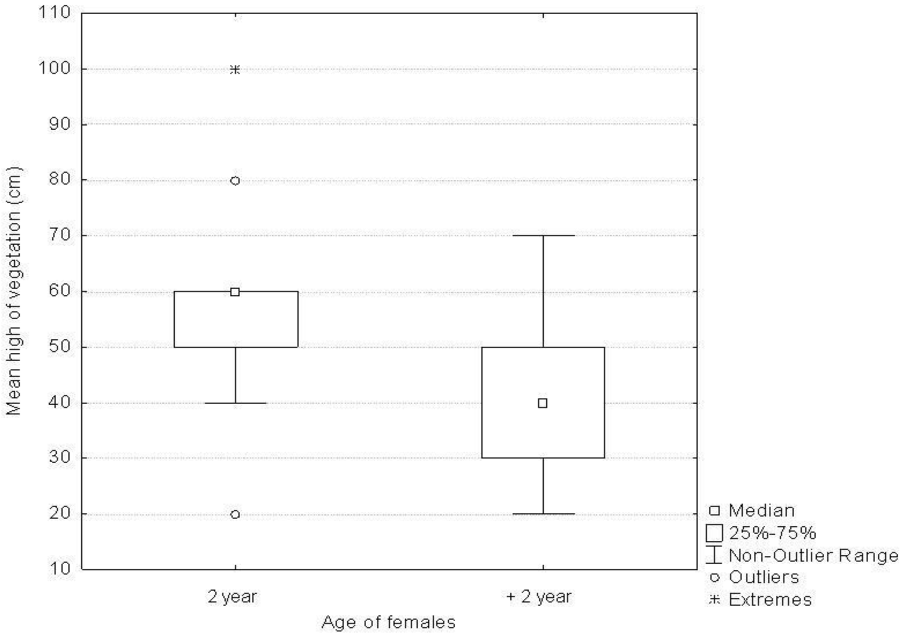


Figure 3. Mean height of vegetation surrounded nest in young and older females.



KAPITOLA II.

Musilová, Z., Musil, P., Fuchs, R. & Poláková, S. Territory settlement and site fidelity in the Reed Bunting *Emberiza schoeniclus* in a patchy environment of fishpond. *submitted after revision*

Territory settlement and site fidelity in the Reed Bunting *Emberiza schoeniclus* in a patchy environment of fishpond

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Short title: Territtory settlement and fidelity in Reed Bunting

Summary

Capsule The highly fragmented fishpond landscape in South Bohemia provides an important breeding habitat for Reed Buntings *Emberiza schoeniclus* (early-arriving species, forming flocks in pre-breeding season).

Aim To investigate the relationship between territory settlement and site fidelity of the target species and to analyse factors affecting settlement and fidelity patterns.

Methods In total, 270 colour marked individuals were investigated on five fishponds in South Bohemia, the Czech Republic, in 2000-2009. We used model selection to test the effect of individual covariates (sex, age, weight and body measurements) on apparent survival and recapture probabilities of Reed Bunting adults.

Results There is a correlation between territory settlement and site fidelity. Older males were more frequently re-sighted in the study area during the year of banding. Moreover, males were more frequently recovered in subsequent breeding seasons. The effect of body measurement as well as body weight did not appear evident. The effect of breeding performance on site fidelity in previous breeding seasons was not confirmed.

Conclusion This study provides evidence that there is a connection between territory settlements and site fidelity in the early-arriving Reed Bunting species. Site fidelity and territory settlement is probably limited by occupancy of suitable sites by males and high mortality in females most likely caused by an extended breeding season in the study area. Moreover, territory settlement, and marginally, site fidelity is associated with the previous experience of the males. Forming pre-breeding flocks probably provides addition of nutrition reserves after spring arrival. High competition in males and lack of suitable breeding habitats, due to occupancy by older residents, indicated crucial importance of small fragmented wetlands to this study species in this particular area.

Key words: *Emberiza schoeniclus*, territory occupancy, early-arriving species, breeding success, site fidelity, patchy environment

Introduction

Individuals of many bird species tend to use the same breeding areas and the same territories in successive years (Berthold 2001, Newton 2008). Site fidelity is widespread in passerine birds, with adults returning to the same area to breed, presumably for as long as they survive (Greenwood & Harvey 1982, Klemp 2003). In general, species with high site-fidelity to the breeding areas show low hatching-site fidelity, presumably because the juveniles are forced to disperse far afield by the dominant adults (Berthold 2001).

There are obvious benefits to a bird returning to the same breeding territory each year, providing conditions permit. Individuals can benefit from local knowledge or familiarity that might give a bird an advantage in a competitive interaction with other individuals. This behaviour makes the birds better able to defend its feeding and breeding sites against potential intruders. Birds may also profit from previous knowledge of food availability and refuges (Greenwood 1980). The benefits of local experience and local adaptation, acting at the level of individuals, could be the main selective forces underlying site fidelity in birds (Berthold 2001, Newton 2008).

Conversely the advantage of dispersal is that birds can leave areas where conditions are poor or overcrowded to find somewhere better (Greenwood 1980, Verhulst *et al.* 1997, Berthold 2001, Hansson at al. 2002a, Hansson *et al.* 2002b, Calabuig *et al.* 2008). Another advantage of dispersal is that it could reduce inbreeding (e.g. Greenwood *et al.* 1978, Bauer 1987, Hansson *et al.* 2002a).

We can summarize these main pattern that affect site fidelity in birds: sex differences in fidelity within species with male biased return rates (e.g. Solonen 1979, Greenwood 1980, Payne & Payne 1993, Verhulst *et al.* 1997, Schlossberg 2009); a tendency for greater fidelity in later life (e.g. Greenwood & Harvey 1982, Pärt 2001, Winkler *et al.* 2004, Vergara *et al.* 2006) and a greater tendency to change territories after a breeding failure (e.g. Harvey *et al.* 1979, Haas 1998, Schjørring *et al.* 2000, Sedgwick 2004). In addition, some birds change territories immediately after arrival, in response to local food depletion or other factors that are likely to reduce breeding success (Newton 2008).

Individuals are under pressure to return to breeding sites early, in order to gain precedence in competition for them (Hopp *et al.* 1999, Klemp 2003, Sergio & Newton 2003, Tryjanowski *et al.* 2004, Sergio *et al.* 2007, Newton 2008). Generally, later arriving species seem to settle directly in their territories, especially those returning to territories of the previous year. Conversely, among the early-arriving species, individuals tend to concentrate in particular places where food is available on arrival. Their numbers are probably higher than the number of potentially suitable territories available in the area. These pre-breeding sites are important in improving the birds body condition (Newton 2008). Factors affecting site fidelity were analysed especially in later arriving long-distance migrants (e.g. in European migratory passerines: Red-backed Shrike - Šimek 2001, Great Reed Warbler - Bensch & Hasselquist 1991, Hansson *et al.* 2002a, 2002b, Lesser Grey Shrike - Krištín *et al.* 2007, Common Redstart - Sedláček & Fuchs 2008). However, empirical evidence and lack of empirical research affecting territory acquisition after the break-up of flocks in early-arriving species and simultaneously the relationship between territory settlement and site fidelity are limited (Newton 2008).

We investigated patterns in territory settlement and site fidelity in the Reed Bunting *Emberiza schoeniclus*, as an example of early-arriving species forming flocks in the pre-breeding season (Blümel 1989, Cramp & Perrins 1994, Glutz von Blotzheim and Bauer 1997) using apparent survival and recapture probabilities. Among investigated variables associated with territory settlement, we predicted lower effect of body weight due to intensive feeding of migrants during pre-breeding period. Furthermore, we assume that the probability of territory settlement and site fidelity in individual birds is correlated. The best quality individuals, who are able to occupied a territory at optimal breeding sites (Sergio & Newton 2003, Sergio *et al.* 2007), can show higher probability of site fidelity in subsequent years. In addition, we examined site fidelity in relation to breeding performance in a sample of birds with known nests. We expected lower site fidelity in subsequent years, when individuals fail to fledge their young.

Methods

The Reed Bunting is a small, short-distance migratory, sexual dimorphic, granivorous passerine that breeds on the ground in open wetland habitats (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997). Consequently it displays highly fragmented (patchy) distribution pattern throughout Central Europe. Males arrive in Czech Republic at the end of February or the beginning of March, a few days before the females. They are usually able to breed twice during one breeding season (e.g. Blümel 1989, Glutz von Blotzheim and Bauer 1997). Moreover, re-nesting usually follows an unsuccessful breeding attempt (Musilová unpubl. data).

This study was carried out in near by fishponds in South Bohemia (district Jindřichův Hradec) located close to Kardašova Řečice (49˚11'– 49˚13' E, 14˚51'-14˚ 54' N, 443-480 m a.s.l.) (four fishponds: Hejtmánků – 1.6 ha, Špitálský – 5.9 ha, Obecní – 10.3 ha, and Šlechtův ponds – 5.6 ha) and close to Lužnice (Černičný fishpond - 49˚05' E, 14˚45' N, 42.6 ha, 425 m a.s.l.). Reed Buntings occupy the edge of fishponds dominated by *Phragmites australis*, *Typha angustifolia*, *Phalaris arundinacea*, *Glyceria sp.* and *Calamagrostis epigeios*. Trees and bushes in the study area are mainly *Salix alba* and *Alnus glutinosa* (for more details of the habitat see Janda *et al.* 1996). Individual fishponds were isolated without the wetlands corridor, surrounded by woods, fields and urban areas. The number of occupied territories varied between 2 and 9 breeding pairs on individual fishponds.

We carried out fieldwork during the breeding season from March to the beginning of July of 2000 to 2009. The majority of adults were mist-netted (Ecotone mist nets) in roosting sites during the pre-breeding period (March and April), when the birds were forming flocks and their numbers were higher than the number of potentially suitable nesting sites available in the area (pre-breeding season). All Reed Buntings caught were marked using unique individual combination of colour rings (Ecotone). Additionally, all birds were ringed with aluminium rings issued by The National Museum Prague. Age was categorized as 2 years or older (2K and +2K in the Euring system) (Bub 1985, Svensson 1992). Accuracy of age determination was verified by long-term ringing and recovery of individually marked birds. Individual birds were body weighed and measured (tarsus and wing). We supposed wing length as a feather component related to body condition or aerodynamic consideration. Tarsus length was used as a body size assumption (Pascual & Senar 1996, Senar &Pascaul 1997, Sutherland *et al.* 2005).

Using a telescope we repeatedly monitored the whole study area during one week intervals to identify individually marked birds and to estimate the total number of occupied territories during the breeding period. We used the following terms: *site fidelity* (also called return rate) is defined as event when residents were recovered in order to breed on fishponds (i.e. on ringing site) in subsequent years. According to our observation, transfers between particular fishponds were very rare in the study area. *Territory settlement* was used for event, when bird banded in pre-breeding season (March and April) was later (i.e. May and June) recovered at breeding and territory sites defending on particular fishponds.

The separated data set comprises 63 nests where there was identified at last one parent. We found nests by systematically searching of the focal area or monitoring of feeding parents. Nests were discovered at various stages of development, including nest building, incubation and brood rearing and these were repeatedly controlled. Nests were considered successful if at least one nestling was fledged. Similarly a breeding season was considered successful if at least one breeding attempt was successful.

We included all recaptures of the same individual in consecutive years in the analysis (Figure 1). Apparent survival and recapture probabilities were estimated applying the Colmack-Jolly-Seber (CJS) model for life recapture data in the program MARK 2.1 (White & Burnham 1999). Individual encounter histories were coded using two criteria: recovered or re-sighted at territory defending (1) or not detected (0). Site fidelity data were analysed with 5 encounter occasions according to maximum recurrence and territory settlement data with 2 encounter occasions. We used 7 individual variables: sex, age, weight, length of wing and tarsus, number of occupied territories on fishpond and date of ringing (dates were given as the Julian day from the beginning of the year) as additive covariates in our models (White and Burnham 1999, Cooch & White 2009) and standardise them in MARK. We use logit-link function to force all estimates of apparent survival and recapture probabilities to the interval (0, 1) (Lebreton *et al.* 1992). Akaike's Information Criterion (AICc) was used to select the best approximating model(s) and differences in AICc between models were also calculated (ΔAICc). A total of 10 candidate models were based on questions of interest (Cooch & White 2009). The model with the lowest value of AICc was considered the most parsimonious explanation for the data. Models were equally parsimonious if the difference in AICc from the best fit model was ≤2 (Burnham & Anderson 2002). Currently, there is no goodness-of-fit test of models with individual covariates in MARK (Cooch & White 2009). Regardless, the program RELEASE (available in MARK) was used to test for goodness of fit of our general model with two groups' parameter to the CJS model. Three standard tests were generated and two of them (TEST 2 and TEST 3) together provided the goodness of fit statistics for the general model.

Similarly, apparent survival and recapture probabilities of parents were estimated applying the CJS model for life recapture data in the program MARK 2.1 (White & Burnham 1999) and Akaike's Information Criterion (AICc) was used to select the best approximating model (see above). Individual encounter histories with 2 encounter occasions were coded using two criteria: recovered or re-sighted at territory defending (1) or not detected (0). We used 4 individual variables: sex, age, breeding outcome and number of occupied territories on fishpond as additive covariates in our models (White and Burnham 1999, Cooch & White 2009). We did not have sufficient data to include weight and body measurements as individual covariates in the models.

Unless otherwise indicated, tests were two-tailed, with significance levels set at $P<0.05$ using STATISTICA 8.0 (StatSoft Inc., 2007).

Results

In the study period in 2000 - 2009, we caught 270 adult Reed Buntings (153 males and 117 females). Program MARK estimated virtually different apparent survival probabilities (probability that a bird remains alive and available for recapture) for males (0.41±0.05, 95% CI 0.32–0.51) and females (0.16±0.06, 95% CI 0.08–0.30). Recapture probabilities (probability of being recaptured conditioned on being alive and in the sample) were 0.80±0.13 (95% CI 0.46–0.95) for males and 0.12±0.05 (95% CI 0.05–0.25) for females. Recovery rate (percentage of re-sighted birds) was 64.8% for males (n = 105) respectively 59.7% for females (n = 72) in year of banding (territory settlement) and 39.7% for males (n = 68) respectively 14.0% for females (n = 43) in subsequent years (site fidelity) (Table 1).

In total, we captured 56 (36.6%) young males (1 year old – 2K) and 97 (63.4%) older males (+2K). The proportion of captured females was 62 (53.0%) one year old and 55 (47.0%)

older birds. The difference of age structure of banded birds in both sexes was significant (χ^2 = 7.24, df = 1, P < 0.01). We banded 146 nestlings in 2000 - 2009. However, only one female (ringed as a nestling) was recovered during the whole study period. All females returned only once to the study area. Conversely, males were more frequently recovered. Maximum recurrence was three breeding season in a female and five breeding season in a male (Figure 1).

