ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE

Fakulta životního prostředí

Katedra ekologie

RIZIKA PREDACE PTAČÍCH HNÍZD VE FRAGMENTOVANÉ SUBURBÁNNÍ KRAJINĚ

PREDATION RISKS OF BIRD NESTS

IN THE FRAGMENTED SUBURBAN LANDSCAPE

(Dizertační práce)

Petr Suvorov

Praha 2013

Školitel: Prof. Mgr. Miroslav Šálek, Dr.

Prohlašuji, že všichni spoluautoři jsou řádně uvedeni a že můj podíl na jednotlivých publikacích zařazených do dizertační práce není menší, než odpovídá pořadí a počtu autorů. Dále prohlašuji, že jsem nepředložil dizertační práci ani její podstatnou část k získání jiného akademického titulu.

V Praze 14. 02. 2013

Petr Suvorov

PODĚKOVÁNÍ

Za přečtení dizertace i jednotlivých jejích částí bych rád poděkoval všem recenzentům a jim i všem členům doktorské komise za to, že si udělali čas na hodnocení výsledků mé práce.

Na závěr si snad už jen dovolím vyslovit dík lidem, kteří mne podpořili po lidské stránce. Byla to především moje maminka *MUDr. Zorka Suvorovová*, která přes velmi obtížnou životní situaci dodržela slib a v doktorském studiu mě podporovala celých šest let. Bez ní bych studium dokončoval jen velmi obtížně. Rád bych zmínil i ty, kteří při mně stáli až do konce. Byli to zejména *Ing. Jana Svobdová, PhD.*, *Mgr. Filip Harabiš, PhD., RNDr. Jaroslav Koleček, Bc. Martin Sládeček* a *Vendulka Bronová*. Díky za podporu!

Tuto práci věnuji památce

Miroslavy Taušové (✝ 10. 6. 1993)

a

pplk. Miloslava Suvorova (✝ 22. 4. 2004)

OBSAH

ÚVOD

Většina změn v krajině Střední Evropy, které ovlivňují ptačí populace, je v současné době ovlivňována člověkem (Pärt et al. 2007). Lidská činnost spojená s osídlením může přinášet značné výhody pro ptačí populace, které jsou schopny se na přítomnost člověka adaptovat. Jsou to např. doplňkové potravní zdroje, nové hnízdní příležitosti nebo mírnější zimy v blízkosti urbanizacovaných zón (Chace & Walsh 2006, Robb et al. 2008). Proto může denzita některých druhů ptáků směrem k suburbánním oblastem narůstat (Šálek et al. 2004). Avšak na druhé straně lidské osídlení s sebou přináší mnohá rizika, se kterými se hnízdící ptáci musí vyrovnávat. Podle Marzluff & Ewing (2004) a Chace & Walsh (2004) se jedná zejména o *(1)* manipulace s klíčovými zdroji (pozměněné potravní spektrum, ztráta vegetačního pokryvu vlivem úprav křovin atp.), *(2)* omezené možnosti disperze a migrace, *(3)* přítomnost nepůvodních prvků (vegetace, predátoři, nemoci a parazité), *(4)* změny v hydrologických a živinových cyklech, *(5)* absenci vrcholových predátorů a následné změny v trofické struktuře a *(6)* zvýšenou míru hnízdní predace a parazitizmu.

Hnízdní predace je velmi významným mortalitním faktorem, který ovlivňuje populační dynamiku i životní strategie ptáků (Wilcove 1985, Weidinger 2002, Remeš 2005, Roos 2006). Riziko hnízdní predace je v urbanizovaných zónách zvýšené zejména díky vysoké denzitě nespecializovaných predátorů, kterými jsou např. krkavcovití ptáci (*Corvidae*), kuny (*Martes* sp.), prase divoké (*Sus scrofa*), někteří hlodavci (*Rodentia*) aj. (Angelstam 1986, Rangen et al. 2000, Roos 2002, Einarsen et al. 2008, Svobodová et al. 2012). Některé práce dokonce prokazují, že směrem z periferie do centra velkých měst predační tlak narůstá (Jökimäki & Huhta 2000, Thorington & Bowman 2003). Většina predátorů na ptačí hnízda narazí náhodou při pátrání po potravě (Vickery et al. 1992). Urbanizovaná krajina je pro ně atraktivní z důvodu vysoké míry heterogenity způsobené antropogenní fragmentací - jemná mozaika odlišných biotopů jim nabízí možnost přístupu k odlišným typům zdrojů (Ries & Sisk 2004, Šálek et al. 2004, Chace & Walsh 2006, Marzluff & Neatherlin 2006). S rostoucí jemnozrnností mozaiky fragmentované krajiny a zmenšující se plochou jednotlivých biotopových fragmentů může riziko hnízdní predace v člověkem osídlené a ovlivňované krajině narůstat (Vander Haegen et al. 2002). Přes zvýšený predační tlak láká možnost využívat více zdrojů najednou do fragmentované krajiny také ptáky. Pokud záměrně zahnízdí v místě, kde je jejich reprodukční úspěch nižší vlivem silného predačního tlaku, dostávají se do slepé uličky tzv. ekologické pasti (Dwernychuk & Boag 1972, Gates & Gysel 1978, Robertson & Hutto 2006, Pelicice & Agostinho 2008). Zejména v suburbánních oblastech dochází velmi často ke změnám v krajině, na které se ptáci nemusí stihnout

adaptovat včas a lze předpokládat, že jsou ekologickými pastmi ohroženi ještě více. Literární review **(I)**, které je součástí rozsáhlejšího textu s názvem Fragmentation and loss of natural habitats, pojednává více o podstatě hypotézy ekologické pasti v širších kontextech včetně mechanizmu jejího vzniku a hlavních faktorů, které její vznik ovlivňují. Volně navazující práce **(II)** zužuje okruh literatury pouze na výskyt ekologických pastí u ptáků. V databázích Web of Science, Wiley, EBSCO a Springer Link jsme vyhledávali práce, vztahující se k tématu ekologických pastí a ptačích populací a zjišťovali jsme, které hlavní příčiny jsou zodpovědné za jejich výskyt. Dále nás zajímalo, zdali se zdokumentované ekologické pasti vyskytovaly pravděpodobněji na některých kontinentech, jestli byly asociované s typem habitatu a mírou jeho podobnosti přírodě blízkých stanovišť a byl-li jejich výskyt u volně žijících ptačích populací ovlivněn typem migrační strategie, umístěním hnízda a zahnízděním v uměle vyrobených hnízdních budkách. Testovat skutečnou ekologickou past je u volně žijících ptačích populací velmi náročné, proto studií na toto téma není příliš. Většina prací, které podporují hypotézu ekologických pastí, pochází z Evropy, i když v Severní Americe se jejímu studiu věnoval téměř dvojnásobek studií. Jedním z možných vysvětlení může být vyšší populační hustota obyvatelstva v Evropě, která může více modifikovat krajinu. Naše výsledky však také ukázaly, že prací, které by studovaly ekologické pasti přímo v urbanizovaných oblastech a jejich periferiích, je velmi málo. Lze dále předpokládat, že populace druhů, které migrují, budou vystaveny riziku ekologické pasti častěji (Battin 2004, Leston et al. 2006), neboť musí v krátkém časovém období najít vhodné místo k hnízdění (Hahn & Silverman 2006, Lindell et al. 2007) a jejich informace mohou být omezené (Kokko & Sutherland 2001, Winter et al. 2006). Navzdory tomu typ migrační strategie výskyt ekologické pasti neovlivnil. Jedno z možných vysvětlení poskytuje hypotéza tzv. *heterospecific habitat copying* (Parejo et al. 2006) spočívající v předpokladu, že migrující ptačí druhy napodobují hnízdní strategie sedentárních druhů, čímž riziko chyby při výběru habitatu mohou snížit. Analýza prací dále prokázala, že jednou z nejčastějších příčin vzniku ekologické pasti je zjevně přítomnost nepůvodního druhu (predátora, kompetitora, vegetace...), na který nejsou domácí druhy evolučně adaptované. Překvapivě malý podíl (2 z 15 prací) ukázal, že by mohly ekologické pasti vznikat cestou fragmentace biotopů nebo managementu krajiny. Je tedy možné, že si ptáci riziko spojené se změnou habitatu fragmentací uvědomují a jsou schopni se mu předem vyhnout.