Fidelity ratio (proportion of re-sighted birds) was higher (Figure 2) in birds recorded in the study area as residents in year of banding (territory settlement) in both sexes. There is a correlation between territory settlement and site fidelity. Nevertheless, this relationship is more pronounced in males (χ^2 = 8.61, df = 1, P < 0.01) than in females (χ^2 = 0.75, df = 1, n.s.).

Results from the program RELEASE for TEST 2 and TEST 3 combined indicated that our general model Φ(.)p(sex) with two attribute groups fitted the data (goodness of fit, χ^2 = 0.53, df = 1, P = 0.47).

The best model of territory settlement data according to AICc criterion included sex and age interaction variation in apparent survival probability and constant recapture probability (Table 2). In this model apparent survival was 0.30±0.04 and recapture probability was 0.99±0.01. There was no support (ΔAICc>2) for variation of apparent survival in body measurements, weight, date of banding or total number of occupied territories on fishpond. Similarly, sex variation in recapture probability was not confirmed (Table 2). Older males (2 year +) were significantly more frequently re-sighted in the study area (n=177). The relationship between age and successful territory settlement was more pronounced in males and conversely less pronounced in females.

The best models of fidelity data for apparent survival and recapture probabilities included sex dependence effect (Table 3). In this model, there was the following apparent survival in subsequent years: 0.32±0.04, 0.28±0.05, 0.24±0.06, 0.20±0.07 and recapture probability was

0.79±0.09. There was marginal support for sex and age interaction differences in apparent survival probabilities (ΔAICc = 2.03, Table 3). Models that included variation in body measurements, weight, date of banding or total number of occupied territories had low support (Table 3). Males were more frequently recovered in the study area in subsequent breeding seasons (n = 111).

In 82 cases (43 in males and 39 in females), we were able to test the effect of previous breeding success or failure based upon the likelihood of a return in subsequent years. The best model for this data according to AICc criterion included sex variation in apparent survival probability and constant recapture probability (Table 4). There was no support for breeding outcome differences in apparent survival probabilities (ΔAICc = 19.07, Table 4). Male parents were more frequently recovered in the study area in subsequent years.

Discussion

In South Bohemia, individually marked Reed Buntings exhibited moderate site fidelity (cf. Newton 2008, Schlossberg 2009), with male-bias return rate and low philopatry. The low philopatry and following wide natal dispersion of this species show only one record of banded nestling in consequent years during the whole study period. This is in accordance with data from the Praha Bird Ringing Centre (Musilová 2008), where nestlings represent only 1.7% of recoveries and supports the general contention of low philopatry in migratory passerines (Weatherhead & Forbes 1994). Simultaneously, this low philopatry can reduce inbreeding in patchy distribution areas (Greenwood *et al.* 1978, Hansson *et al.* 2002a).

Site fidelity correlated with territory settlement, whereas, this difference is more pronounced in males than in females (Figure 2). This similar pattern in fidelity probably reflects quality of individuals. Males which stay in breeding site during breeding season after catching show higher probability to return to previous breeding site in the next spring. Moreover, we found support for sex-dependent variation in apparent survival with stronger probabilities for males remaining alive and available for re-capture. Apparent survival (0.41±0.05 for males and 0.16±0.06 for females) was similar with recovery rate (39.7% for males and 14.0% for females) which express site fidelity. To compare these findings, we can indicate that apparent survival follows site fidelity in our study. Sex differences in site fidelity have been noted in more than a half of the studied bird species (Newton 2008). Male biased return rates were defined in many European open landscape migratory passerines (Krištín *et al.* 2007, Sedláček & Fuchs 2008, Vadasz C. *et al.* 2008). Newton (2008) mentioned male-biased return patterns in 13 of 20 passerines species. Moreover, Schlossberg (2009) summarizes sex differences in site fidelity in 32 of 35 North American migratory bird species. To compare species with similar habitat preferences, there were similar male-biased return rates in following common species: Garden Warbler *Sylvia borin* (25% males and 6% females, Solonen 1979), Willow Warbler *Phyloscopus trochilus* (30% males and 17% females, Pratt & Peach 1991), Winchat *Saxicola rubetra* (74% males and 57% females, Bastian 1992) and Red-backed Shrike *Lanius collurio* (28% males and 20% females, Šimek 2001). On the contrary, no differences in breeding dispersal pattern of males (54%) and females (57%) were confirmed in the rare Great Reed Warbler *Acrocephalus arundinaceus* (Bensch & Hasselquist 1991, Hansson *et al.* 2002a, Hansson *et al.* 2002b). Sex differences in site fidelity with males more likely to return is possibly related to sex differences in territory acquisition and defense (Siriwardena *et al.* 1998, Artl & Part 2008, Newton 2008). Greater parental investment and extended breeding season in the Reed Bunting (Blümel 1982, Hudec 1983, Dyrcz 1984, Okulewicz 1989) results in a higher rate of mortality in females and a lower return rate of them. Reproduction is costly and therefore reduces subsequent survival (Lack 1954). Moreover, there was shown negative relationship between reproduction effort and subsequent survival (Benett & Owens 2005). If we take into an account that females express lower survival and males need experience for territory acquisition, we can assume there are differences in female and male life-histories due to different age at first time breeding (Benett & Owens 2005). Furthermore, female-bias in mortality (e.g. Newton 1992, Newton 1998, Berthold 2001) and dispersion (Greenwood 1980) is generally known. Nevertheless, when marked birds are not re-sighted in a study area, we generally do not know whether they have dispersed or died (Haas 1998, Schlossberg 2009).

We found that age plays an important role in the likelihood of apparent survival (resp. re-sighting) of birds banded in the pre-breeding season and consecutively controlled the same year. Older males were more frequently re-sighted. The effect of age in territory settlement, especially in males, could confirm the advantage of local knowledge, experience and age-related social dominance to occupied territories (Harvey *et al.* 1984, Sedgwick 2004, Winkler *et al.* 2004, Newton 2008, Sergio *et al.* 2009) and simultaneously high competition in the study area with a higher proportion of former residents. The importance of local knowledge and the experience to occupy territory indicates also marginal support for the model that analyzes age and sex interaction on the apparent survival in subsequent years. Old residents seem to be recovered or re-sighted more frequently than young ones in the study area in subsequent years. This finding could confirm that young birds are often re-legated to poorer nesting sites, and only acquire better sites as they grow older (Greenwood & Harvey 1982), because older individuals often breed in better habitats than first-time breeders (Pärt 2001).

The effect of body measurements and body weight on territory settlement using apparent survival modelling was not confirmed, thus supporting the theory of the importance of the formation of pre-breeding flocks in early arriving species (Newton 2008). The Reed Buntings improve their body condition due to intensive feeding after arrival. Therefore, competing males could less profit from the advantage of better body conditions after flock break up and acquired territory. In this case, greater importance from past experiences, expressed by age (mentioned above), can be shown. According to significant correlation between territory settlement and site fidelity, it seems that stable residents tend to return to their territories till they die.

We showed no significant effect of breeding success to apparent survival probabilities of parents in subsequent years. This is not in accordance with general patterns where breeding outcomes (success vs. failure) affect site fidelity and thereby successful birds are more likely to return to the same breeding site in the following year to that of those that fail to fledge their young (e.g. Harvey *et al.* 1979, Howlett *et al.* 2003, Wesołowski 2006, Johnson & Walters 2008, Berkunsky & Reboreda 2009). We suggest that there is a lack of suitable breeding sites in the study area and probably due to high competition between males, the effect of previous breeding outcome on site fidelity in males couldn't be expressed. Moreover, the relationship between reproduction success and site fidelity was found to be greater in females than males (Murphy 1996, Haas 1998, Sedgwick 2004). No effect of breeding outcome on fidelity in females could cause extended breeding period, which allows repeated breeding attempts, loose of nutrition resources and the following higher mortality in consequent years (see above). Moreover, this higher mortality of females supports high proportion of predation in the study area (Musilová unpubl. data). Survival of first-year male was higher than females of Reed bunting in Britain (Siriwardena *et al.* 1998). Mezquida & Villaran (2006) showed higher mortality of females than males in Reed Bunting wintering in central Spain. The geographical differences in site-fidelity caused by differences in female mortality were confirmed in Pied Flycatcher (Sanz 2001). We assume that lower survival of Reed Bunting female makes site fidelity affected by previous breeding outcome more difficult. The likelihood of high competition in males, as well as higher mortality in females, seems to be important factor affecting territory settlement in year of banding and fidelity probability in consequent years. On the other hand, in a few bird species, reproductive outcome did not affect the likelihood of return in successive years (e.g. Gavin & Bollinger 1988, Haig & Oring 1988, Payne & Payne 1993, Pyle *et al.* 2001, Shutler & Clark 2003, Hallworth *et al.* 2008). These studies indicate that the effect of previous breeding success is not important in high-quality territories, which are occupied in any case. Individual decision to reoccupied territory could be related to site quality (Greenwood 1980, Newton 2008). Therefore, the low effect of breeding performance on fidelity could reflect optimal breeding habitat in the study area. Moreover, Pasinelli *et al*. (2008) showed that large and small wetlands fragments are equally suited as breeding grounds for Reed Bunting. High male competition and lack of suitable breeding habitats occupied by older residents in the study area support high importance of these fragmented wetlands (fishponds) for Reed Bunting in Central European fishpond landscape.

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References

Artl, D. & Part, T. 2008. Sex-biased dispersal: A result of a sex difference in breeding site availability. *American Naturalist* **171**: 844–850.

Bastian, H.V. 1992. Breeding and natal dispersal of Whinchats *Saxicola rubetra*. *Ringing & migration* **13**: 13–19.

Bauer, H.G. 1987. [Geburtsortstreue und Streuungsverhalten junger Singervögel.] *Vogelwarte* **34**: 15–32 (in German).

Benett, P.M. & Owens, P.F. 2005. *Evolutionary Ecology of Birds.* Oxford University Press, New York.

Bensch, S. & Hasselquist, D. 1991. Territory infidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *J. Anim. Ecol.* **60**: 857–871.

Berkunsky, I. & Reboreda, J.C. 2009. Nest-site fidelity and cavity reoccupation by Blue-fronted Parrots Amazona aestiva in the dry Chaco of Argentina. *Ibis* **151**: 145–150.

Berndt, R. & Sternberg, H. 1968. Terms, studies and experiments on the problems of bird dispersion. *Ibis* **110**: 256–269.

Berthold, P. 2001. *Bird Migration: A General Survey,* English edn. Oxford University Press, New York.

Blümel, H. 1982. [*Die Rohrammer. Die Neue Brehm-Bucherei.*] Die Neue Brehm-Bucherei. Nr. 544. A. Ziemsen, Wittenberg Lutherstadt (in German).

Bollinger, E. K. & Gavin, T. A. 1989. The effects of site quality on site fidelity in Bobolinks. *Auk* **106**: 584–594.

Bub, H. 1985. [Kennzeichen und Mauser europäischer Singvögel.] Die Neue Brehm-Bucherei. Nr. 570. A. Ziemsen, Wittenberg Lutherstadt (in German).

Burnham, K.P. & Anderson, D.R. 2002: *Model selection and multimodel inference: a practical information-theoretic approach.* Springer-Verlag, New York.

Calabuig, G., Ortego, J. Cordero, P.J., & Aparicio, J.M. 2008. Causes, consequences and mechanism of breeding dispersal in the colonial lesser kestrel, *Falco neumanni*. *Anim. Behav*. **76**: 1989–1996.

Cooch, E. & White, G. 2009. *Program MARK. A Gentle Introduction.* 8th edition. Department of fish, Wildlife, and Cons. Biol. Colorado State University, Fort Collins.

Cramp, S. & Perrins C.M. 1994. *The birds of the Western Palearctic*. Vol. IX.: Buntings and New World Warblers. Oxford UniversityPress, Oxford and New York.

Diquinzio, D.A., Paton, P.W.C. & Eddleman, W.R. 2001. Site fidelity, phylopatry, and survival of promiscuous saltmarsh sharp-tailed sparrows in Rhode Island. *Auk* **118:** 888–899.

Dyrcz, A. 1984. Mating systems in European Marsh-nesting Passeriformes. *Proc. Int. Ornithol. Congr*. **19:** 2613–2623.

Gavin, T. A. & Bollinger, E. K. 1988. Reproductive correlates of site fidelity in Bobolinks (*Dolichonyx oryzivorus*). *Ecology* **69**: 96–103.

Glutz von Blotzheim, U. & Bauer, K. (eds.) 1997. [Hand buch der Vogel Mitteleuropas]. Ba 14; Anea Verlag, Wiesbaden (in German).

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematic* **13**: 1–21.

Greenwood, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim.Behav*. **28:** 1140–1162.

Greenwood, P.J., Harvey, P.H. & Perrins, C.M. 1978. Inbreeding and dispersal in the Great Tit. *Nature* **271**: 52–54.

Haas, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* **115**. 929–936.

Haig, S.M. & Oring, L.W. 1988. Mate, site and territory fidelity in Piping Plovers. *Auk* **105**: 268–277.

Hallworth, M., Ueland, A., Anderson, E., Lambert, J.D. & Reitsma, L. 2008. Habitat selection and site fidelity of Canada Warblers (*Wilsonia canadensis*) in Central New Hampshire. *Auk* **125**: 880–888.

Hansson, B., Bensch, S. & Hasselquist, D. 2002a. Restricted dispersal in a long-distance migrant bird with patchy distribution, the Great Reed Warbler. *Oecologia* **130**: 536–542.

Hansson, B., Bensch, S. & Hasselquist, D. 2002b. Predictors of natal dispersal in Great Reed Warblers: results from small and large census areas. *J. Avian Biol.* **33**: 311–314.

Harvey, P.H., Greenwood, P.J. & Perrins, C.M. 1979. Breeding area fidelity to Great Tits (*Parus major*). *J. Anim. Ecol.* **48**: 305–313.

Harvey, P.H., Greenwood, P.J., Campbell, B. & Stenning, M.J. 1984. Breeding dispersal of the Pied Flycatcher (*Fycedula hypoleuca*). *J. Anim. Ecol*. **53**: 727–736.

Honza, M., Literák, I. & Petro, R. 1993. Postbreeding occurence of the Reed Bunting (*Emberiza schoeniclus*) in the upper reaches of the Odra River and its migration to the Paduan Lowland. *Ornis Hungarica*. **4**: 49–55.

Hopp, S. L., Kirby A. & Boone C. A. 1999. Banding returns, arrival pattern and site fidelity of White Eyed Viros. *Wilson Bull.* **111**: 46–55.

Howlett, J.S. & Stutchbury, B.J. 2003. Determinants of between-season site, territory, and mate fidelity in hooded warblers (*Wilsonia citrina*). *Auk* **120**: 457–465.