Zejména při opakované fragmentační události velkého rozsahu bez možnosti obnovení přirozené sukcese, jako jsou např. rychlé změny v suburbánních oblastech, je pravděpodobné, že budou druhy žijící v krajině vykazovat negativnější efekt, než při jednorázové fragmentaci

(Hagan et al. 1996). Nejsilněji budou ovlivněny druhy úzce specializované na konkrétní typy biotopu (Howell et al. 2000). Podle Bayne et al. (2005) existují tři způsoby, jak může pták reagovat na antropogenní fragmentaci v krajině: *(1)* Jedná-li se o habitatového generalistu, nebude jej změna příliš ovlivňovat a změněný habitat zahrne do svého teritoria. *(2)* Alternativně může zmenšit plochu svého teritoria o plochu změněného habitatu. Dokáží-li adaptabilní ptačí druhy maximálně využít zdroje pozměněné krajiny, mohou žít v prostředí se zvýšeným rizikem hnízdního neúspěchu, aniž by to na jejich populace mělo negativní vliv. Např. u krkavcovitých bylo prokázáno, že velikost teritoria může negativně korelovat s množstvím zdrojů, které v nich najdou (Marzluff & Neatherlin 2006). Jejich prostorové požadavky nemusí být tedy příliš veliké. Naopak úzce specializované druhy ptáků *(3)* budou chápat pozměněný habitat jako suboptimální a budou nuceny přesídlit jinam – např. populace ptačích druhů citlivých na zmenšování krajinných fragmentů (tzv. *area-sensitive species*; Villard 1998, Davis 2004, Fraser & Stutchbury 2004) s klesající velikostí fragmentů v krajině ubývají. Někdy mohou být změny v početnosti ptačích populací, ale i rozdíly v míře predačního tlaku v daném krajinném fragmentu, ovlivňovány nejen vlastnostmi fragmentu samotného, ale mohou záležet na složení okolní krajiny (Jokimäki & Huhta 2000, Dunford & Freemark 2004). Zatímco krajina fragmentovaná zemědělstvím může mít na ptačí společenstva negativní vliv (Andrén 1995), lesní hospodářství ptačí populace negativně ovlivňovat nemusí (Bayne & Hobson 1997, Marzluff & Ewing 2004). V urbanizované krajině fragmentované lidskou zástavbou dosahuje druhové bohatství ptáků i jejich hnízdních predátorů svého vrcholu už při střední míře fragmentace (Fernandez-Juricic & Jökimäki 2001, Evans et al. 2009). V interní urbanizaci je totiž již vliv člověka tak silný, že mnohdy dochází k úplnému vymizení přírodě podobných stanovišť a živočichové nemají kde žít (Donovan et al. 1997, Evans et al. 2009, Howard et al. 2001). Je možné, že populace živočichů silně urbanizovaných zón by bez imigrantů zcela zanikly (Baker et al. 2008). Většina prací porovnává vliv konkrétních komponent okolní krajiny na denzitu a diverzitu ptáků a míru predačního tlaku, ale pouze málo z nich se pokouší zhodnotit komplexně vliv celé okolní krajiny na ptačí populace žijící v daném krajinném fragmentu.

Reakce samotných ptačích populací na antropogenní fragmentaci se může měnit v závislosti na rychlosti, intenzitě a prostorovém měřítku, s jakými je krajina fragmentovaná (Marzluff & Ewing 2004). Je pravděpodobné, že negativní vliv fragmentace může být vidět zejména u fragmentů vzniklých v nedávné minulosti, protože ptáci, kteří je osídlili, se na člověkem pozměněnou krajinu nestihli adaptovat (Hagan et al. 1996). Negativním vlivem fragmentace pak mohou být ohroženy druhy obývající zejména raně sukcesní stádia jako např.

ruderální biotopy a fragmenty s náletovou vegetací. Zároveň ale může odpověď ptačích společenstev na fragmentaci vykazovat určité zpoždění (Winter et al. 2006) a negativní vliv disturbancí se může projevit až v delším časovém měřítku. Vzhledem k časové náročnosti nejsou dlouhodobé studie odpovědí ptačích společenstev příliš časté (Donázar et al. 2002).

V naší studii **(III)** jsme se zaměřili na recentně vzniklé ruderální fragmenty v okolí Prahy, ve kterých jsme zkoumali míru hnízdní predace za pomocí umělých zemních hnízd opatřených slepičími vejci s cílem simulovat hnízdění zemních hrabavých ptáků. I když umělá hnízda neposkytují úplně nejvěrnější odhad míry hnízdní predace, jsou stále užitečnou metodou stanovení přibližného obrazu míry predačního tlaku na zemní hnízda (Söderström et al. 1998, Pärt & Wrettenberg 2002, Martin & Joron 2003, Burke et al. 2004). Předchozí práce prokázaly, že např. pro ubývající populace koroptve polní (*Perdix perdix*) jsou fragmenty ruderálních biotopů v okrajové zóně Prahy atraktivní díky jejich heterogenitě, spjaté s vyšší nabídkou zdrojů, takže je v nich početnost koroptví vyšší (Šálek et al. 2004). Zároveň jsou ale zde žijící ptáci vystaveni vyššímu predačnímu riziku díky zvýšené denzitě hnízdních predátorů (M. Šálek et al., nepublikovaná data).

V naší studii míra predačního tlaku na umělá hnízda dosáhla 57.8 % a nebyla závislá na vnitřních vlastnostech ruderálních fragmentů (velikost, tvar atp.), ale měnila se s proporcemi okolní krajiny – nejvyšší byla v oblastech, kde ruderální fragment obklopovaly zejména raně sukcesní stádia nebo krajina silně pozměněná člověkem (lidské osídlení, dopravní infrastruktura). Naopak s rostoucím podílem přírodě podobných, pozdně sukcesních stanovišť (louka, les) predační tlak klesal, což podtrhuje význam výše zmiňovaného vlivu skladby okolní krajiny v souladu se studiemi Jokimäki & Huhta (2000) a López-Flores et al. (2009).

Role okrajových zón v míře hnízdní predace ve fragmentované krajině

Fragmentace krajiny zvyšuje podíl okrajových zón, což podporuje míru diverzity dostupných zdrojů (Ries & Sisk 2004). Zdrojově pestřejší okrajové biotopy mohou preferovat ptáci při hledání hnízdních míst a následně i hnízdní predátoři. S rostoucí denzitou predátorů v okrajových zónách roste riziko, že některý z nich náhodně najde hnízdo s vejci a vyplení jej (tzv. okrajový efekt na hnízdní predaci; Albrecht 2004, Schiegg et al. 2007). V některých případech vyplenění hnízda se může jednat o kompetici - na vnitrodruhové úrovni byla tato situace popsána u strak obecných (*Pica pica*) (Baeyens 1981, Tatner 1982, Jerzak 2001) a na mezidruhové úrovni u vrabců domácích (*Passer domesticus*) a salašníků modrých (*Sialia sialis*) (Gowaty 1984). V případě kompetice mohou kvalitní jedinci vytlačovat slabší

z okrajových (atraktivnějších) biotopů do vnitřních (kvalitních, ale nepreferovaných) biotopů s nižšími skrytými riziky, kde mohou mít slabší jedinci následně vyšší reprodukční úspěšnost (Miner et al. 2005).

Okrajový efekt na míru hnízdní predace se ve většině studií projevil nejsilněji do vzdálenosti cca 50 – 200 metrů od habitatového přechodu (Andrén & Angelstam 1988, Paton 1994, Batáry & Báldi 2004). Existují ale práce, které ho potvrdily až do vzdálenosti 4 - 5 km (Laurance 2000, Storch et al. 2005). S rostoucí mírou fragmentace mohou predátoři pronikat hlouběji do jádrového habitatu zmenšujících se krajinných fragmentů a šíře okrajového efektu se může zvětšovat (Lahti 2001, Bátary & Báldi 2004). Fragmenty s menším vzájemným poměrem délek stran, tj. čtvercovitější, popř. kulovitější, vykazují nižší podíl okrajového biotopu než fragmenty úzké a protáhlé (Johnson & Temple 1990, King & Byers 2002).

Intenzita okrajového efektu na hnízdní predaci se může měnit s ostrostí přechodu jednoho habitatu v druhý (Deng et al. 2003, Schneider et al. 2012). Nejvíce prací je zatím známo v mozaikové krajině s ostrými přechody (např. pole – les, les – sečená louka atp. – např. Huhta et al. 1996, Conner & Perkins 2003, Bátary et al. 2004 aj.), které jsou většinou vyvolané lidskou činností. Naopak, u graduálních přechodů mezi biotopy podobné fyziognomie (většinou přirozená stanoviště) je počet prací zkoumajících okrajový efekt sporý (např. Wallander et al. 2006, Schneider et al. 2012), obzvláště pak v oblastech s minimálním vlivem člověka, a jednoznačně z ní nevyplývá, zdali ptáci i jejich hnízdní predátoři chápou dva biotopy jako odlišné nebo jako jeden celek.

Zvýšená denzita predátorů v okrajové zóně může být podle Ries & Sisk (2004) ovlivněna třemi příčinami. Jedná-li se o tzv. efekt přelévání (*spillover*; *matrix effect* sensu Lidicker 1999) přes okrajovou zónu *(1)*, dva vzájemně přiléhající habitaty obsahují jeden a ten samý zdroj. Je-li jeho množství v preferovaném habitatu vyšší než v nepreferovaném, může početnost druhu, který spotřebovává daný zdroj, klesat směrem do nepreferovaného habitatu. Nepředpokládá se ale, že by druh do nepreferovaného habitatu pronikal do přílišné vzdálenosti. Příkladem můžou být volavky, které můžou navštěvovat louku přilehlou k mokřadu, protože do ní proniká menší množství mokřadních obojživelníků, kterými se živí. Pokud obsahují dva sousedící habitaty dva odlišné zdroje, které se vzájemně doplňují, bude existence v okrajové zóně zlepšovat možnost přístupu k oběma – jedná se o tzv. distribuci doplňkových zdrojů *(2)*. Ve výše uvedeném případu by volavky v louce hledaly hlodavce, kteří v mokřadu nežijí. Nemusely by létat nikam daleko a zdržovaly se ve větších počtech poblíž předělové linie mokřadu a louky. Pokud by se ovšem jednalo o hlodavce, kteří by žili pouze v okrajovém biotopu a ne jinde, koncentrace volavek by byla zvýšená právě v něm. V

tomto případě se jedná o zesílení vlivu okrajové zóny *(3)*. Při svém průchodu či pohybu v okrajové zóně by volavky mohly vyplenit každé náhodně nalezené hnízdo. Bod (2) a (3) je v práci Lidicker 1999 shrnut pod termín *ecotonal effect*.

Naprostá většina studií se zabývala pouze okrajovým efektem v jednom biotopu. Proto jsme v naší studii **(IV)** zvolili design nepřímo navržený Riesem a Siskem, abychom ověřili gradient míry hnízdní predace na přechodu dvou odlišných biotopů. Jako studijní plochu jsme vybrali krajinu Vltavského luhu v Národním parku Šumava, protože ve Střední Evropě kromě prací z oblastí se silným vlivem člověka chybí práce, které by se věnovaly míře hnízdní predace v přírodě blízkým biotopům s minimálním vlivem člověka. Součástí našeho pokusu bylo zkoumat míru hnízdní predace na přechodu mokřadu a přilehlých luk, protože prací, které by se věnovaly hnízdní predaci v biotopech s vzájemně podobnou fyziognomií je také málo. Jednostranný okrajový efekt na míru hnízdní predace zde již byl prokázán Albrechtem (2004) na hnízdící populaci hýlů rudých (*Carpodacus erythrinus*). Oboustranný okrajový efekt jsme testovali pomocí umělých zemních hnízd, vyplněných křepelčími vajíčky. Posléze jsme testovali také jednostranný okrajový efekt s použitím umělých křovinných hnízd. Okrajový efekt se na míře predace zemních hnízd projevil na postupném gradientu z mokřadu do louky a mohl odpovídat hypotéze distribuce doplňkových zdrojů nebo zesílení vlivu okrajové zóny. Na gradientu z mokřadu do lesa se projevil nekonzistentně pouze v některých sezónách s proměnlivým charakterem. Okrajový efekt na míru predace umělých křovinných hnízd byl v jedné ze dvou studovaných sezón také znatelný, což podporuje výsledky Albrechta (l. c.). Nezjištění okrajového efektu na hnízdní predaci v dané sezóně může mimo jiné znamenat, že se okrajový efekt v krajině projevuje, ale na daleko širších prostorových škálách, než jsme zkoumali (viz také výsledky ze studie **III**). Nekonzistence v jeho výskytu výskytu může být naopak způsobena změnou potravních preferencí hnízdních predátorů podle míry produktivity aktuální sezóny. Ptačí vajíčka totiž tvoří pouze doplňkovou část jídelníčku predátorů (Angelstam 1986) a mohou být v případě dostupnosti výživnější potravy nahrazena (viz výsledky studie **V**). Z otisků nalezených v našich hnízdech se podařilo určit pouze jen velmi malou část. Komunitu hnízdních predátorů Vltavského luhu z našich dat tedy popsat nelze.

Predátoři ptačích hnízd a jejich chování při samotné predaci

Společenstva predátorů v mírném pásu jsou tvořena zejména savci, kteří se při hledání potravy orientují čichem, a vizuálně se orientujícími ptáky, kteří se při pátrání po potravě řídí výraznými (orientačními) body – např. stromy, lidskými sídly, pásy živých plotů atp.

(Wallander et al. 2006). Ptačí hnízdní predátoři, jako např. krkavcovití, většinou spíše vyplení hnízda v křovinách (Santisteban et al. 2002), zatímco savci ve větší míře hnízda umístěná na zemi, která jsou pro ně lépe přístupná (Söderström 1999). Savčí predátoři jsou také většinou zodpovědni za predaci v mnohdy homogenním prostředí interního lesa (Marini et al. 1995), zatímco ptáci častěji predují hnízda v otevřené krajině nebo mozaice malých lesních fragmentů a otevřených habitatů (Andrén 1992, Nour et al. 1993, Vander Haegen et al. 2002). V našem pokusu **(III)** z ruderálních biotopů predovali ptáci více jak dvojnásobný počet hnízd než savčí predátoři.

Krkavcovití ptáci, kteří v našich podmínkách tvoří majoritní složku vizuálně se orientujících predátorů (Andrén 1992, Albrecht 2004), mnohdy nalézají hnízdo ukryté ve vegetaci díky aktivitě rodičů kolem něj (Yahner & Mahan 1999, Martin et al. 2000, Eggers et al. 2005, Schneider et al. 2012). V případě experimentálních hnízd si mohou zapamatovat jejich polohu, vidí – li výzkumníka při práci (Báldi 2000). Někteří z nich si dokonce mohou vytvořit na hledání hnízd searching image (Sonerud & Fjeld 1987, Santisteban et al. 2002, Olsen & Schmidt 2004). Míra hnízdní predace ptáků hnízdících v blízkosti hnízd nebo pozorovatelen některých druhů krkavcovitých ptáků může být díky tomu zvýšená (Söderström et al. 1998, Roos 2002, Roos & Pärt 2004, Šálek 2004, Wallander et al. 2006). U některých krkavcovitých ptáků byla v některých částech hnízdní sezóny zaznamenána zvýšená tendence predovat ptačí hnízda (Nisbet 1975, Sieving & Willson 1999). Nicméně o samotném chování krkavcovitých přímo při predaci ptačích hnízd jsou z literatury informace sporé. Náš terénní pokus **(V)** testoval chování straky obecné (*Pica pica*) vůči dvěma odlišným typům umělých snůšek (křepelčí a slepičí) ve dvou různých částech hnízdní periody (perioda sezení strak na vejcích, perioda krmení mláďat). Straky přednostně predovaly naše umělé snůšky v období sezení na vejcích. Je možné, že v období krmení mláďat přednostně hledaly výživnější potravu, jako jsou např. bezobratlí, a proto si vajec všímaly méně. Při predaci nerozlišovaly mezi umělými a reálnými vejci. K hnízdům s křepelčími vejci přistupovaly častěji a odnášely je z hnízda pryč. Naproti tomu, slepičí vejce byla konzumována přímo na hnízdě nebo u něj. Protože dospělá straka neumí otevřít zobák tak, aby do zobáku vzala celé slepičí vejce a zároveň napichování a transport může být náročnější, je pravděpodobné, že možnost odnést křepelčí vajíčko okamžitě pryč zvýšila atraktivitu křepelčích hnízd pro predující ptáky. Slepičí vejce jsou tedy při identifikaci středně velkých ptačích hnízdních predátorů vhodnější než vejce křepelčí.