Hudec, K. (ed.) 1983: [*Fauna ČSSR. Sv. 24. Ptáci III (2)*]. Ac ademia, Praha (in Czech).

Janda, J. & Pechar, L. et al. 1996. Sustainable use of fishponds in the Třeboňsko protected landscape area and biosphere reserve. *České koordinační středisko IUCN - Světového svazu ochrany přírody Praha a IUCN Gland, Švýcarsko a Cambridge, Velká Británie, 189 pp.*

Johnson, M. & Walters, J.R. 2008. Effects of mate and site fidelity on nest survival of Western Sandpipers (*Calidris mauri*). *Auk* **125**: 76–86.

Klemp S. 2003. Altitudinal dispersal within the breeding season in the Grey Wagtail *Motacilla cinerea*. *Ibis* **145**. 509–511.

Krištín A., Hoi H., Valera F. & Hoi C. 2007. Philopatry, dispersal pattern and nest-site reuse in Leader Grey Shrikes (*Lanius minor*). *Biodivers. Conserv*. **16**. 987–995.

Lack, D. 1954. *The natural regulation of animal numbers.* Clarendon Press, Oxford.

Lebreton, J.D., Pradel, R. & Clobert, J. 1993. The statistical analysis of survival in animal populations. *Trend. Ecol. Evol.* **8**: 91–95.

Mezquida, E.T. & Villaran, A. 2006. Abundance variations, survival and site fidelity of Reed Buntings *Emberiza schoeniclus* wintering in central Spain. *Ornis fenn*. **83**: 11–19.

Murphy, M.T. 1996. Surviorship, breeding dispersal and mate fidelity in Eastern Kingbirds. *Condor* **98**: 82–92.

Musilová, Z. 2008. Reed Bunting *Emberiza schoeniclus.* In: Cepák, J., Klvaňa P., Škopek, J., Schröpfer, L., Jelínek, M., Hořák, D., Formánek, J. & Zárybnický J., (eds.) 2008. *Czech and Slovak Bird Migration Atlas.* Aventinum. Praha, Czech Republic. [In Czech with English summary.]

Newton, I. 1992. *Life time reproduction in Birds*. Academic Press, London.

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

Newton, I. 2008. *The migration ecology of birds.* Academic Press, London.

Okulewicz, J. 1989. [Biologia i ekologia Rozrodu Potrzosa (*Emberiza schoeniclus*) w rejonie stawów Milickich.] *Ptaki Slaska 7:*1–39 (in Polisch).

Pärt, T. 2001. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe. Anim. Behav*. **62:** 379–388.

Pascual, J. & Senar, J.C. 1996. What are different biometric measurements of avian body size actually measuring? *Butll. GCA* **13**: 1–8.

Pasinelli, G., Mayer, Ch., Gouskov, A. & Schiegg, K. 2008. Small and large wetland fragments are equally suited breeding sites for a ground-nesting passerine. *Oecologia* **156:** 703–714.

Payne, R. B. & Payne, L. L. 1993. Breeding dispersal in Indigo Buntings: Circumstances and consequences for breeding success and population structure. *Condor* **95**: 1–24.

Pyle, P., Sydeman, W.J. & Hester M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin´s auklets. *J. Anim. Ecol*. **70**: 1088–1097.

Sanz, J.J. 2001. Latitudinal variation in female local return rate in the philopatric Pied Flycatcher (*Ficedula hypoleuca*). *Auk* **118**: 539–543.

Schjørring, S., Gregersen, J. & Bregnballe, T. 2000. Sex difference in criteria determining fidelity towards breeding sites in the great cormorant. *J. Avian Ecol*. **69**: 214–223.

Schlossberg, S. 2009. Site fidelity of shrubland and forest birds. *Condor* **111**: 238–246.

Sedgwick, J.A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). *Auk* **121** (4): 1103–1121.

Sedláček, O. & Fuchs, R. 2008. Breeding site fidelity in urban Common Redstarts *Phoenicurus phoenicurus*. *Ardea* **96:** 261–269.

Senar, J.C. & Pascual, J. 1997. Keel and tarsus length may provide a good predictor of avian body size. *Ardea* **85**: 269–274.

Sergio, F. & Newton, I. 2003. Occupancy as a measure of territory quality. *J. Anim. Ecol.* **72**: 857–865.

Sergio, F., Blas, J., Forero, M.G., Donázar, J.A. & Hiraldo, F. 2007. Sequential settlement and site dependence in a migratory raptor. *Behav.Ecol*. **9**: 811–821.

Sergio, F., Blas, J. & Hiraldo, F. 2009. Predictors of floater status in a long-lived bird: a cross sectional and longitudinal test of hypotheses. *J.Anim.Ecol.* 78: 109–118.

Shutler, D. & Clark, R.G. 2003. Causes and consequences of Tree Swallow (*Tachycineta bicolor*) dispersal in Saskatchewan. *Auk* **120**: 619–631.

Šimek, J. 2001. Patterns of breeding fidelity in the Red-backed Shrike (*Lanius collurio*). *Ornis fenn.* **78**: 61–71.

Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. 1998. Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study* **45**: 276–292.

Solonen, T. 1979. Population dynamics of the Garden Warbler *Sylvia borin* in southern Finland. *Ornis Fenn.* **56**: 3–12.

Sutherland, W.J, Newton, I. & Green, R.E. 2005. *Bird Ecology and Conservation. A Handbook of Techniques*. Oxford University Press, New York.

Svensson, L. 1992. *Identification guide to European passerines.* Fourth edition. Stockholm.

Swanson, D.L., Liknes, E.T. & Dean, K.L. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant Ruby-crowned Kinglets. *Wilson Bull.* **111**: 61–69.

Tryjanowski, P., Sparks, T.H., Ptaszyk, J. &Kosicki, J. 2004. Do White Storks Ciconia ciconia always profit from an early return to their breeding grounds? *Bird Study* **51**: 222–227.

Vadász, C., Német, Á., Karcza, Z., Loránt, M., Biró, C. & Csörgő, T. 2008. Study of site fidelity of Acrocephalus Warblers in Central Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae* **54:** 167–175.

Vergara, P. Aguirre, J. I., Fargallo, J. A. & Dávila, J. A. 2006. Nest-site fidelity and breeding success in White Stork *Ciconia ciconia*. *Ibis* **148**. 672–677.

Verhulst, S., Perrins, C.M. & Riddington, R. 1997. Natal dispersal of Great Tits in a patchy environment. *Ecology* **78**: 864–872.

Weatherhead, P.J. & Forbes, M.R.L. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behav. Ecol.* **5**: 426–433.

Wesołowski, T. 2006. Nest-site re-use: March Tit *Poecile palustris* decision in a primeval forest. *Bird Study* **53**: 199–204.

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

Winkler, D.W., Wrege, P.H., Allen, P.E., Kast, T.L., Senesac, P., Wasson, M.F., Llambías, P.E., Ferretti, V. & Sullivan, P.J. 2004. Breeding dispersal and philopatry in the Tree Swallow. *Condor* **106**: 768–776.

Young, W. & Moore, F. R. 1997. Spring stopover of intercontinental migratory trushes along the northern coast of the Gulf of Mexico. *Auk* **114**: 263–278.

Table 1. Number of banded and recovered Reed Buntings in the study area in 2000-2009 (between rounds brackets is proportion of birds banded in previous years).

	Males				Females			
	No. ringed	year 0	year + 1	years + 1 ≤	No.ringed	year 0	year + 1	years + 1 ≤
2000	16 (-)	8	6	7	12 (-)	3	2	2
2001	25 (2)	16	7	7	14 (1)	7	1	1
2002	27 (4)	15	6	7	20 (-)	14	3	3
2003	23 (5)	9	4	5	17 (3)	8	0	0
2004	16 (3)	6	6	6	18 (0)	5	3	3
2005	15 (4)	3	2	3	16 (1)	7	3	4
2006	8 (2)	3	4	4	2 (1)	1	0	0
2007	16 (4)	8	1	2	10 (-)	0	0	0
2008	3 (1)	0	1	1	6 (-)	0	0	0
2009	4 (-)	1	-	-	2 (-)	-	-	-

year 0 – birds recovered in year of banding, year + 1 – birds recovered in subsequent year, years + 1 ≤ - birds recovered in any subsequent years

Table 2. Model selection of territory settlement for adult Reed Bunting (birds recorded in year of banding in study area) using different models (n=177; 105 males and 72 females).

Model	np	AICc	ΔAICc	AICc weight	Deviance
Φ(sex*age)p(.)	3	207.31	0.00	0.77	201.17
Φ(wl)p(.)	2	211.79	4.48	0.08	207.72
Φ(.)p(sex)	2	212.36	5.05	0.06	208.29
Φ(sex)p(.)	3	214.43	7.12	0.02	208.29
Φ(w)p(.)	2	220.46	13.15	0.00	216.39
Φ(age)p(.)	4	220.64	13.33	0.00	212.41
Φ(tl)p(.)	4	220.95	13.64	0.00	212.71
Φ(ter)p(.)	2	225.59	18.28	0.00	221.52
Φ(date)p(.)	2	226.52	19.21	0.00	222.45
Φ(.)p(.)	3	228.53	21.22	0.00	222.39

AICc = Akaike´s information criterion, ΔAICc = differences between that model and the model with the lowest AICc, np = number of parameters, Φ = apparent survival probability, p = recapture probability, . time independent effect, * interaction of terms, wl = wing length, w = weight, tl = tarsus length, ter = number of occupied territories.

Table 3. Model selection of site fidelity for Reed Bunting (residents recorded in subsequent years) using different models (n=111; 68 males and 43 females).

Model	np	AICc	ΔAICc	AICc weight	Deviance
Φ(sex)p(.)	3	207.25	0.00	0.49	201.10
Φ(sex)p(sex)	4	208.20	0.95	0.30	199.94
Φ(sex*age)p(.)	4	209.29	2.03	0.18	201.02
Φ(.)p(sex)	4	212.91	5.65	0.03	204.64
Φ(tl)p(.)	3	217.45	10.20	0.00	211.29
Φ(wl)p(.)	3	217.51	10.26	0. 00	211.36
Φ(w)p(.)	3	218.28	11.03	0.00	212.12
Φ(ter)p(.)	3	219.99	12.74	0.00	213.83
Φ(.)p(.)	6	222.53	15.28	0.00	209.97
Φ(date)p(.)	3	262.19	54.94	0.00	256.03

AICc = Akaike´s information criterion, ΔAICc = differences between that model and the model with the lowest AICc, np = number of parameters, Φ = apparent survival probability, p = recapture probability, . time independent effect, * interaction of terms, wl = wing length, w = weight, tl = tarsus length, ter = number of occupied territories.

Table 4. Model selection of site fidelity for Reed Bunting parents using different models (n=82; 44 males and 38 females).

Model	np	AICc	ΔAICc	AICc weight	Deviance
Φ(sex)p(.)	2	84.17	0.00	0.67	80.02
Φ(.)p(sex)	3	86.33	2.16	0.23	80.02
Φ(sex*age)p(.)	4	88.05	3.89	0.10	79.53
Φ(age)p(.)	2	96.02	11.85	0.00	91.87
Φ(ter)p(.)	2	98.09	13.92	0.00	93.94
Φ(.)p(.)	2	98.90	14.73	0.00	94.75
Φ(suc)p(.)	4	103.24	19.07	0.00	94.72

AICc = Akaike´s information criterion, ΔAICc = differences between that model and the model with the lowest AICc, np = number of parameters, Φ = apparent survival probability, p = recapture probability, . time independent effect, * interaction of terms, suc = breeding success, ter = number of occupied territories.

Figure 1. Recurrence of banded adults in the study area in 2000-2009 (0 - the same year, 1-4 the following years).

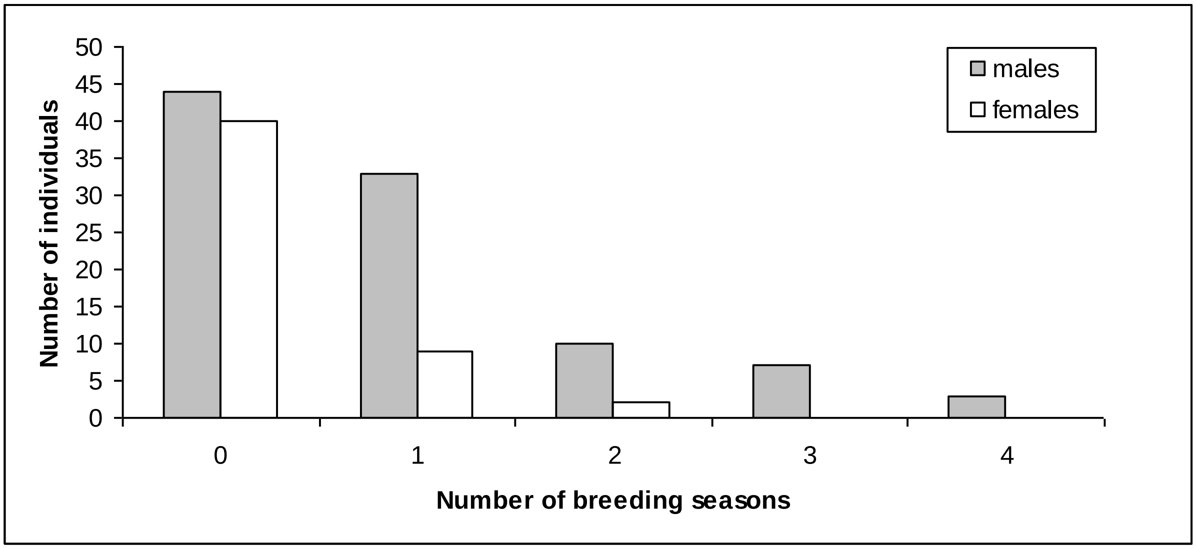
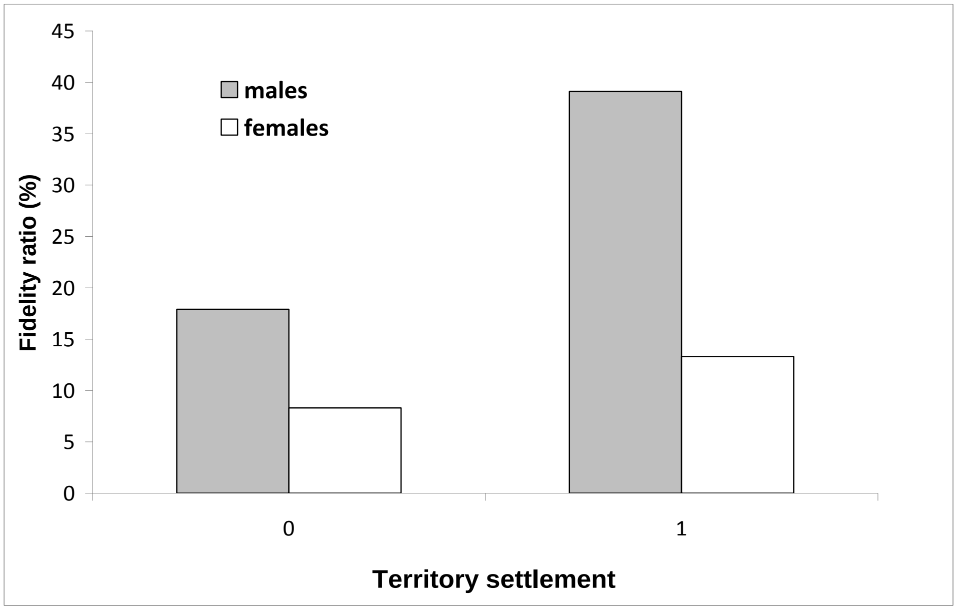


Figure 2. Fidelity ratio of males and females in relation to territory settlement in the study area (0 -not detected, 1 - re-sighted in the study area).



KAPITOLA III.

Musilová, Z., Musil, P. & Poláková S. Males try to attract neighbouring females during incubation in the Reed Bunting *Emberiza schoeniclus*. *submitted*

Males try to attract neighbouring females during incubation in the Reed Bunting *Emberiza schoeniclus*

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Key words: song in the Reed Bunting, incubation, song type, honest signal, *Emberiza schoeniclus*, mate choice

Running title: Song types in the Reed Bunting

Introduction

In many bird species, females tend to choose mates on the basis of differences in male's song and it could serve as an assessment of the condition of the potential mate (Marler & Slabbekoorn 2004). In this case, the quality of the singer should be related to cost of the signal to be honest (Grafen 1990). We can summarise the following main song characteristics which could be important in mate-choice communication: specific song structure called "sexy syllables" (e.g. Vallet & Kreutzer 1995), song repertoire (e.g. Lambrechts & Dhont 1986), song rate (e.g. Radesäter *et al.* 1987) and song performance (e.g. Hofstad *et al.* 2003). Correlations between male song rate and mating success suggest that females prefer mates that sing at the highest rates (e.g. Radesäter *et al.* 1987, Eens *et al.* 1991, Collins *et al.* 1994). Moreover, in some species males may dramatically shift the use of a certain song after attracting a female (Highsmith 1989).

In the Reed Bunting *Emberiza schoeniclus* was shown that males use different singing styles (Figure 1) related to male mating status. Unpaired males sing a rapid song (type I) and paired males sing a slow one (type II) (Nemeth 1996). Type III was classified as a continuous song of the type II, which is mainly produced during the dawn chorus and it is an honest signal of quality due to a connection between its production and a level of extra-pair paternity (EPP) (Suter *et al.* 2009). Moreover, song expressed as the "all-clear" signal, an example of a non-sexual function in acoustic communication between male and female, was investigated during incubation and feeding of nestlings. In this case, the sonogram analyses were not accomplished. This signal shows that there is no risk of predation and it is safe for the female to exit the nest or feed the young, as was ascertained using observation of singing males and incubating or feeding females (Wingelmaier *et al.* 2007).

The main aim of this study is to assess seasonal timing of different song types in the Reed Bunting *Emberiza schoeniclus* and its relation to various stages of the breeding cycle. We predicted an increase of the song type III, as an honest signal of male's quality, during fertile stage of female and conversely the decrease of this song type during incubation and feeding of nestlings. We assume that the "all-clear" signal to incubating and feeding female likely belongs to the type II.

Methods

The Reed Bunting is a short-distance migratory, granivorous passerine that breeds on the ground in open wetland habitats and shows highly fragmented (patched) distribution in Central European landscape (Hudec 1983, Blümel 1989, Cramp & Perrins 1994). Even though socially monogamous species, Reed Buntings show a high level of extra-pair paternity (Dixon et al. 1994, Bowmann & Komdeur 2005, Kleven & Lifjeld 2005). They are able to breed usually twice during one breeding season (e.g. Blümel 1989).

The study was carried out on fishponds in South Bohemia (Jindřichův Hradec district, the Czech Republic) located close to Kardašova Řečice town (49˚11'–49˚13' E, 14˚51'–14˚ 54' N, 443–480 m a.s.l.) (four fishponds: Hejtmánků - 1.6 ha, Špitálský - 5.9 ha, Obecní - 10.3 ha, and Šlechtův ponds - 5.6 ha) and close to Lužnice village (Černičný fishpond - 49˚05' E, 14˚45' N, 42.6 ha, 425 m a.s.l.). Particular fishponds were isolated, without wetlands corridors, surrounded by mixture of forest patches, fields and villages (for more details of the habitat see Janda *et al.* 1996). The number of occupied territories varied between 2 and 8 breeding pairs on individual fishponds.

In total, we monitored 122 territories of the study species in 2003–2007. Nests were found with the use of a systematic searching of the focal area or monitoring of feeding parents. Nests were repeatedly controlled and current stage of each brood was recorded. Age of clutch/nestlings estimates allowed back-calculation of first egg-laying date for the nest according to Blümel

(1982), Hudec (1983) and Okulewicz (1989). We defined the following stages of breeding: 1 - more than a week and less than two weeks before egg laying (pre-breeding stage), 2 - a week before egg laying (1st fertile stage), 3 - egg laying (2nd fertile stage), 4 - incubation, 5 - nestlings in a nest, 6 - a week after nestlings abandonment (movement of nestlings recorded in males territory), 7 - more than a two weeks after nestlings abandonment, 8 - uncertain because of a predation or an abandonment of the clutch. Our research activities were carried out during the breeding season from March to the beginning of July. Adult Reed Bunting males were caught and marked using unique individual combination of colour rings (Ecotone) and aluminium rings of the National Museum Prague.

Songs of males were recorded using directional microphone (Sennheiser ME 66) and Marantz cassette recorder (PMD 201). We noted date, time, locality, position on the map and if possible, phase of the nest and individual colour rings of the male for each recording. We recorded songs between 6 am and 8 pm. Repeated recordings of the same male in one day were not included in the analysis. Recordings were digitalised and categorised using Avisoft SASLab Pro version 4.38 (Avisoft Bioacoustics, Berlin). We saved Wav-files with the following parameters: input sample rate 44 100 Hz, sample format 16 bit. Correspondingly, sonograms were produced with the following parameters: type Hamming, FFT Length 256 and frame 50%. We used three types of Reed Bunting song according to Nemeth (1996) and Suter *et al.* (2009). Recordings were categorised as rapid song (type I), slow song (type II) and continuous song (type III) by time measurement. We applied Nemeth (1996) for the definition of a syllable.

We compared differences in using of song types and the date during the breeding season and the number of territories per the pond. For these analyses, we used ANOVA in program STATISTICA 8.0 (StatSoft Inc. 2007) and all data were ln-transformed. Then we tested relationship between nesting stage and fertile or infertile period and the types of songs by contingency tables and Fisher exact test in STATISTICA 8.0.

Results

Using of the three types of song significantly differed according to the total number of territories on fishpond ($n = 422$, $F = 7.2$, $df = 2$, $p < 0.01$), the type II was used more in the ponds with a smaller number of territories than type III ($p < 0.01$). There was no difference in using of the song types during progress of the breeding season ($n = 422$, $F = 1.8$, $df = 2$, $p = 0.174$).

Different song type was explained significantly by the stage of breeding cycle (Pearson chi square = 32.8, df = 14, p = 0.003). Song type I occurs in pre-breeding stage of the cycle, more than two weeks after nestling abandonment and after predation or clutch abandonment (Figure 2). When comparing only recordings from the 1^{st} fertile stage and egg-laying of singer's female (stage 3 and 4) and incubation and feeding (stage 4 and 5), we were able to compare proportion of song type II and III in fertile (stage 3 and 4) and infertile period (stage 4 and 5) of the female (Figure 2). The difference was not confirmed ($n = 91$, Fisher exact test, $p = 0.6$).

Discussion

We found out that the number of pairs on the fishpond affects the proportion of different singing types with an increased use of song type III as an honest signal of quality (Suter *et al.* 2009) on more populated localities. In this case, conspecific density could affect the honesty of call features as signals of male and/or territory quality (Penteriani 2003). Our finding could be also connected with a higher pressure of male competition in more suitable habitat and a possible role of song type III in male-male competition. On the contrary, Nemeth (1996) indicated that different singing styles seem to be directed to females. We incline to his finding because song overlapping is likely connected with male-male competition in this species (unpubl. data). It means that a male can set the time of singing in aim to overlap song with that of another male (Marler & Slabbekoorn 2004). Reed Bunting's males probably direct the song type III to motivate females and overlap another male to vocal fight.

We found out that Reed Bunting males use different song types in different stages of their breeding cycle. The distribution of song type I during the breeding cycle confirmed the Nemeth's (1996) definition of the song type I which belongs to unpaired male. We recorded song type I in a pre-breeding stage (possible absence of singer's female) or more than two weeks after nestling abandonment and in a case of predation or an abandonment of the clutch (possible death of singer's mate). No recordings of song type I were registered in the confirmed breeding period (fertile stage or an active nest).

Conversely, we did not confirm any significant differences in proportion of song type II and III in fertile period of singer's female and successive incubation and feeding of nestlings. This is in contrast with the assumption that male tends to communicate with his female using non-sexual "all-clear" signal during incubation in the aim to minimise the risk of predation of the clutch (Wingelmaier *et al.* 2007). We can emphasise that the continuous song type III is an honest signal of male's quality. The amount of song produced per unit time might depend directly on male energy balance and could depend on the availability of food on his territory (Searcy & Nowicki 2005). Moreover, Sutter *et al.* (2009) confirmed that song type III plays an important role in the female's choice of extrapair mates. Furthermore, Reed Bunting shows one of the highest levels of EPP within passerines (Dixon *et al.* 1994, Bowmann & Komdeur 2005, Kleven & Lifjeld 2005). According to our findings, we can assume that males of Reed Bunting seek extra-pair mates using song type III during incubation period of their own nests. High level of EPP could be also connected with increased song type III on more populated localities (see above). Moreover, Hofstad *et al.* (2002) showed that extended breeding season could lead to a better option for the male to attract a second female or to practice extra-pair copulation (EPC) during the incubation period of the first female in the Snow Bunting *Plectrophenax nivalis*. There was no trend in the timing of different song types during the whole breeding season. Nevertheless, Reed Buntings show extended breeding season with little synchronisation of the breeding pairs in the study area (pers. obs.).

According to our study, more research to confirm the connection between proportion of song type III during incubation and following individual male's fitness using proportion of his extra-pair nestlings in neighbour nest is needed.

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References

Blümel, H. 1982. *Die Rohrammer.* Die Neue Brehm-Bucherei. Die Neue Brehm-Bucherei. Nr. 544. A. Ziemsen, Wittenberg Lutherstadt.

Bouwman, K.M. & Komdeur, J. 2005. Old female Reed Buntings (*Emberiza schoeniclus*) increase extra-pair paternity in their broods when mated to young males. *Behaviour* **142**: 1449–1463.

Collins, S.A., Hubbard, C. & Houtman A.M. 1994. Female mate choice in the zebra finch: The effect of male choice beak colour and male song. *Behav. Ecol. and Sociol*. **35**: 21–25.

Cramp, S. & Perrins, C.M. 1994. *The birds of the Western Palearctic*. Vol. IX.: Buntings and New World Warblers. Oxford UniversityPress, Oxford and New York.

Dixon, A., Ross, D., Omalley, S.L.C. & Burke, T. 1994. Parental investment inversely related to degree of extra-pair paternity in the Reed Bunting. *Nature* **371**: 698–700.

Eens, M., Pinxten, R. & Verheyen, R.F. 1991. Male song as a cue for mate choice in the European Starling. *Behav.* **116:** 210–238.

Grafen, A. 1990. Biological signals as handicaps. *J. Theor. Biol.* **144**: 517–546.

Highsmith, R.T. 1989. The singing behaviour of golden-winged warblers. *Wils. Bull.* **101**: 36–50.

Hofstad, E., Espmark, Y., Moksnes, A., Haugan, T. & Ingebrigsten, M. 2002. The relationship between song performance and male quality in Snow Buntings (*Plectrophenax nivalis*). *Can. J. Zool.* **80**: 524–531.

Hudec, K. (ed.) 1983*: Fauna of ČSSR*. Birds III (2). Academia, Praha.

Janda, J. & Pechar, L. et al. 1996. *Sustainable use of fishponds in the Třeboňsko protected landscape area and biosphere reserve.* České koordinační středisko IUCN - Světového svazu ochrany přírody Praha a IUCN Gland, Švýcarsko a Cambridge, Velká Británie, 189 pp.

Kleven, O. & Lifjeld, J.T. 2005. No evidence for increased offspring heterozygosity from extrapair mating in the Reed Bunting (*Emberiza schoeniclus*). *Behav.Ecol.* **16**: 561–565.

Lambrechts, M.M. & Dhont, A.A. 1986. Male quality, reproduction, and survival in the Great Tit (*Parus major*). *Behav.Ecol. Sociobiol*. **19**: 57–63.

Marler, P & Slabbekoorn, H. (Eds) 2004. *Nature´s Music - the Science of Birdsong*. New York.

Nemeth, E. 1996. Different singing styles in mated and unmated Reed Buntings Emberiza schoeniclus. *Ibis* **138**: 172–176.

Okulewicz, J. 1989. Breeding biology and ecology of the Reed Bunting (*Emberiza schoeniclus*) in the region of the Milicz fishpond area. *Ptaki Slaska* **7**:1–39.

Penteriani, V. 2003. Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality. *Ibis* **145**: 127–135.

Radesäter, T., Jakobsson, S., Andbjer, N., Bylin, A. & Nyström, K. 1987. Song rate and pair formation in the willow warbler, Phylloscopus trochilus. *Anim. Behav*. **35**: 1645–1651.

Searcy, W.A. & Nowicki, S. 2005. *The evolution of animal communication.* Princeton University Press. New Jersey.

Suter, S.M., Ermacora, D., Rielle, N. & Meyer, D.R. 2009. A distinct reed bunting dawn song and its relation to extrapair paternity. *Anim. Behav*. **77**: 473–480.

Vallet, E. & Kreutzer, M. 1995. Female canaries are sexually responsive to special song phrases. *Anim. Behav*. **49**: 1603–1610.