V rámci dizertační práce se nám podařilo potvrdit, že přestože je fenomén ekologických pastí významným pro poznání ptačích populací, prací na toto téma, zejména

v určitých typech biotopů, stále mnoho není a je velmi obtížné jej testovat. Hlavním cílem by mělo být další testování ekologické pasti v co nejvíce možných typech biotopů u druhů s odlišnými životními strategiemi s důrazem na silně narušovanou krajinu suburbánní i naopak krajinu člověkem vůbec nenarušovanou.

Prokázali jsme, že zvýšená míra hnízdní predace, která může v některých případech s ekologickou pastí přímo souviset, je v ruderálních fragmentech situovaných do silně fragmentované krajiny ovlivněna zejména kompozicí svého okolí. Přesto je naše studie jednou z mála, které se kontextem okolní krajiny v Evropě zabývaly. Protože výsledky takové studie mohou být jedním z podkladů pro územní plánování, je další výzkum obdobného charakteru žádoucí v jiných oblastech Evropy i v jiných typech biotopů. Na příkladu člověkem nepříliš ovlivňované lokality jsme také potvrdili nekonzistenci výskytu okrajového efektu mezu mezi sezónami a typy studovaných biotopů. Částečně jsme zároveň podpořili evidenci případů, ve kterých míra hnízdní predace umělých hnízd může odrážet míru hnízdní predace hnízd reálných.

Na příkladu straky obecné jsme prokázali, že středně velký ptačí hnízdní predátor může dávat přednost vejcím, které je schopen z hnízda ihned odnášet. Pro identifikaci středně velkých ptačích hnízdních predátorů se tedy hodí vejce, která predátor nemůže z hnízda odnést a je nucen je konzumovat na nebo u něj. Našimi výsledky jsme rozšířili poznatky o chování hnízdních predátorů v průběhu predace ptačích hnízd. Vzhledem k tomu, že naše studie zahrnuje ale pouze jediný druh predátora, je v budoucnu více než žádoucí testovat chování jiných druhů v jiných typech prostředí a nenaruší-li to průběh hnízdění, pak také u hnízd reálných a nejen umělých.

LITERATURA

Albrecht T., 2004: Edge effect in wetland – arable land boundary determines nesting success of Scarlet Rosefinch (*Carpodacus erythrinus*) in the Czech republic. *The Auk 121 (2):* 361 – 371.

Andrén H., 1992: Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology. 73 (3),* 794-804.

Andrén H. & Angelstam P., 1988: Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 60 (2): 544 – 547.

Angelstam P., 1986: Predation on ground – nesting birds´ nests in relation to predator densities and habitat edge. *Oikos 47:* 365 – 373.

Baeyens G.1981. The role of the sexes in territory defence in the Magpie (*Pica pica*). *Ardea*

69: 69 - 82

Baker P. J., Molony S. E., Stone E., Cuthill I. C. & Harris S., 2008: Cats about town: is predation by free-ranging pet cats Felis catus likely to affect urban bird populations? *Ibis 150 (Suppl 1):* 86 – 99.

Báldi, A., 2000: Different depredation rates between daylight and twilight placed artificial nests. *Folia Zool. 49(2):* 157 – 159.

Bátary P. & Báldi A., 2004: Evidence of an edge effect on avian nest success. *Conservation Biology 18 (2):* 389 – 400.

Bátary P., Winkler H. & Báldi A., 2004: Experiments with artificial nests on predation in reed habitats. *J Ornithol 145:* 59 – 63.

Battin J., 2004: When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology 18 (6):* 1482 – 1491.

Bayne E. M. & Hobson K.A. 1997: Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conserv Biol, 11, 1418 - 1429.*

Bayne E. M., Van Wilgenburg S. L., Boutin S. & Hobson K. A., 2005: Modeling and field testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. *Landscape Ecology 20:* 203 – 216.

Burke D. M., Elliott K., Moore L., Dunford W., Nol E., Phillips J., Holmes S. & Freemark K., 2004: Patterns of nest predation on artificial and natural nests in forests. *Conservation Ecology 18 (2):* 381 – 388.

Conner L. M. & Perkins M. W., 2003: Nest predator use of food plots within a forest matrix: an experiment using artificial nests. *Forest Ecology and Management 179 (1 – 3):* 223 – 229.

Davis S., 2004: Area sensitivity in grassland passerines: effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in Southern Saskatchewan. *The Auk 121 (4):* 1130 – 1145.

Deng W.-H., Zheng G.-M. & Gao W., 2003: Nesting success of the meadow bunting along habitat edges in northeastern China. *J Field Ornithology 74 (1):* 37 – 44.

Donázar J. A., Blanco G., Hiraldo F., Soto-Largo E. & Oria J., 2002: Effects of forestry and other land-use practices on the conservation of Cinereous Vultures. *Ecological Applications 12 (5):* 1445 – 1456.

Donovan T. M., Jones P. W., Annand E. M. & Thompson F. R., 1997: Variation in local-scale

edge effects: mechanisms and landscape context. *Ecology 78 (7):* 2064 – 2075.

Dunford W. & Freemark K., 2004: Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. *Landscape Ecology 20:* 497 – 511.

Dwernychuk L. W. & Boag. D. A., 1972: Ducks nesting in association with gulls - an ecological trap? *Canadian Journal of Zoology 50:* 559 - 563.

Eggers S., Griesser M., Anderssen T. & Ekman J., 2005: Nest predation and habitat change interact to influence numbers. *Oikos 111:* 150 – 158

Einarsen G., Hausner V. H., Yoccoz N. G. & Ims R. A., 2008: Predation on artificial ground nests in birch forests fragmented by spruce plantations. *Écoscience 15 (2):* 141 – 149.

Evans K. L., Newson S. E. & Gaston K. J., 2009: Habitat influence on urban avian assemblages. *Ibis 151:* 19 – 39.

Fernández-Juricic E. & Jokimäki J., 2001: A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation 10:* 2023 – 2043.

Fraser G. S. a Stutchbury B. J. M., 2003: Area-sensitive forest birds move extensively among forest patches. Biological Conservation 118: 377 – 378.

Gates E. J. & Gysel L. W., 1978: Avian nest dispersion and fledging success in field – forest ecotones. *Ecology 59 (5):* 871 – 883.

Gowaty P. A., 1984: House Sparrows kill Eastern Bluebirds. *Journal of Field Ornithology 55:* 378 – 380.

Hagan J. M., Vander Haegen M. & McKinley P. S., 1996: The early development of forest fragmentation effects on birds. *Conservation Biology 10 (1):* 188 – 202.

Hahn B. A. & Silverman E. D., 2006: Social cues facilitate habitat selection: American Redstarts establish breeding territories in response to song. *Biology Letters 2 (3):* 337 – 340.

Howard M. N., Skagen S. K. & Kennedy P. L., 2001: Does habitat fragmentation influence nest predation in the shortgrass prairie? *The Condor 103 (3):* 530 – 536.

Howell C. A., Latta S. C., Donovan T. M., Porneluzi P. A., Parks G. R. & Faaborg J., 2000: Landscape effects mediate breeding bird abundance in midwestern forests. *Landscape Ecology 15:* 547 – 562.

Huhta E., Mappes T. & Jokimaki J., 1996. Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. *Ecography 19:* 85-91

Chace J. F. & Walsh J. J., 2006: Urban effects on native avifauna: A review. *Landscape and Urban Planning. 74*, 46 - 69.

Jerzak L., 2001: Synurbanization of the magie in the Paleartic. *In* J. M. Marzluff, R. Bowman and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. *Kluwer Academic*, Norwell, MA.

Johnson R. G. & Temple S. A., 1990: Nest predation and brood parasitism of tallgrass prairie birds. *J Wildlife Management 54:* 106 – 111.

Jokimäki J. & Huhta E., 2000: Artificial nest predation and abundance of birds along an urban gradient. *Condor 102 (4):* 838 – 847.

King D. I. & Byers B. E., 2002: An evaluation of powerline rigths-of-way as habitat for early-succesional shrubland birds. *Wildlife Soc. Bulletin 30:* 868 – 874.

Kokko H. & Sutherland W. J., 2001: Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research 3:* 537 – 551.

Lahti D. C., 2001: The „edge effect on nest predation" hypothesis after twenty years. *Biological Conservation 99:* 365 – 374.

Laurance W., 2000: Do edge effects occur over large spatial scales? *Tree 15 (4):* 134 – 135.

Lidicker W. Z. Jr., 1999: Responses of mammals to habitat edges: an overview. *Landscape Ecology 14:* 333 - 343.

Leston L. F. V. & Rodewald A. D., 2006: Are urban forests ecological traps for understory birds? An examination using Northern Cardinals. *Biological Conservation 131:* 566 – 574.