Wingelmaier, K., Winkler, H. & Nemeth, E. 2007. Reed Bunting (*Emberiza schoeniclus*) males sing an “all-clear” signal to their incubating females. *Behav.* **144**: 195–206

Figure 1. Spectrograms of different song type in the Reed Bunting males

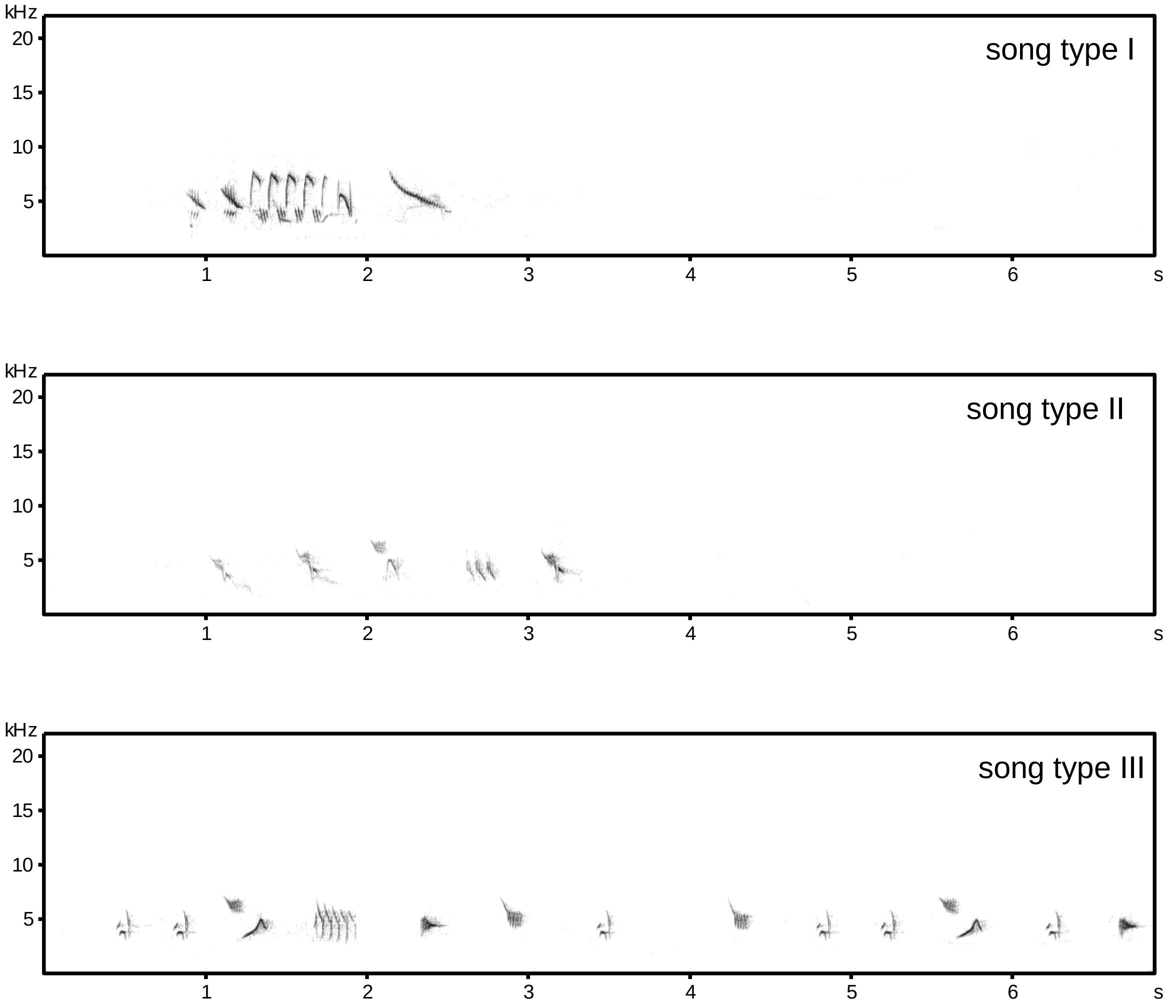
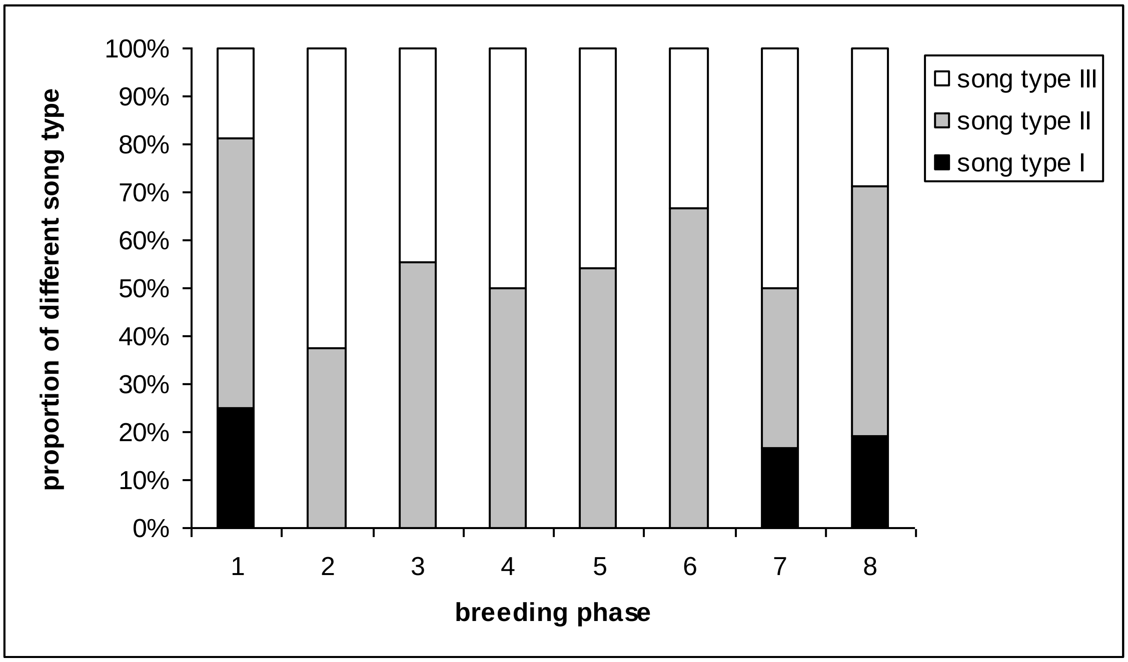


Figure 2. Proportion of different song type in relation to different stage of the singer's breeding cycle (1 - more than a week before egg laying, 2 - a week before egg laying, 3 - egg laying, 4 - incubation, 5 - nestlings in a nest, 6 - nestlings close to the nest, 7 - more than two weeks after nestlings abandonment, 8 - a predation or an abandonment of the clutch). n=164



PŘÍLOHA

(Další publikace, které nejsou součástí disertační práce, ale jsou přiloženy jako doklad širšího vědeckého směru autorky)

Musil, P., Nachtigalová, M., Hořák, D., Albrecht, T., Brožová, M., Klvaňa, P. & **Musilová, Z.** 2006. Survival and movements in relation to condition in individually-marked broods of diving ducks on South Bohemian fishponds. *J Ornithol. 147 (suppl.):* 216.

Musilová, Z. & Musil, P. 2006. Current status of International Waterbird Census in the Czech Republic. In: G.C. Boere, C.A. Galbraith & D.A. Stroud (eds.) *Waterbirds around the world. TSO Scotland Ltd, Edinburgh, UK:* 484–486.

Musilová, Z. 2008. Reed Bunting *Emberiza schoeniclus.* In: Cepák, J., Klvaňa P., Škopek, J., Schröpfer, L., Jelínek, M., Hořák, D., Formánek, J. & Zárybnický J., (eds.) 2008. *Czech and Slovak Bird Migration Atlas.* Aventinum. Praha, Czech Republic. [In Czech with English summary.]

Musil, P., Darolová, A., Jureček, J., **Musilová, Z.**, Podhrazský, M. & Slabeyová, K. 2008: Dlouhodobé změny početnosti zimujících hus v České republice a na Slovensku v letech 1991–2007. *Tichodroma 20:* 61–67.

Musilová, Z., Musil, P., Poláková, S. & Fuchs, R. 2009. Wintering ducks in the Czech Republic: population size, changes in population trends and distribution. *Wildfowl Special Issue*: 73–85.

Musil, P. **Musilová, Z.**, Fuchs, R. & Poláková, S. Long-term changes in numbers and distribution of wintering waterbirds in the Czech Republic (1966–2008). *Submitted to Bird Study.*

Long-term changes in numbers and distribution of wintering waterbirds in the Czech Republic (1966-2008)

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Short title: Trends in wintering waterbirds in Czechia

Key words: wintering waterbirds, changes in distribution, trends in numbers, Czech Republic, International Waterbird Census

Summary

Capsule Increasing species prevailed among wintering waterbirds in the Czech Republic in 1966-2008.

Aim To assess long-term trends in the numbers and distribution of the 37 most abundant wintering waterbird species in the Czech Republic.

Methods We used International Waterbird Census data from 48–639 wetland sites counted annually in the Czech Republic from 1966 to 2008, using log-linear poisson regression analysis.

Results Increasing trends were found for 16 species, 7 species were found to be declining and stable (5) or uncertain trends (7) amongst the remaining species. Wintering distribution (the ratio of sites occupied by a given species to the total number of sites counted) increased in 16 species and decreased in 3 species, broadly correlated with the species changes in distribution.

Conclusion Fish-eating birds, geese, dabbling and diving ducks and gulls increased, while waders decreased. Trends in numbers, as well as changes in distribution, of particular species were mostly explained by Western Palearctic population trends, although Teal decreased in the Czech Republic (in contrast general increases) and Bean Goose, Pochard, Common Gull increased in the Czech Republic compared with decreasing trends in the Western Palearctic. Rare, southern species were generally more increasing in numbers.

Introduction

Many waterbird species, recognized as being species of conservation concern, have significantly changed their numbers in the last decades (e.g. Birdlife International 2004, Wetlands International 2002, 2006). The population dynamics of waterbird species, as in many bird groups, is affected by various factors throughout the whole year, including the breeding season, spring and autumn migration and wintering season. Waterbirds generally breed in low densities over large areas (Scott & Rose 1996, Kear 2005) but aggregate in large numbers in winter when limited habitat may cause large temporal and spatial variability (Ridgill and Fox 1990). Inter-seasonal variation in numbers and distribution of particular species are considerably affected by weather and habitat changes (Wahl & Sudfeldt 2005; Maclean *et al*. 2008, Musil *et al.* 2008a, Musilová *et al.* 2009). Changes in wintering conditions can be assumed as a key-factor affecting wintering numbers, over-wintering survival and consequently the population dynamics of a particular species.

Among wintering waterbirds in Europe, significant population trends (either increases or decreases) have been found in roughly half of all species (52 %: Wetlands International 2002; 48 %: Wetlands International 2006), while the remaining species are considered as stable or species with uncertain trends. Although counting effort and coverage of particular countries by monitoring programmes should be taken into consideration, it still remains remarkable that the proportion of species with marked increasing or decreasing trends is highest in Europe amongst all the Ramsar regions (e.g. Kear 2005, Wetlands International 2006). Thus various analyses of wintering waterbirds trends at a national (Crove *et al*. 2008, Nilsson 2008, Slabeyová *et al.* 2008, 2009, Fouque *et al.* 2009), or regional (Mclean *et al.* 2008) level have been carried out. Nevertheless, a deeper, more-specific analysis of long-term trends in the numbers of wintering waterbirds from central Europe has been missing.

The Czech Republic is not a core waterbird wintering area because most wetlands usually freeze at some time during the winter (Hudec 1994; Delany *et al.* 1999; Musil *et al.* 2001; Gillisen *et al.* 2002). Despite this, its relatively mild climate and high diversity of smaller wetland habitats may provide some feeding opportunities throughout the winter period for birds which breed in northern Europe, particularly when freezing conditions in the Baltic region may limit the birds´ access to feeding areas e.g. Švažas *et al.* 2001, Nilsson 2008). Conversely, species with a more southerly distribution, which usually leave central Europe to winter in Mediterranean areas (Musil *et al*. 2001; Cepák *et al.* 2008), may delay their southbound movement in milder winters when non-freezing wetlands are more frequently available. The Czech Republic can therefore provide attractive wintering areas for waterfowl species with differing wintering strategies (Hudec 1994; Hudec *et al.* 1995).

The long tradition of wintering waterbird monitoring in the Czech Republic started with contributions to the International Waterbird Census in 1966 and now covers almost all sites of national importance. We use these data to try to answer the following questions:

Do numbers of Czech wintering waterbirds show long-term changes? Are the changes in numbers and distribution among individual waterbird species inter-correlated? What species-specific variables are responsible for changes in numbers and distribution of individual species? We test the effect of the following species-specific variables: body size, Western Palearctic population size and trend, mean wintering numbers and distribution in the Czech Republic, biogeographic position and conservation status at the national and European level.

Are there any differences in trends in numbers on running and standing waters? We might expect more conspicuous changes amongst individual species on standing waters compared to running water, because standing waters are more affected by a global warming that can extend the non-freezing water bodies suitable for wintering waterbirds.

Methods

Waterbird data

Long-term trends in the numbers and distribution of waterbird species were analysed using count data recorded in the Czech Republic for the International Waterbird Census (IWC), which is conducted in mid-January each winter, for the years 1966–2008 inclusive. Within the Czech Republic, the IWC counts have been carried out annually at 48 to 639 wetland sites in January from 1966 onwards, the year 2008 being the last year included in this study (Fiala 1980; Musil *et al.* 2001, Musilová & Musil 2006; Musilová *et al.* 2008). Altogether, 3,289,871 birds of 98 waterbird species were counted on 1,078 wetland sites in the Czech Republic during the study period. Data for the 37 most abundant waterbird species (i.e. 3,116,390 waterbirds in total) were included in the analysis. Large gulls (i.e. *Larus argentatus, Larus cachinnans and Larus michahellis)* were considered as only one bird species in accordance with the taxonomical situation current at the beginning of the study period (i.e. in 1966).

Trend analysis

Trend analyses were carried out using IWC data from 847 of the 1,078 sites. Only those sites which had been counted in at least two winters over the 1966 – 2008 period were included. Log-linear Poisson regression analysis was used to estimate missing data using TRIM software (Statistic Netherlands version 3.52, Pannekoek & Van Strien 2001). Serial correlation between annual numbers and over-dispersion in the data were taken into account while developing the models used to calculate the trends of wintering populations of investigated species. The models included change points to allow for changes in the slope parameters at some points in the time series (Pannekoek & Van Strien 2001; Fouque *et al.* 2007).

The multiplicative slope (*i.e.* the change in indices from one year to the next) was the value used to express population trends over the study period. Additionally, two separate analyses (using the TRIM software) were carried out for trends in numbers of birds occurring on two main wetland habitat types, *i.e*. running water (444 sites) and standing water (403 sites). For running waters (rivers and streams), sites were defined as river sections with known boundaries, such as dams, weirs and bridges; standing water sites included fishponds, reservoirs, gravel and sand-pit lakes, and industrial settling ponds (Chytil *et al.* 1999).

Distribution of species

The distribution of each species was described as the ratio (arcsin transformed) of the number of sites occupied by that species to the total number of sites investigated. Linear regression analysis was then used to identify potentially significant long-term changes in species distribution. Correlation coefficients derived from the linear regression analysis were used to describe the change in species distribution over the study period for each species (Table 1).

Species- specific variables

We use the following species specific-variables in aim to find ecological factors responsible for analysed changes in numbers and distribution of individual species. In total, 7 eco-taxonomical group were distinguished, i.e. fish-eating birds, geese, dabbling ducks, diving ducks, waters, gulls and others. Moreover, we used mean body weight as the measurement of body size (from Snow and Perrins 1998). Data about population trends and sizes in western Palearctic were used from Wetlands International (2006) and, in particular, from Birdlife International (2004). The geographical distribution of an investigated species was classified using the latitudinal midpoint

(Lemoine 2007), i.e. the difference between the southernmost and northernmost latitudes of the species breeding range (Snow and Perrins 1998).

We used the Czech IWC data as values expressing mean numbers (annual number of individuals) and mean distribution (mean number of occupied sites) in the Czech Republic for the period 1966-2008. The conservation status of a particular species was classified using its listing in Annex 1 of the EU Bird directive (European level) and using the classification of the species under Czech legislation Act No. 114/92 Coll. and Regulation No. 395/1992 Coll., Annex No. III (list of Specially-Protected Animals: endangered, strongly-endangered and critically-endangered; Hudec *et al.* 1999).

The influences of species-specific variables on trends in numbers or changes in distribution of individual species were tested by GLM for normal distribution with the identity link function in STATISTICA 8.0 (StatSoft Inc 2008).

Results

Trend in numbers

Population trends were recorded in the 37 most common wintering waterbird species in the Czech Republic in 1966-2008. Among those investigated, 18 species were found out to be increasing and only 7 species were recorded as decreasing (using TRIM ver. 3.52, Pannekoek & Van Strien 2001). The trends of 5 species were assessed as being 'stable' and the trends of 7 species were assessed as 'uncertain'.

A 'strong increase' was apparent in Cormorant, Great White Egret, White-fronted Goose, Greylag Goose, Tufted Duck, White-tailed Eagle and in 'large gulls' (i.e. *Larus argentatus, Larus cachinnans and Larus michahellis)*. A 'moderate increase' was recorded in Grey Heron, Mute Swan, Wigeon, Mallard, Pochard, Smew, Goosander, Common Gull, Kingfisher, Grey

Wagtail and Dipper. On the other hand, a moderate decrease was recorded in Little Grebe, Great Crested Grebe, Teal, Moorhen, Coot and Black-headed Gull. Stable species included: Pintail, Scaup, Velvet Scooter, Goldeneye and Green Sandpiper. No trend (i.e. 'uncertain') was found in the case of the less abundant Whooper Swan, Gadwall, Shoveler, Red-crested Pochard, Feruginous Duck and Lapwing.

Changes in distribution

Distribution (i.e. the ratio of occupied sites to total number of investigated sites) increased in 16 species, and, by contrast, decreased in only 3 of the species during the study period. No significant changes in distribution were found in 18 species during the study period. A significant increase in distribution ($P < 0.05$) was recorded in Cormorant, Great White Egret, Grey Heron, Mute Swan, Bean Goose, White-fronted Goose, Greylag Goose, Wigeon, Gadwall, Mallard, Red-crested Pochard, Tufted Duck, Goosander, White-tailed Eagle, Common Gull, 'large gulls' (i.e. *Larus argentatus, Larus cachinnans and Larus michahellis)* and Kingfisher. On the other hand, the distribution decreased in three species: i.e. in Little Grebe, Teal and Ferruginous Duck.

Changes in numbers (indicated by the multiplicative rate of change of values) generally correlated with changes in distribution (correlation coefficient) among the waterbird species analysed ($y = -3.446 + 3.603x$; $r = 0.695$, $n = 37$, $P < 0.0001$; Fig. 1). Nevertheless, the increase in distribution (i.e ratio of occupied sites) was more marked than the increase in numbers in, for example, Grey Heron, Wigeon, Mallard, Goosander, and White-tailed Eagle. On the other hand, the decrease in numbers was more marked than the decrease in distribution in, for example, Great Crested Grebe, Moorhen, Coot, Snipe and Black-headed Gull. Moreover, the distribution of Ferruginous Duck decreased significantly during the study period, whereas its numbers show an 'uncertain trend' (Table 1).

Changes in number of waterbirds on standing and running waters

Population trends of wintering waterbirds were analysed separately (using TRIM ver. 3.52, Pannekoek & Van Strien 2001) for two main wetland habitats in the Czech Republic (i.e. for standing and running waters). Overall, 13 increasing, 5 decreasing and 4 stable species were found on standing waters, and 18 increasing, 4 decreasing and 5 stable species recorded on running waters. The number of species with an uncertain trend was higher on standing waters (15) than on running waters (10). Changes in numbers (indicated by the multiplicative rate of change of values) on standing and running waters were generally correlated among the waterbird species analysed ($y = 0.452 + 0.575x$; $r = 0.568$, $n = 37$, $P < 0.001$; Fig. 2).

Nine species increased in both habitat types, i.e. Cormorant, Grey Heron, Mute Swan, Wigeon, Mallard, Goosander, White-tailed Eagle, Common Gull and Kingfisher. Moreover, 4 waterbird species (i.e. Greylag Goose, Pintail, Green Sandpiper, ‘large gulls’) increased on standing waters, whereas 9 species (i.e. Great White Egret, Bean Goose, White-fronted Goose, Gadwall, Pochard, Tufted Duck, Smew, Grey Wagtail, Dipper) increased on running waters. Among these latter 9 species, only Pochard numbers increased on rivers and, on the other hand, decreased on standing waters. Numbers of Little Grebe and Coot decreased in both standing and running waters. Moreover, numbers of Pochard (see above), Moorhen and Black-headed Gull decreased on standing waters, and numbers of Great Crested Grebe and Teal decreased on running waters. Numbers of Goldeneye were stable in both types of wetland habitat. Stable wintering populations were found in Great Crested Grebe, Teal and Tufted Duck on standing waters, and in Pintail, Moorhen, Green Sandpiper and Black-headed Gull on running waters.

Effect of species- specific variables

Trends in numbers, as well as changes in distribution, of particular species were affected by similar species-specific variables (Tables 2 and 3). Both these values were significantly affected by a species' population trend in the Western Palearctic and by its eco-taxonomical group. An increase in both numbers and distribution prevailed in fish-eating birds, geese, dabbling and diving ducks and gulls. Only in waders did a decrease in numbers prevail. Changes in numbers, as well as changes in distribution, of gulls varied remarkably among species: including the decreasing Black-headed Gull and increases in other species (Common Gull, 'large gulls'). The values in 'Changes in numbers' and 'Changes in distribution' in most species reflected the species population trends in the Western Palearctic. There were only a few exceptions: firstly, wintering numbers and distribution of Teal decreased significantly in the Czech Republic; in contrast, numbers and/or distribution of three species (Bean Goose, Pochard, Common Gull) which were decreasing in the Western Palearctic increased in the Czech Republic.

The wintering distribution (mean number of occupied sites in the Czech Republic) and geographical distribution of the species (latitudinal midpoint of breeding range) affected a species trend in numbers: rare and southern species were generally increasing more in numbers. Conservation status in the Czech Republic also affected changes in distribution: increases in distribution were more frequent in non-protected species.

Furthermore, changes in numbers on standing and running waters were also affected significantly by a species' population trend in the Western Palearctic, wintering species distribution and by eco-taxonomical group. The geographical distribution of a species (latitudinal midpoint of breeding range) and the conservation status of a species in the Czech Republic affected wintering numbers only on running waters, where southern and non-protected species were increasing.

Discussion

Numbers and distribution of wintering waterbird species changed significantly in the Czech Republic between 1966 and 2008. Among the 37 species analysed, significant changes were found in the numbers of 25 species and in the distribution of 19 species. Increases in numbers were recorded in 18 species and increases in distribution in 19 species. In contrast, decreasing numbers were recorded in 7 species and decreasing distributions in only 3 species. The proportion of waterbird species that changed their numbers (68 %) in the Czech Republic seems to be higher than the proportion of waterbird species in Europe with changing (decreasing and increasing) waterbird populations, which reached 48 – 51 % of all species populations recorded in this Ramsar region (Wetlands International 2002, 2006). Although changes in numbers and distribution of particular waterbird species in the Czech Republic follow the trends in the European populations, increasing trends are more frequent in this country. It can be assumed that wintering waterbirds in the Czech Republic are affected by the status of that particular species in Europe (or in the Western Paleartic), and moreover they are also affected by the suitable wintering conditions in the Czech Republic.

Differences between population trends of wintering waterbird species in the Czech Republic and their general European trends are probably a consequence of regional (national) variability in wintering trends, but which can be also explained by a shift in the wintering range due to climatic changes (Ridgill & Fox 1990, Keller 2006, Maclean 2008, Musil *et al*. 2008a). Nevertheless, a comparison of population trends at a national level is limited by the differences of published studies in their length of study period, number of species covered, methods of trend analysis, etc. Moreover, we can omit species whose distribution is related (especially in the wintering period) to coastal habitats, (for example, most waders, seaducks and several goose species). Comparative multi-specific trend analyses covering more than 10 waterbird species are available from, for example: Slovakia (1991-2006, Slabeyová *et al.* 2008, 2009); Sweden (1967-2006, Nilsson 2008); Ireland (1994-2004, Crowe *et al.* 2008); the United Kingdom (1966-2007, Austin *et al.* 2008); France (1987-2008, Fouque *et al.* 2009) and Bulgaria (1977-2001, Michev & Profirov 2003). Despite of methodological differences, we can compare the proportion of species with increasing, decreasing or no (i.e. stable, uncertain, unknown, fluctuating) trends. In most of these countries (Sweden, Czech Republic, Slovakia, United Kingdom and Bulgaria), the number of increasing species was higher than the number of decreasing species. Nevertheless, increasing species only prevailed in Sweden (Nilsson 2008), where an increase was recorded in 13 out of 17 species. The second highest proportion of increasing species was recorded in the Czech Republic (49 %). By contrast, the decreasing species prevailed in the Irish study (Crowe et al. 2008). Surprisingly, perhaps, in the United Kingdom (Austin *et al.* 2008) and France (Fouque *et al.* 2009) increasing species were more dominant among the relevant species than decreasing ones. Nevertheless, it seems that certain species have been increasing in the northern and eastern parts of Europe and decreasing in some western countries. Some slight north-south differences can be also seen by comparing the Czech data (49 % of increasing species) with Slovakia, where only 41 % of species were increasing in wintering numbers.

Generally, the changes in numbers and distribution of waterbird species in the Czech Republic correlated with species population trends in the Western Palearctic. However, there were a few species with a difference in their trends. Numbers and the distribution of Teal have been declining significantly in the Czech Republic, whereas this species has been increasing in other European countries. The decrease of Teal in the Czech Republic can be related to the negative impact of intensive fishpond management (see, for example, Musil *et al* 2001, Musil 2006), which has affected the breeding, migrating and consequently also the wintering numbers of this species. On the other hand, the numbers of three species (Bean Goose, Pochard and Common Gull) have been decreasing in the Western Palearctic, whereas their numbers and /or distribution have increased in the Czech Republic. Among these species, Pochard and Common Gull have expanded their breeding and wintering range - not only in the Czech Republic but in other central European countries as well (e.g. Slovakia, Slabeyová *et al.* 2008). The increasing national distribution of Bean Goose can be related to a shift in wintering sites within Europe (Madsen et al. 1999, Wetlands International 2002, 2006). Nevertheless, the trend in the wintering numbers of this species has been classified as 'uncertain' due to its fluctuations in relation to climatic conditions (Musil et al. 2008a). Another interesting species is Mallard, whose numbers and distribution have increased in the Czech Republic, whereas there has been a decrease in wintering numbers reported from northwest and northeast Germany (Wahl & Sudfeldt 2005) and Slovakia (Slabeyová *et al.* 2008, 2009). Numbers of Mallard in the Czech Republic have been affected by the long-term releasing of this species for hunting purposes.

Changes in numbers generally correlated with changes in distribution among the analysed waterbird species (Fig. 1). Nevertheless, increases in distribution were more visible than increases in numbers in, for example, Grey Heron, Wigeon, Mallard, Goosander and White-tailed Eagle. These species seem to have become more widespread as opposed to being concentrated in relatively few sites. These expanding waterbird populations can exhibit a large-scale buffer effect, in which numbers in sub-optimal sites will tend to increase more than in the more optimal sites (Gill *et al.* 2001). On the other hand, a significant decrease in numbers was recorded in Great Crested Grebe, Moorhen, Coot, Snipe and Black-headed Gull, whereas these species don't appear to have had significant changes in distribution. Moreover, the distribution of Ferruginous

Duck has decreased significantly during the study period, whereas its numbers show an 'uncertain trend' (Table 1). This species seems to be concentrated in just a few sites, where they could be more vulnerable to possible habitat changes.

Running (streams, rivers) and standing waters (including fish ponds, reservoirs, gravel and sand-pit lakes, and industrial settling ponds) represents two main wetland habitats (Chytil *et al.* 1999) available for wintering birds in the Czech Republic. Although the changes in numbers for these two habitat types were generally correlated among the waterbird species analysed (Fig. 2), there are noticeable differences in changes in numbers related to habitat. Overall, 13 increasing, 5 decreasing and 4 stable species were found on standing waters, and 18 increasing, 4 decreasing and 5 stable species recorded on running waters. The number of species with uncertain trends were higher on standing waters (15, i.e. 41 %) than on running waters (10, i.e. 27 %); this difference can be explained by within-year fluctuations in numbers of wintering waterbirds on standing waters in response to variable climatic conditions (especially the ice-cover period). Species with a highly-significant trend in numbers throughout the entire Czech Republic changed their numbers similarly in both habitat types. Thus a similar trend was recorded in 9 increasing species (Cormorant, Grey Heron, Mute Swan, Wigeon, Mallard, Goosander, White-tailed Eagle, Common Gull and Kingfisher), 2 decreasing (Little Grebe and Coot), and one stable species (Goldeneye). Similar uncertain trends in numbers were found in 8 less abundant species (Whooper Swan, Shoveler, Red-crested Pochard, Ferruginous Duck, Scaup, Common Scooter, Lapwing and Snipe). In another 17 species, we find differences in trends on standing and running waters which can be related to the habitat preferences of the particular species (Hudec 1994; Snow & Perrins 1999, Delany *et al.* 1999; Musil *et al.* 2001; Gillisen *et al.* 2002, Musil *et al.* 2008b). The numbers of 4 waterbird species (i.e. Greylag Goose, Pintail, Green Sandpiper and 'large gulls') increased only on standing waters, whereas 9 species (i.e. Great White Egret, Bean

Goose, White-fronted Goose, Gadwall, Pochard, Tufted Duck, Smew, Grey Wagtail and Dipper) increased only on running waters. Among these species, only numbers of Pochard increased on rivers and conversely decreased on standing waters. Those species which are increasing only on standing waters use these habitats more frequently in mild winters. On the other hand, 9 species increasing only on running waters represent species with a general ‘strong increase’ in numbers and/or species which avoid intensively-managed fish ponds. An increase in the importance of non-freezing standing waters can be expected in the coming years in accordance with the global climate change forecasts which predict milder winters across Europe, including the Czech Republic (*e.g*. Huntley *et al.* 2007; IPCC 2007).