Lindell C. A., Riffell S. K., Kaiser S. A., Battin A. L., Smith M. L. & Sisk T. D., 2007: Edge responses of tropical and temperate birds. *The Wilson Journal of Ornithology 119 (2):* 205 – 220.

López-Flores V., MacGregor-Fors I. & Schondube J. E., 2009: Artificial nest predation along a neotropical urban gradient. *Landscape Urban Plan 92:* 90 – 95.

Marini M. A., Robinson S. K. & Heske E. J., 1995: Edge effects on nest predation in the Shawnee – national – forest, Southern Illinois. *Biological Conservation 74 (3):* 203 – 213.

Martin J. – L. & Joron M., 2003.: Nest predation in forest birds: Influence of predator type and predator´s habitat quality. *Oikos 102:* 641 – 653.

Martin T. E., Scott J. & Menge C., 2000: Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc Biol Sci. 267 (1459):* 2287 – 2293.

Marzluff J. M. & Ewing K., 2004: Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology 9 (3):* 280 – 292.

Marzluff J. M. & Neatherlin E., 2006: Corvid response to human settlements and campgrounds: causes, consequences and challenges for conservation. *Biological Conservation 130:* 301 – 314.

Nisbet I. C. T., 1975: Selective effects of predation in a tern colony. *The Condor 77 (2):* 221.

Nour N., Matthysen E. & Dhont A., 1993: Artificial nest predation and habitat fragmentation – different trends in bird and mammal predators. *Ecography 16:* 111 - 116

Olsen H. & Schmidt N. M., 2004: Response of Hooded Crow *Corvus corone cornix* and Magpie *Pica pica* to exposure to artificial nest. *Bird Study 51:* 87 – 90.

Parejo D., Oro D. & Danchin E., 2006: Testing habitat copying in breeding habitat selection in a species adapted to variable environments. *Ibis 148:* 146-154.

Pärt T. & Wretenberg J., 2002: Do artificial nests reveal relative nest predation risk for real nests? *Journal of Avian Biology 33:* 39 – 46.

Pärt T., Arlt D. & Villard M.-A., 2007: Empirical evidence for ecological traps: a two-step model focusing on individual decisions. *Journal of Ornithology 148 (suppl 2):* S327 - S332.

Paton P. W. C., 1994: The effect of edge on avian nest success – how strong is the evidence. *Conservation Biology 8 (1):* 17 – 26.

Pelicice F. M. & Agostinho A. A., 2008: Fish-passage facilities as ecological traps in large neotropical rivers. *Conservation Biology 22 (1):* 180-188.

Remeš V., 2005: Nest concealment and parental behaviour interact in affectingnest survival in the Blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis. *Behavioral Ecology and Sociobiology 58:* 326 – 333.

Ries L. & Sisk T. D., 2004: A predictive model of edge effects. *Ecology 85 (11):* 2917 – 2926.

Robb G. N., McDonald R. A., Chamberlain D. E. & Bearhop S., 2008: Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment 6 (9):* 476 – 484.

Robertson G. A. & Hutto R. L. 2006: A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology 87*: 1075 - 1085.

Roos S., 2002: Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia 133:* 608 – 615.

Roos S., 2006: Habitat selection and reproduction of Red-backed Shrikes (*Lanius collurio*) in relation to abundance of potential avian nest predators. Osnabrücker Naturwissenschaftliche Mitteilungen Brand 32: S. 167 – 173.

Roos S. & Pärt T. 2004. Nest predators and spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology 73:* 117 – 127.

Santisteban L., Sieving K. E. & Avery M. L., 2002: Use of sensory cues by Fish Crows *Corvus ossifragus* preying on artificial bird nests. *Journal of Avian Biology 33:* 245 – 252.

Schiegg K., Eger M. & Pasinelli G. 2007: Nest predation in Reed Buntings (*Emberiza schoeniclus*): an experimental study. *Ibis 149:* 365 – 373.

Schneider N. A., Low M., Arlt D. & Pärt T., 2012: Contrast in edge vegetation structure modifies the predation risk of natural ground nests in an agricultural landscape. *Plos One 7 (2):* available online on: http://dx.plos.org/10.1371/journal.pone.0031517

Sieving K. E. & Willson M. F. 1999. A temporal shift in Steller's Jay predation on bird eggs. *Canadian Journal of Zoology 77:* 1829 – 1834.

Soderström B, 1999: Artificial nest predation rates in tropical and temperate forests: a review of the effects of edge and nest site. *Ecography 22:* 455 – 463.

Soderström B, Pärt T. & Ryden J. 1998: Different predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia 117:* 108-118.

Sonerud G. A. & Fjeld P. E., 1987: Long – term memory in egg predators: an experiment with a Hooded Crow. *Ornis Scand. 18:* 323 – 325.

Storch I., Woitke E. & Krieger S., 2005: Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe. *Landscape Ecology 20:* 927 – 940.

Svobodová J., Koubová M., Mrštný L., Albrecht T. & Kreisinger J., 2012: Temporal variation in nest predation risk along habitat edges between grassland and secondary forest in Central Europe. *European Journal of Wildlife Research 58:* 315 – 323.

Šálek M., 2004: The spatial pattern of the Black – billed Magpie, *Pica pica* to predation risk on dummy nests. *Folia Zoologica 53:* 57 – 64.

Šálek M., Pintíř J. & Marhoul P., 2004: Vliv zástavby a lesa na prostorový výskyt populace koroptve polní (*Perdix perdix*) v zemědělské krajině. *Sylvia 40:* 89 – 97.

Tatner P., 1982: Factors influencing the distribution of Magpies *Pica pica* in an urban environment. *Bird Study (29):* 227 – 234.

Thorington K. K. & Bowman R., 2003: Predation rate on artificial nests increases with human housing density in suburban habitats. *Ecography 26:* 188 – 196.

Vander Haegen W. M., Shroeder M. A. & DeGraaf F. M., 2002: Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. *Condor 104:* 496 – 506.

Vickery P. D., Hunter M. L. Jr. & Wells J. V., 1992: Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos, 63, 281-288.*

Villard M.-A., 1998: On forest – interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. The Auk 115 (3): 801 – 805.

Wallander J., Isaksson D. & Lenberg T., 2006: Wader nest distribution and predation in relation to man – made structures on coastal pastures. *Biological conservation 132:* 343 – 350.

Weidinger K., 2002: Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology 71 (3):* 424 – 437.

Wilcove D S. 1985: Nest predation in forest tracts and the decline of migratory songbirds. *Ecology 66:* 1211 - 1214.

Winter M., Johnson D. H., Shaffer J. A., Donovan T. M. & Svedarsky W. D., 2006: Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management 70 (1):* 158 – 172.

Yahner R. H. & Mahan C., 1999: Potential for predator learning of artificial arboreal nest locations. *Wilson Bulletin 111 (4):* 536 – 540.

SOUBOR ČLÁNKŮ

I.

Koubová M., **Suvorov P.,** Svobodová J., Albrecht T. & Kreisinger J.,

2011: **Fragmentation and loss of natural habitats.** Subhead 6: Suvorov

P.: **Ecological traps.** Chapter 6 in: Daniels J. A. (ed.): Advances in

Environmental Research 14. pp 195 – 197. *Nova Science Publishers Inc*.

Chapter 6

PREDATION IN LANDSCAPES AFFECTED BY FRAGMENTATION AND LOSS OF NATURAL HABITATS

Martina Koubová[*1]*, Petr Suvorov[1], Jana Svobodová[1], Tomáš Albrecht[2, 3] and Jakub Kreisinger[2]*

[1] Department of Ecology, Faculty of Environmental Science,
Czech University of Life Sciences Prague,Czech Republic
[2] Faculty of Science, Department of Zoology,
Charles University in Prague, Czech Republic
[3] Institute of Vertebrate Biology v.v.i., Brno,
Academy of Sciences of the Czech Republic, Czech Republic

6. ECOLOGICAL TRAPS

Rapid habitat changes, especially of anthropogenic origin, can have detrimental consequences not only because they alter interspecies interactions, as described above. Faced with rapid changes in environments, individuals from natural populations may have only limited ability to alter their modes of behavior, and that can lead to suboptimal exploitation of resources in the altered habitats (Miner et al. 2005, Shochat et al. 2005). For example, (micro) habitat parameters (food abundance, vegetation density available for breeding etc.) in undisturbed landscapes indicate the quality of an environment and hence they have a positive effect on individual fitness (Schlaepfer et al. 2002). In a disturbed landscape, however, these characters do not necessarily indicate the quality of the environment (Gates and Gysel 1978, Vergara and Simonetti 2003, Igual et al. 2007, Mannan et al. 2008). If a particular individual living in an altered environment still orients itself based on the evolved preferences for indicators of environmental quality that are no longer relevant, then this leads to a direct negative effect on its fitness (Kokko and Sutherland 2001, Ries and Fagan 2003, Gilroy and Sutherland 2007, Pärt et al. 2007, Kriska et al. 2008, Lindell 2008). In an extreme case, this can cause extinction of the population (Schlaepfer et al. 2002, Ries and Fagan 2003). This phenomenon

* Corresponding Author: e-mail koubova@fzp.czu.cz, Czech University of Life Sciences Prague, Department of Ecology, Faculty of Environmental Science, Kamýcká 1176, Prague 6 165 21, Czech Republic

is known as an "ecological trap." Put in another way, an ecological trap typically occurs in situations where behavioral or sensory capabilities estimating habitat quality are limited (Donovan and Thompson 2001, Kokko and Sutherland 2001, Battin 2004, Robertson and Hutto 2007) even as habitats are undergoing rapid changes from an evolutionary point of view.