The changes in wintering numbers and distribution of particular species were affected by many inter-correlated species-specific variables. Among these, a species’ eco-taxonomical group and its trend in the Western Paleartic (Birdlife International 2004, Wetlands International 2006, Figures 4a,b) were the most significant. The relationship between changes in wintering numbers and distribution in the Czech Republic and wintering trends have been discussed in the previous paragraphs. Amongst the various eco-taxonomical groups (Figure 3a, 3b), the most remarkable increases in numbers and distribution were shown by the fish-eating birds, followed by the geese, dabbling ducks, diving ducks, and gulls, while large inter-specific variability was found in several groups, especially in the gulls. Only in waders did a decrease in numbers prevail. This pattern of changes is similar to the published data for population changes in whole Europe (e.g. Birdlife International 2004, Wetlands International 2006).

Moreover, we found that species with increasing wintering numbers were more frequent in southern (especially on running waters) and rare species. This phenomenon can be explained by the northwards expansion of wintering waterbirds in central Europe , similar to the changes recorded in western or northern Europe (Maclean *et al.* 2008, Nilsson 2008) or expected for most of Europe (Huntley *et al.* 2007) in response to the expected climatic changes (IPCC 2007). Finally, we found that species protected under Czech conservation law decreased more frequently in distribution and in numbers on running waters. Negative trends of these species (e.g. Little Grebe, Teal, Ferruginous Ducks) were not reversed by Czech conservation law. This result corresponds with a similar analysis carried out on mostly terrestrial birds in the Czech Republic (Voříšek *et al.* 2008).

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References

Austin, G.E., Collier, M.P., Calbrade, N.A., Hall, C. & Musgrove, A.J. 2008. *Waterbirds in the UK 2006/07: The Wetland Bird Survey*. BTO/WWT/RSPB/JNCC. Thetford.

Birdlife International 2004. *Birds in Europe: populations, estimates, trends and conservation status*. BirdLife Conservation Series No. 12, Birdlife International, Cambridge, UK.

Chytil, J., Hakrová, P., Hudec, K., Jandová, J. & Pellantová, J. (eds) 1999. *Wetlands of the Czech Republic – inventory of wetlands in the Czech Republic.* Czech Ramsar Committee, Mikulov, Czech Republic.

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

Crove, O., Austin, G.E., Colhoun, K., Cranswick, P.A., Kershaw, M & Musgrove, A.J. 2008. Estimates and trends of waterbird numbers wintering in Ireland, 1994/95 to 2003/04. *Bird Study* **55**: 66–77.

Delany, S., Reyes, C., Hubert, E., Pihl, S., Rees, E., Haanstra, L. & van Strien, A. 1999. *Results of the International Waterbird Census in the Western Palearctic and Southwest Asia, 1995 and 1996.* Wetlands International Publication No. 54, Wetlands International, Wageningen, The Netherlands.

Gilissen, N., Haanstra, L., Delany, S., Boere, G. & Hagemeijer, W. 2002. *Numbers and distribution of wintering waterbirds in the Western Palearctic and Southwest Asia in 1987, 1988 and 1999.* Results from the International Waterbird Census. Wetlands International Global Series No. 11, Wetlands International, Wageningen, The Netherlands.

Fiala, V. 1980. Changes in winter numbers of the Mallard (*Anas platyrhynchos*) in the Czech Socialist Republic 1970-71 – 1977-78. *Folia Zoologica* **29**: 251–266. (In German with English summary).

Fouque, C.; Guillemain, M., Benmergui, M., Delacour, G., Mondain-Monval, J.-Y. & Schricke V. 2007. Mute swan (*Cygnus olor*) winter distribution and numeric trends over a 16-year period (1987/1988–2002/2003) in France. *J. Ornithol.* **148**: 477–487.

Fouque, C.; Guillemain, M. & Schricke, V. 2009. *Wildfowl. Special Issue* **2***: 42*–59.

Hudec, K. (ed.) 1994. [*Fauna ČR a SR. Ptáci 1*.] Academia, Praha, The Czech Republic. (In Czech with German summary).

Hudec, K., Chytil, J., Šťastný, K. & Bejček V. 1995. Birds of the Czech Republic. *Sylvia* **31**: 94–149. (In Czech with English summary).

Hudec K., Flousek J. & Chytil J. 1999. Checklist of birds of the Czech Republic and relevant conservation rules. *Příloha Zpráv ČSO* **48:** 1–16. [In Czech with English summary.]

Huntley, B., Green, R.E., Vollingham, Y.C. & Willis, S.G. 2007: *A climatic atlas of European breeding birds. Durnham University.* The RSPB and Lynx Edicions, Barcelona, Spain.

Intergovernmental Panel on Climate Change 2007. *Climate Change 2007: The Physical Science Basis.* Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. Cambridge, Cambridge University Press, Cambridge, UK.

Kear, J. 2005. Bird Families of the World: Ducks, Geese and Swans. *Oxford University Press, Oxford, UK.*

Keller, V. 2006. Population size and trend of the Red-crested Pochard *Netta rufina* in southwest/central Europe: an update. *In* G.C. Boere, C.A. Galbraith & D.A. Stroud (eds.), *Waterbirds around the World*, pp. 503-504. The Stationery Office, Edinburgh, UK.

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

MacLean, I.M.D., Austin, G.E., Rehfish, M.M., Blew, J., Crowe, O., Delany, S., Devos, K., Deceucnick, B., Günther, K., Laursten, K., Van Roomen, M. & Wahl, J. 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Climate Change Biology* **14**: 2489–2500.

Madsen J., Cracknell G. & Fox A. D. 1999: *Goose populations of the Western Palearctic. A review of status and distribution.* Wetlands International Publ. No. 48, Wetlands International, Wageningen.

Michev, T.& Profirov L. 2003. Midwinter Numbers of Waterbirds in Bulgaria: Results from 25 years of mid-winter counts carried out at the most important Bulgarian wetlands. *Publ. House Pensoft, Sofia,* 160 pp (In English with Bulgarian summary).

Musil, P., Cepák, J., Hudec, K. & Zárybnický, J. 2001: *The long-term trends in the breeding waterfowl populations in the Czech Republic.* Oiseaux Migrateurs du Paléarctique Occidental & Institute of Applied Ecology, PB tisk Příbram, Czech Republic.

Musilová, Z. & Musil, P. 2006. Current status of International Waterbird Census in the Czech Republic. *In* G.C. Boere, C.A. Galbraith. & D.A. Stroud (eds), *Waterbirds around the World,* pp. 484-486. The Stationery Office, Edinburgh, UK.

Musilová, Z., Musil, P. & Neužilová, Š. 2008. The International Waterbird Census in the Czech Republic in January 2006 and 2007. *Aythya* **1**: 5–13. (In Czech with English summary).

Musil, P., Darolová, A., Jureček, J., Musilová, Z., Podhrázský, M. & Slabeyová, K. 2008a. Dlouhodobé změny početnosti zimujících hus v České republice a na Slovensku v letech 1991–2007. *Tichodroma* **20**: 61–67 (In Czech with English summary).

Musil, P., Musilová, Z., Strnad, M. & Neužilová, Š. 2008b. Numbers and distribution of common waterbird species in January 2006 and 2007. *Aythya* **1***:* 14–67.

Musilová, Z., Musil, P., Poláková, S. & Fuchs, R. 2009. Wintering ducks in the Czech Republic: population size, changes in population trends and distribution. *Wildfowl. Special Issue* **2***:* 73–85.

Nilsson, L. 2008. Changes in numbers and distribution of wintering waterfowl in Sweden during forty years, 1967-2006. *Ornis Svecica* **18***:* 135–236.

Pannekoek, J. & van Strien, A. J. 2005. *TRIM 3 Manual (TRends and Indices for Monitoring Data).* Statistics Netherlands, Voorburg, The Netherlands.

Ridgill, S. C. & Fox, A. D. 1990. *Cold Weather Movements of Waterfowl in Western Europe*. IWRB Special. Publ. No.13, International Waterfowl & Wetlands Research Bureau, Slimbridge, UK.

Slabeyová, K., Ridzoň J., Darolová A., Karaska D. & Topercer J. 2008. Výsledky sčítania zimujícího vodného žáctva na Slovensku 2004/05. *SOS/Birdlife Slovensko, Bratislava.*

Slabeyová, K., Ridzoň J., Topercer J. Darolová A. & Karaska D. 2009. Výsledky sčítania zimujícího vodného žáctva na Slovensku 2005/06. *SOS/Birdlife Slovensko, Bratislava.*

Scott, D.A. & Rose, P.M. 1996: *Atlas of Anatidae Populations in Africa and Western Eurasia.* Wetlands International Publication No. 41, Wetlands International, Wageningen, The Netherlands, 336 pp.

Snow D.W. & Perrins C.M. (eds) 1998: *The Birds of the Western Palearctic.* Concise Edition Vol. 1, Non-Passerines. Oxford University Press, New York.

Švažas, S., Meissner, W., Serebryakov, V., Kozulin, A. & Grishanov, G. 2001. *Changes of wintering sites of waterfowl in Central and Eastern Europe*. Vilnius: OMPO & Institute of Ecology.

Wahl, J & Sudlfeldt, C. 2005. Phenology and population trends of dabbling ducks (*Anas* sp.). *Vogelwelt* **126**: 75–91 (In German with English summary).

Wetlands International 2002: *Waterbird Population Estimates – Third Edition.* Wetlands International Global Series No 11, Wageningen, The Netherlands.

Wetlands International 2006. *Waterbird Population Estimates – Fourth Edition*. Wetlands International, Wageningen, The Netherlands.

Table 1. Changes in distribution (correlation coefficient (*r*) and significance: * $P < 0.05$, ** $P < 0.01$, n.s. = not significant; $n = 43$) and changes in numbers in waterbird species 1966–2008 (multiplicative rate of change ± std.err.) on all wetlands, rivers and standing waters. The trend categories provided by TRIM software are: SI = strong increase; MI = moderate increase; U = uncertain; MD = moderate decline; S = stable.

Species	**Changes in distribution**		**Changes in numbers**					
			All wetlands		**Running waters**		**Standing waters**	
Little Grebe	-0.367		0.973 ± 0.002	MD	0.974 ± 0.002	MD	0.961 ± 0.009	MD
Great Crested Grebe	0.182	n.s.	0.982 ± 0.006	`MD	0.949 ± 0.010	MD	1.009 ± 0.012	S
Great Cormorant	0.842	**	1.172 ± 0.009	SI	1.194 ± 0.013	SI	1.109 ± 0.011	SI
White Egret	0.778	**	1.262 ± 0.064	SI	1.251 ± 0.048	SI	1.268 ± 0.172	U
Grey Heron	0.916	*	1.045 ± 0.002	MI	1.046 ± 0.003	MI	1.043 ± 0.004	MI
Mute Swan	0.734	*	1.018 ± 0.002	MI	1.019 ± 0.003	MI	1.013 ± 0.004	MI
Whooper Swan	0.047	n.s.	1.023 ± 0.020	U	1.022 ± 0.022	U	1.011 ± 0.068	U
Bean Goose	0.476	*	1.022 ± 0.015	U	1.063 ± 0.018	MI	1.011 ± 0.034	U
White-fronted Goose	0.691	**	1.114 ± 0.016	SI	1.157 ± 0.043	SI	1.081 ± 0.215	U
Greylag Goose	0.554	**	1.160 ± 0.018	SI	1.357 ± 0.284	U	1.139 ± 0.024	SI
Wigeon	0.726	**	1.061 ± 0.011	MI	1.062 ± 0.014	MI	1.047 ±0.023	MI
Gadwall	0.619	**	1.163 ± 0.132	U	1.052 ± 0.017	MI	1.321 ± 1.401	U
Teal	-0.319	*	0.974 ± 0.003	MD	0.957 ± 0.004	MD	1.005 ± 0.008	S
Mallard	0.576	**	1.008 ± 0.001	MI	1.004 ± 0.001	MI	1.014 ± 0.003	MI
Pintail	0.122	n.s.	1.016 ± 0.009	S	0.998 ± 0.011	S	1.055 ± 0.022	MI
Shoveler	0.216	n.s.	1.018 ± 0.020	U	0.973 ± 0.139	U	1.040 ± 0.034	U
Red-crested Pochard	0.392	*	1.051 ± 0.033	U	1.071 ± 0.040	U	0.994 ± 0.080	U
Pochard	0.276	n.s.	1.031 ± 0.006	MI	1.045 ± 0.008	MI	0.965 ± 0.012	MD
Ferruginous Duck	-0.317	*	0.942 ± 0.032	U	0.943 ± 0.033	U	0.993 ± 0.041	U
Tufted Duck	0.685	**	1.092 ± 0.006	SI	1.100 ± 0.008	SI	1.011 ± 0.008	S
Scaup	0.114	n.s.	1.201 ± 0.013	S	1.024 ± 0.015	U	1.015 ± 0.031	U
Velvet Scooter	-0.206	n.s.	1.016 ± 0.016	S	0.977 ± 0.037	U	1.084 ± 0.067	U
Goldeneye	0.181	n.s.	1.004 ± 0.003	S	1.005 ± 0.004	S	0.995 ± 0.007	S
Smew	0.236	n.s.	1.057 ± 0.009	MI	1.056 ± 0.011	MI	1.053 ± 0.029	U
Goosander	0.672	*	1.021 ± 0.003	MI	1.019 ± 0.004	MI	1.030 ± 0.007	MI
White-tailed Eagle	0.874	**	1.088 ± 0.007	SI	1.084 ± 0.012	SI	1.088 ± 0.009	SI
Moorhen	-0.202	n.s.	0.995 ± 0.003	MD	0.996 ± 0.003	MD	0.953 ± 0.008	S
Coot	0.013	n.s.	0.992 ± 0.002	MD	0.993 ± 0.002	MD	0.964 ± 0.006	MD
Lapwing	0.161	n.s.	0.980 ± 0.031	U	1.007 ± 0.035	U	0.911 ± 0.313	U
Snipe	0.062	n.s.	0.905 ± 0.036	MD	1.009 ± 0.028	U	0.784 ± 0.310	U
Wood Sandpiper	0.021	n.s.	1.006 ± 0.009	S	0.938 ± 0.012	S	1.034 ± 0.017	MI
Black headed Gull	-0.251	n.s.	0.996 ± 0.002	MD	0.998 ± 0.002	S	0.973 ± 0.008	MD
Common Gull	0.336	*	1.052 ± 0.006	MI	1.061 ± 0.008	MI	1.048 ± 0.011	MI

large gulls	0.826	**	1.197 ± 0.014	SI	1.277 ± 0.169	U	1.187 ± 0.019	SI
Kingfisher	0.544	**	1.043 ± 0.004	MI	1.041 ± 0.004	MI	1.057 ± 0.013	MI
Grey Wagtail	0.232	n.s.	1.071 ± 0.014	MI	1.071 ± 0.014	MI	1.074 ± 0.078	U
Dipper	0.096	n.s.	1.013 ± 0.003	MI	1.012 ± 0.003	MI	1.052 ± 0.031	U

Table 2. Result of the GLZ model to explain effect of species-specific variables on changes in numbers (multiplicative rate of change) in all investigated wetlands.

Species-specific variables	χ^2	df	P
Body size	0.091	1	0.764
Western Palearctic trend	**17.742**	**1**	**0.0001**
Wintering distribution in CZ	**7.976**	**1**	**0.005**
Wintering numbers in CZ	1.686	1	0.194
Western Palaearctic population size	0.036	1	0.849
Latitudinal midpoint	**5.048**	**1**	**0.025**
Species protection (Bird Directive)	0.264	1	0.607
Species Protection (Czech legislation)	3.651	1	0.056
Eco-taxonomical group	**21.215**	**6**	**0.002**

Table 3. Result of the GLZ model to explain effect of species-specific variables on changes in distribution (correlation coefficient between arcsin-transformed ratio of occupied size and year) in all investigated wetlands.

Species-specific variables	χ^2	df	P
Body size	2.748	1	0.097
Western Palearctic trend	**4.557**	**1**	**0.033**
Wintering distribution in CZ	0.428	1	0.513
Wintering numbers in CZ	0.571	1	0.500
Western Palaearctic population size	0.325	1	0.569
Latitudinal midpoint	0.865	1	0.352
Species protection (Bird Directive)	1.719	1	0.190
Species Protection (Czech legislation)	**5.475**	**1**	**0.019**
Eco-taxonomical group	**25.282**	**6**	**0.0003**

Table 4. Result of the GLZ model to explain effect of species-specific variables on changes in numbers (multiplicative rate of change) on standing waters.

Species-specific variables	χ^2	df	P
Body size	0.237	1	0.626
Western Palearctic trend	**7.661**	**1**	**0.006**
Wintering distribution in CZ	**5.871**	**1**	**0.015**
Wintering numbers in CZ	1.854	1	0.173
Western Palaearctic population size	0.522	1	0.470
Latitudinal midpoint	2.668	1	0.102
Species protection (Bird Directive)	0.002	1	0.964
Species Protection (Czech legislation)	1.773	1	0.183
Eco-taxonomical group	**18.024**	**6**	**0.006**

Table 5. Result of the GLZ model to explain effect of species-specific variables on changes in numbers (multiplicative rate of change) on running waters.

Species-specific variables	χ^2	df	P
Body size	0.341	1	0.559
Western Palearctic trend	**28.320**	**1**	**0.0001**
Wintering distribution in CZ	**8.787**	**1**	**0.003**
Wintering numbers in CZ	2.464	1	0.116
Western Palaearctic population size	0.040	1	0.841
Latitudinal midpoint	**9.768**	**1**	**0.002**
Species protection (Bird Directive)	0.429	1	0.513
Species Protection (Czech legislation)	**5.880**	**1**	**0.015**
Eco-taxonomical group	**34.545**	**6**	**0.0001**

Figure 1. Relationship between changes in distribution (correlation coefficient describing trend in the ratio of the number of sites occupied to sites counted) and changes in numbers (multiplicative rate of change).

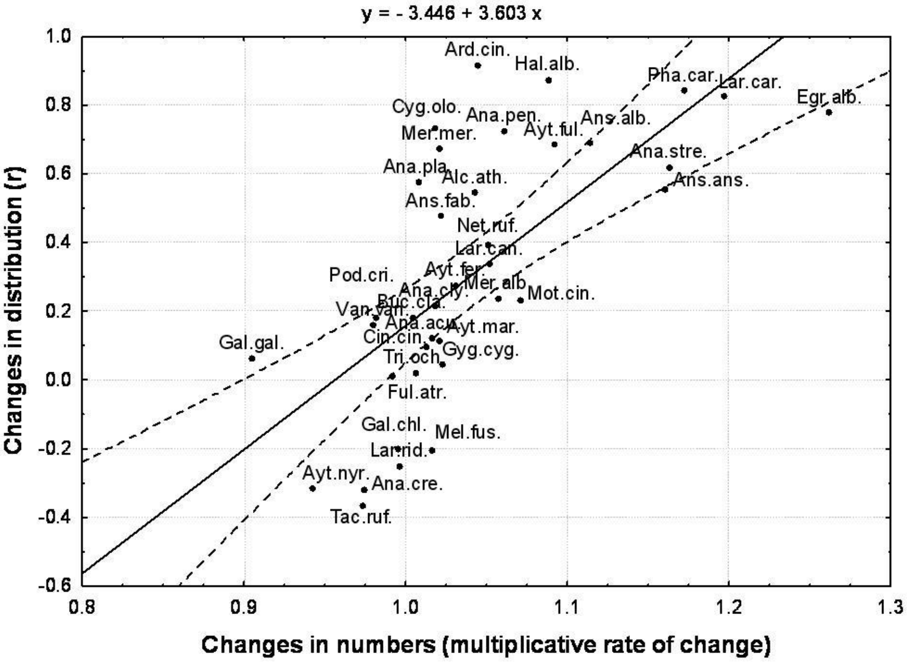

Figure 2. Relationship between changes in numbers (multiplicative rate of change) on standing and running waters.

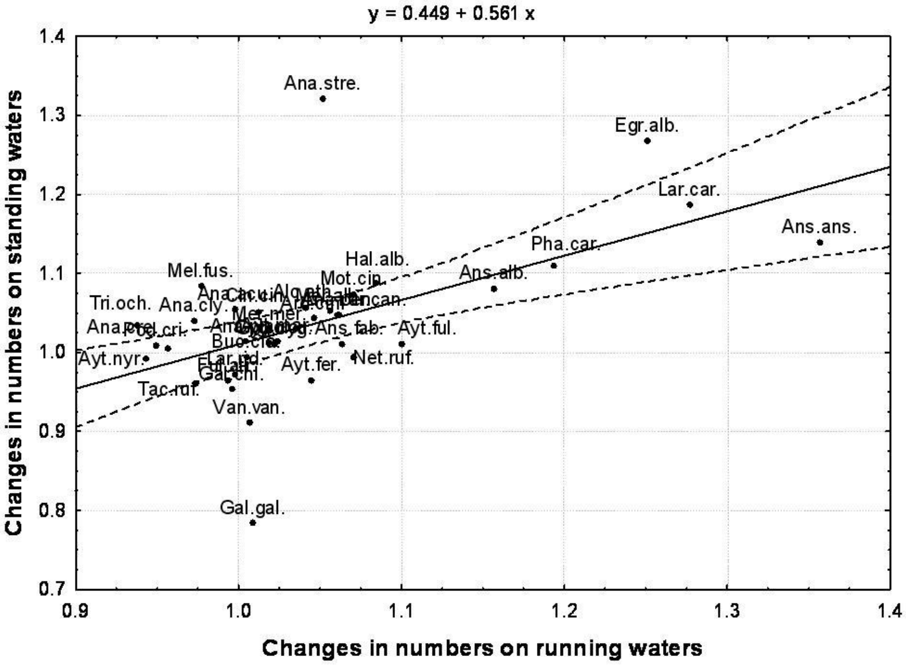

Figure 3a. Changes in numbers (multiplicative rate of change) among waterbird groups.

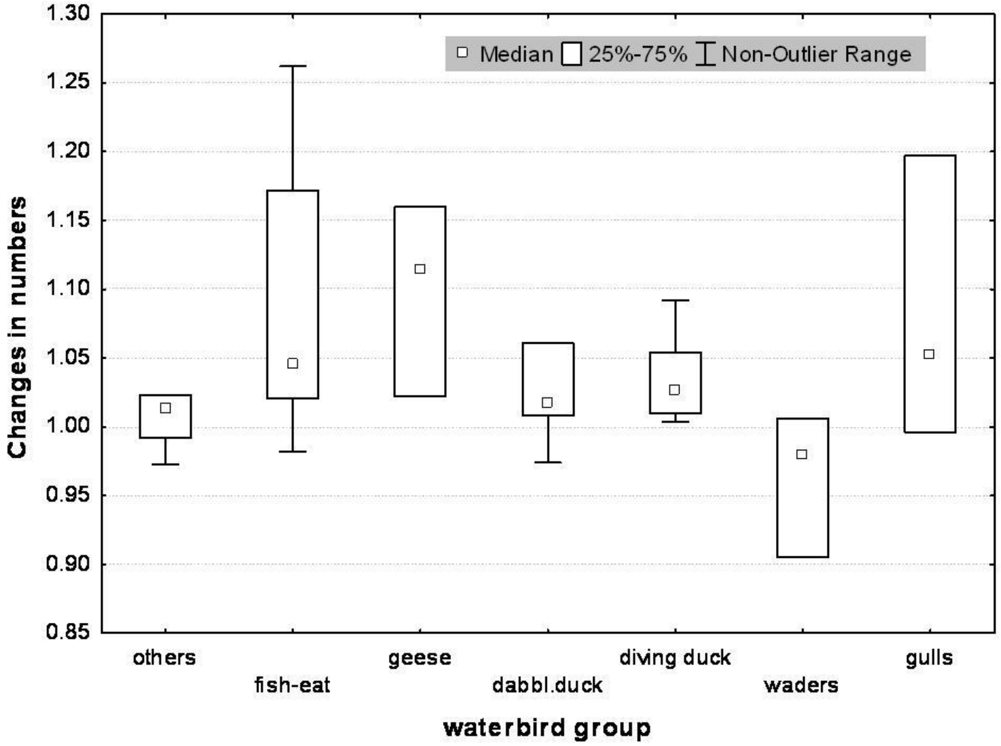

Figure 3b. Changes in distribution (correlation coefficient describing trend in the ratio of the number of sites occupied to sites counted) among waterbird groups.

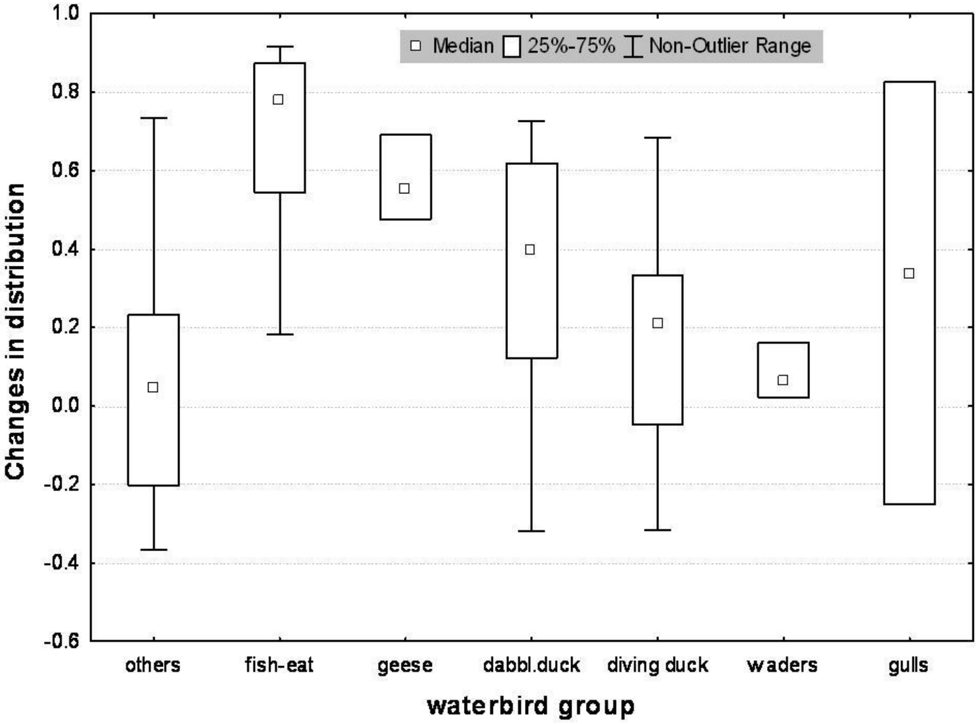

Figure 4a. Relationships between changes in numbers (multiplicative rate of change) in the Czech Republic and changes in numbers in the Western Palearctic (Wetlands International 2006).

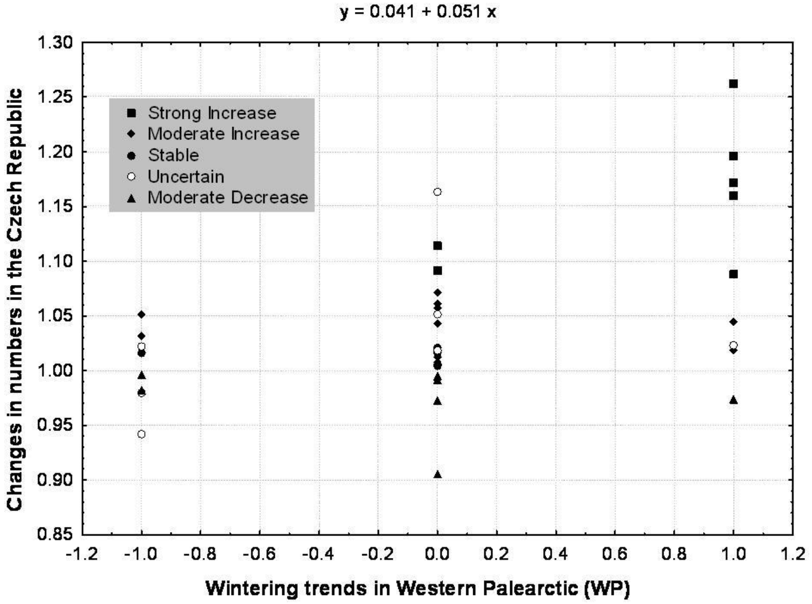

Figure 4b. Relationships between changes in distribution (correlation coefficient describing trend in the ratio of the number of sites occupied to sites counted) in the Czech Republic and changes in numbers in the Western Palearctic (Wetlands International 2006)