An individual choice of nesting site is based on the evolutionary history of a given species and also on individual experience (Kokko and Sutherland 2001, Miner et al. 2005, Keeler and Chew 2008). The selection of habitat itself takes place on the basis of direct (e.g., amount of food resources) or indirect (e.g., number of individuals of the same species, predator absence) clues (Andrén 1990, Kokko and Sutherland 2001, Schlaepfer et al. 2002, Roos and Pärt 2004, Eggers et al. 2005,). In some species, the habitat choice is driven by imprinting (i.e. natal habitat preference induction (Kokko and Sutherland 2001, Gilroy and Sutherland 2007). Nevertheless, if an individual has more complete information about a given habitat, its estimation of habitat quality is better (Kokko and Sutherland 2001, Battin 2004).

Although some habitat parameters may increase the probability of survival (better food resources, more nesting places, etc.), their presence in some types of altered habitats can often be associated with factors that negatively affect individual fitness and which can outweigh the effect of positive characters (rate of parasitism and nest predation, disturbance, direct losses caused by humans etc.). For example, although North American Cooper's hawks *(Accipiter cooperii)* were shown to have a high adult survival rate, enough food availability and nesting places in an urban habitat of Arizona, the numbers of surviving nestlings were low because of infection caused by *Trichomonas gallinae*, which occurs in urban habitats (Mannan et al. 2008).

Even a relatively simple ecological trap model can be influenced by the existence of a number of ecological phenomena. According to the despotic model of habitat colonization (IDD – ideal despotic distribution), for example, if competitively more capable individuals occupy the preferred habitat, individuals less competitively fit are forced to nest in less attractive habitat (Andrén 1990, Hunt 1996, Kokko and Sutherland 2001, Battin 2004). In a disturbed environment, however, the individuals of higher fitness may estimate habitat quality according to irrelevant indicators. Consequently, they breed in preferred but qualitatively poorer habitat (e.g., edge habitat, see below) and their reproductive success is lower (Donovan and Thompson 2001) than it would be in non-preferred but higher-quality habitat. Individuals of higher fitness and competitively less capable individuals may achieve similar breeding success due to different conditions of their breeding habitats (Van Horne 1983, Miner et al.

2005). Hence, this phenomenon may compensate for the effect of the ecological trap (Flashpohler et al. 2001a, McGowan 2001).

Two main causes of ecological traps related to nesting success of birds have so far been described in the literature: introductions of exotic species outside their usual area of distribution (Mack et al. 2000, Chace and Walsh 2004) and habitat fragmentation. In addition, a combination of both these influences may occur (Marzluff and Ewing 2004).

Habitat fragmentation increases the proportion of edge to interiors, and habitat edges can be attractive for some nesting birds due to various reasons (Hansson 1994, Fernández–Juricic and Jokimäki 2001, Schlaepfer et al. 2002). Vegetation heterogeneity, which positively correlates with nesting success (Martin and Joron 2003), is usually higher in edge habitats. Another potential advantage of edge habitat is that individuals have easier access to complementary resources from two neighboring habitats (Ries and Sisk 2004). For the same reasons, however, habitat edges can be preferred by omnivorous predators (rats, foxes, martens, corvids etc.; Wegner and Merriam 1979, Andrén 1992, Lahti 2001, Chace and Walsh 2004) that are responsible for higher nest predation along edges compared to interior habitat (Andrén 1992, Paton 1994, Zanette and Jenkins 2000, Albrecht 2004).

Habitat edges as ecological traps can be best documented in situations where the rate of nesting success is lower in edge habitat than in interior parts (so-called edge effect on nest predation) and when birds more frequently place their nests in edge habitats (Andrén and Angelstam 1988, Paton 1994, Batáry et al. 2004, Batáry and Báldi 2004, Hoover et al. 2006, Weldon 2006, Schiegg et al. 2007). Although the edge effect on nest predation has been supported by many studies using both real (Albrecht 2004, Driscoll and Donovan 2004, Pasinelli and Schiegg 2006) and artificial (Donovan et al. 1997, Storch et al. 2005, Schiegg et al. 2007) nests, however, their direct connection with an ecological trap has been demonstrated in only a few of these, because most studies were not able simultaneously to document the habitat preference of birds and predation rate in the compared habitats (e.g., Flashpohler et al. 2001b, Weldon and Haddad 2005, Robertson and Hutto 2007). In one such study, for example, nests of Hermit thrushes *(Catharus guttatus)* and ovenbirds *(Seiurus aurocapillus)* suffered higher predation especially in the edge habitat, and, consistent with the prediction of the ecological trap hypothesis, this was also the place of increased density of their nests (Flashpohler et al. 2001b). Interestingly, a subsequent study claims that the clutch size of ovenbird was by as much as 16% larger in the edge habitat (Flashpohler et al. 2001a), and that can to a certain extent compensate the effect of the ecological trap. Nevertheless,

there are other studies that did not reveal habitat edges acting as ecological traps (Ratti and Reese 1988, Ball et al. 2008).

In the past decade, many studies have described various examples of ecological traps in the human-altered landscape (Horváth et al. 2007, Igual et al. 2007, Robertson and Hutto 2007, Keeler and Chew 2008, see also a summary table in Schlaepfer et al. 2002), but only a few of them studied the exact mechanisms and factors predicting the existence of ecological traps (Flaspohler et al. 2001). It is possible that ecological traps also occur in pristine regions (Battin 2004) after extensive natural disturbances such as windstorms, floods or wildfires or in connection with finer changes in habitats (e.g., habitat changes following the fall of a tree, a change in water regime caused by a newly built beaver dam). However, these subtle changes clearly need not affect the population dynamics of birds, and their importance for conservation management is not as high as in cases of anthropogenic changes on a larger scale. A study involving Argentinean burrowing owls *(Athene cunicularia)* provides an example. The owls prefer habitats with a vegetation cover of less than 40% (Machicote et al. 2004). Nesting success of owls was observed to be 35% if they nested in viscacha *(Lagostomus maximus)* burrows, whereas no single nest survived when placed in an armadillo *(Chaetophractus villosus)* burrow (Machicote et al. 2004) because, in contrast to armadillos, viscachas regularly graze the surroundings of their burrows. Results from other localities proved that nesting in armadillo burrows was successful if the surrounding soil was bare (Machicote et al. 2004). Therefore, the authors proposed armadillo burrows as constituting a local ecological trap, although owl preference for particular burrows was not tested. Works dealing with the relationship between reproductive success of birds and ecological traps in undisturbed landscapes are not very common, and studies which would compare landscapes disturbed and undisturbed by humans are altogether absent.

The extent to which ecological traps are a common phenomenon is still unclear. Studies often present results that could support the ecological traps hypothesis (Best 1986, Ellison and Brush 2004, Klein et al. 2007), but some substantial parameters that would enable testing it are missing (e.g., habitat preferences of nesting birds). In addition to environmental characteristics and nesting success, it is also crucial to measure the physical condition of adult birds (Igual et al. 2007) or their offspring (Weldon and Haddad 2005) because population density is not always the best parameter for testing of an ecological trap.

Although local studies in small areas can often help to understand this phenomenon, the study of ecological traps on wider scales of habitat type is essential for conservation management (e.g., Robinson et al. 1995). Methods of studying ecological traps are still not completely

reliable and often do not reveal the whole truth about the local functioning of particular biospheric units. The improvement of these techniques and use of new approaches to study habitat preference and individual fitness can help protect biodiversity in a more effective way.

REFERENCES

Albrecht T (2004) Edge effect in wetland – arable land boundary determines nesting success of Scarlet Rosefinch (*Carpodacus erythrinus*) in the Czech Republic. *The Auk* 121: 361–371.

Andrén H (1990) Despotic distribution, unequal reproductive success, and population regulation in the Jay *Garrulus glandarius Landscape Ecology* 71: 1796–1803.

Andrén H (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73: 794–804.

Andrén H, Angelstam P (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69: 544–547.

Ball JR, Bayne EM, Machtans CS (2008): Energy sector edge effects on songbird nest fate and nest productivity in the boreal forest of Western Canada: a preliminary analysis. Proceedings of the Fourth International Partners in Flight Conference: *Tundra to Tropics*: 161–170.

Batáry P, Báldi A (2004): Evidence of an edge effect on avian nest success. *Conservation Biology* 18: 389–400.

Batáry P, Winkler H, Báldi A (2004) Experiments with artificial nests on predation in reed habitats. *Journal of Ornithology* 145: 59–63.

Battin J (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* 18: 1482–1491.

Best L. B. (1986). Conservation tillage: ecological traps for nesting birds? *Wildlife Society Bulletin. 14,* 308-317.

Chace JF, Walsh JJ (2004) Urban effects on native avifauna: A review. *Landscape and Urban Planning* 74: 46–69.

Donovan TM, Jones PW, Annand EM, Thompson FR (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78: 2064–2075.

Donovan TM, Thompson III FR (2001) The ecological trap hypothesis: A habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11: 871–882.

Driscoll MJ, Donovan TM (2004) Landscape context moderates edge effects: nesting success of Wood Thrushes in Central New York. *Conservation Biology* 18: 1330–1338.

Eggers S, Griesser M, Anderssen T, Ekman J (2005) Nest predation and habitat change interact to influence numbers. *Oikos* 111: 150–158.

Ellison K. & Brush T. (2004). Hooded Oriole nest silure associated with a novel nest site. *Western Birds. 35*, 71-78.

Fernández-Juricic E, Jokimäki J (2001) A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation* 10: 2023–2043.

Flashpohler DJ, Temple SA, Rosenfield RN (2001a) Effects of forest edges on Ovenbird demography in a managed forest landscape. *Conservation Biology* 15: 173–183.

Flashpohler DJ, Temple SA, Rosenfield RN (2001b) Species-specific edge effects on nest success and breeding density in a forested landscape. *Ecological Applications* 11: 32–46.

Gates JE, Gysel LW (1978) Avian nest dispersion and fledging success in field – forest ecotones. *Ecology* 59: 871–883.

Gilroy JJ, Sutherland WJ (2007) Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology and Evolution* 22: 351–356.

Hansson L (1994) Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. *Landscape Ecology* 9: 105–115.

Hoover JP, Tear TH, Baltz M (2006) Edge effects reduce the nesting success of Acadian Flycatchers in a moderately fragmented forets. *Journal of Field Ornithology* 77: 425–436.

Horváth G, Malik P, Kriska G, Wildermuth H (2007) Ecological traps for dragonflies in a cemetery: the attraction of Sympetrum species (*Odonata: Libellulidae*) by horizontally polarizing black gravestones. *Freshwater Biology* 52: 1700–1709.

Hunt P (1996) Habitat Selection by American Redstarts along a successional gradient in Northern Hardwoods forest: evaluation of habitat quality. *The Auk* 113: 875–888.

Igual JM, Forero MG, Gomez T, Oro D (2007) Can an introduced predator trigger an evolutional trap in a colonial seabird? *Biological Conservation* 137: 189–196.

Keeler MS, Chew FS (2008) Escaping an evolutionary trap: preference and performance of a native insect on an exotic invasive host. *Oecologia* 156: 559–568.

Kokko H, Sutherland WJ (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research* 3: 537–551.

Klein Á., Nagy T., Csörgő T. & Mátics R. (2007). Exterior nest-boxes may negatively affect Barn Owls *Tyto alba* survival: An ecological trap. *Bird Conservation International. 17*, 273-281.

Kriska G, Malik P, Szivák I, Horváth G (2008) Glass buildings on river banks as "polarized light traps" for mass-swarming polarotactic caddis flies. *Naturwissenschaften* 95: 461–467.

Lahti DC (2001) The „edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* 99: 365–374.

Lindell CA (2008) The value of animal behavior in evaluations of restoration success. *Restoration Ecology* 16: 197–203.

Machicote M, Branch LC, Villarreal D (2004) Burrowing Owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? *Oikos* 106: 527–535.

Mannan RW, Steidl RJ, Boal CW (2008) Identifying habitat sinks: a case study of Cooper´s Hawks in an urban environment. *Urban Ecosystems* 11: 141–148.

Martin JL, Joron M (2003) Nest predation in forest birds: Influence of predator type and predator´s habitat quality. *Oikos* 102: 641–653.

Marzluff JM, Ewing K (2004) Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* 9: 280–292.

McGowan KJ (2001): Demographic and behavioral comparisons of suburban and rural American Crows. Chapter 17 in Marzluff et al.2001*: Avian Ecology and Conservation in an Urbanizing* World. Kluwer Academic Press, Norwell, MA: 365–381.

Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* 20: 685–692.

Pärt T, Arlt D, Villard MA (2007) Empirical evidence for ecological traps: a two-step model focusing on individual decisions. *Journal of Ornithology* 148: 327–332.

Pasinelli G, Schiegg K (2006) Fragmentation within and between wetland reserves: the importance of spatial scales for nest predation in reed buntings. *Ecography* 29: 721–732.

Paton PWC (1994) The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8: 17–26.

Ratti JT, Reese KP (1988) Preliminary test of ecological trap hypothesis. *The Journal of Wildlife Management* 52: 484–491.

Ries L, Fagan WF (2003) Habitat edges as a potential ecological trap for an insect predator. *Ecological Entomology* 28: 567–572.

Ries L, Sisk TD (2004) A predictive model of edge effects. *Ecology* 85: 2917–2926.

Robertson BA, Hutto RL (2007) Is selectively harvested forest an ecological trap for Olive – sided Flycatchers? *The Condor* 109: 109–121.

Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987–1990.

Schiegg K, Eger M, Pasinelli G (2007) Nest predation in Reed Buntings Emberiza schoeniclus: an experimental study. *Ibis* 149: 365–373.

Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17: 474–480.

Shochat E, Patten MA, Morris DW, Reinking DL, Wolfe DH, Sherrod SK (2005) Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos* 111: 159–169.

Storch I, Woitke E, Krieger S (2005) Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe. *Landscape Ecology* 20: 927–940.

Van Horne B (1983) Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management* 417: 893–901.

Vergara PM, Simonetti JA (2003): Forest fragmentation and rhinocryptid nest predation in central Chile. *Acta Oecologica* 24: 285–288.

Wegner JF, Merriam G (1979) Movements by birds and small mammals between a wood and adjoining farmland habitats. *Journal of Applied Ecology* 16: 349–357.

Weldon AJ (2006) How corridors reduce Indigo Bunting nest success. *Conservation Biology* 20: 1300–1305.

Weldon AJ, Haddad NM (2005) The effects of patch shape on Indigo Buntings: Evidence for an ecological trap. *Ecology* 86: 1422–1431.

Zanette L, Jenkins B (2000) Nesting success and nest predators in forest fragments: a study using real and artificial nests. *The Auk* 117: 445–454.

II.

Suvorov P. & Svobodová J.: **The occurence of ecological traps in birds: Is our knowledge sufficient? A review.** *Submitted manuscript (Journal of Landscape Ecology).*

THE OCCURENCE OF ECOLOGICAL TRAPS IN BIRDS: IS OUR KNOWLEDGE SUFFICIENT? A REVIEW

Petr Suvorov, Jana Svobodová

Czech University of Life Sciences, Faculty of Environmental Science, Kamýcká 129, CZ-165 21 Prague 6

e-mail: petr.suvorov@hotmail.com, svobodovajana@fzp.czu.cz

ABSTRACT

Anthropogenic changes in a landscape create new cues for birds, which must permanently adapt to these. If landscape changes come too quickly, individuals have insufficient time to develop adequate reactions. They may therefore preferentially nest in low-quality habitats, which can lead to diminished nesting success and to reduction of their population size. This is usually termed the ecological trap hypothesis. We reviewed 38 studies investigating this phenomenon and analysed whether there exist relationships between ecologic trap occurrence and geographical region, habitat type, and/or life strategies of bird species. Ecological traps were most often associated with the presence of exotic species. Exotic species can modify environmental conditions in ways to which native communities are not adapted. They have been mainly detected in open habitats. Such open habitats as arable fields and meadows are under greater human pressure, and rapid changes probably occur there more frequently. Although more studies from North America were investigated, the hypothesis was supported more frequently in European studies. This possibly is due to higher human population density and, hence, more frequent habitat changes. Our results show that an ecological trap is not likely associated with migration. Ground nests suffered less by the consequences of such trap than did other nest types. Although the implications of the ecological trap hypothesis in species conservation are undisputable, a still-more detailed approach is needed. For instance, some habitat types, such as suburban areas, have been neglected in the context of ecological traps as has been the phenomenon's appearance in pristine habitats.

Key words: edge effect, exotic species, habitat fragmentation, life strategies, nest predation, nesting success

INTRODUCTION

Correct selection of a nesting site is one of the most essential points of nesting success in birds (e.g. Bayne and Hobson 2001; Shochat et al. 2005). Birds choose their nesting sites based on environmental characteristics such as species composition or density of vegetation, because, in a natural environment, these indicate sufficiency of food and shelters, which, in turn, have positive effects on individuals' reproductive success (Schlaepfer et al. 2002; Aldridge and Boyce 2007; Powell et al. 2010). In a rapidly changing environment, however, these characteristics do not necessarily possess the same indicative value (Gates and Gysel 1978; Vergara and Simonetti 2003; Shochat et al. 2005), because they may be associated with factors, such as high rate of nest predation, parasitization and disturbance (Marzluff and Ewing 2004; Mannan et al. 2008), that can outweigh the effects of positively acting factors. If individuals of higher fitness preferentially nest in biotopes where they nevertheless achieve lower nesting success, then this habitat is said to be an ecological trap (Dwernychuk and Boag 1972; Gates and Gysel 1978; Robertson and Hutto 2006; Pelicice and Agostinho 2008). This phenomenon can cause decrease in bird abundance (Kokko and Sutherland 2001; Ries and Fagan 2003; Gilroy and Sutherland 2007; Lindell 2008; Pärt et al. 2007; Kriska et al. 2008) and, in extreme cases, can lead to local extinction of entire populations (Reed 1999; Schlaepfer et al. 2002; Ries and Fagan 2003).

An ecological trap is usually linked to a human-altered habitat, and mostly due to habitat fragmentation or the presence of exotic species (Battin 2004). If a new species of animal or plant is introduced into a particular environment, it can either directly (through predation, competition, parasitization or genetic hybridization) or indirectly (e.g. by affecting vegetation structure, which can lead to higher nest predation) negatively influence the reproductive success of native species (Mack et al. 2000; Schlaepfer et al. 2005; Campomizzi et al. 2009). In many places, birds must cope with excessive habitat fragmentation (Fernández – Juricic and Jokimäki 2001), which causes a loss of suitable nesting biotopes and increases the proportion of marginal biotopes relative to inner ones (Andrén and Angelstam 1988; Bosschieter and Goedhart 2005; Fahrig 2003; Manu et al. 2007). Some biotope interfaces, however, can be attractive to nesting birds for such reasons as vegetation heterogeneity (Hansson 1994; Fernandez – Juricic et al. 2001; Brotons and Herrando 2003; Batáry et al. 2004; Berg 2008) or easy access to complementary resources from neighbouring biotopes (Ries and Sisk 2004). Due to a higher concentration of resources, however, there is also an elevated density of especially omnivorous (non-specialized) species of predators such as Red Fox (*Vulpes vulpes*), martens (*Martes* sp.) or corvids (*Corvidae*) (Andrén 1992; Paton 1994; Chace and Walsh 2004; Marzluff and Neatherlin 2006), which profit from the presence of

humans and can lower the reproductive success of birds through increased predation of their nests (i.e. due to so-called edge effect on nest predation). When birds nest in edge habitats in higher densities than in interior biotopes and simultaneously achieve lower reproductive success there because of higher nest predation, they may have been lured into an ecological trap (Weldon and Haddad 2005).

Birds choose their nesting sites based not only on their evolutionary history but also on their acquired experiences (Kokko and Sutherland 2001; Miner et al. 2005; Parejo et al. 2006, Keeler and Chew 2008). Nevertheless, to gain experience takes time. Therefore, individuals that do not remain at their nesting sites all year round (i.e. migrants) can be more vulnerable to negative effects of ecological traps than are sedentary birds because they have shorter time to evaluate the actual conditions of their nesting sites after their arrival (Kokko and Sutherland 2001; Kristan 2003; Battin 2004; Winter et al. 2006). To our knowledge, however, this issue has never been evaluated in studies investigating bird ecology.

The aim of this article is to review the literature studying the ecological trap phenomenon in birds. We analyse whether existence of ecological traps is associated with particular habitat types, geographic areas, and/or life strategies of bird species such as migration and nesting place. We also discuss if ecological traps appear in habitats not altered by humans and the utility of this concept for species protection.

MATERIAL AND METHODS

Articles investigating the ecological trap phenomenon in birds were mainly searched according to the key words "ecological trap" and "birds" using the databases of Web of Science, Wiley, EBSCO and Springer Link, as well as according to the references of papers identified in this way. Those studies examining ecological trap using artificial nests were not included into our analysis, because this methodological approach does not sufficiently enable testing of nesting birds' habitat preferences (Söderström et al. 1998, Yahner and Piergallini 1998).

To analyse whether the existence of an ecological trap is linked to specific geographical regions and/or habitat types, we distinguish among six geographical regions (Europe inclusive of Fuerteventura, North America, South America, Asia, Africa, Australia + New Zealand) and five habitat types (forest, open habitats, suburban habitats, coastal zones and small islands, and unclassified mosaic of different habitats). Open habitats contained such habitat types as arable fields, meadows or wetlands. In addition, habitat types such as cities with suburban zones and farmland were considered as man-affected habitats whereas those

like forests, meadows, wetlands or deserts as natural habitats. From the viewpoint of life strategies, we distinguished between migratory and sedentary species. Moreover, birds were divided into four groups according to their nesting sites (ground, shrub, tree, cavity in the ground or tree; del Hoyo et al. 1992–2011).

RESULTS

We identified 47 articles examining the ecological trap hypothesis in birds. However, nine studies (19.2%) only discussed possible effects of ecological trap on bird nesting success and did not test it. Therefore, only 38 papers were included into the ensuing analyses. We found that existence of an ecological trap has and has not been supported in 14 (29.8%) and 24 (51.1%) studies, respectively (Table 1). In addition, most studies examining the ecological trap hypothesis had tested the effect of habitat fragmentation and management (39.5%, n = 15) or the effect of direct human influence (29.0%, n = 11). The existence of an ecological trap has mainly been supported in studies examining the presence of exotic species (80.0%, n = 4; Table 1).

Most studies examining the ecological trap phenomenon have been conducted in North America (60.5%, n = 23), followed by Europe (34.2%, n = 13). Whereas 57.1% (n = 8) of European studies supported the hypothesis, among the North American studies this figure was only 42.9% (n = 6; Table 1). Just a few studies have been done in other regions (South America, n = 1; Australia + New Zealand, n = 1) and none of these have supported the ecological trap phenomenon. Moreover, to our knowledge, no such study has been conducted either in Africa or the Asian region.

Regarding habitat type, the ecological trap hypotheses has been most studied in open habitats (i.e. arable fields, meadows and wetlands; n = 16) and forest habitats (n = 15). Only 3 studies came from urban habitats and 2 investigations were in coastal zones and small islands (5.3%, Table 1). We revealed that ecological traps appeared more in open habitats (60.0%) than in forests habitats (50.0%). There was no difference in detection of ecological traps between anthropogenic and natural biotopes, however, because the hypothesis was supported in 4 (36.4%) of 11 studies in anthropogenic habitat types and in 9 (39.13%) of 23 studies in natural habitat types.

We found that the ecological trap phenomenon has been tested more frequently in migratory species (n = 24) than in sedentary species (n = 9). In addition, it has been supported in the same proportion in relation to migratory (41.7%) and sedentary species (44.4%). In two works it was not possible to distinguish its effect on sedentary versus migratory species because

these had investigated migratory and sedentary species simultaneously. From the viewpoint of nest position, we found that ground nesters suffered less from ecological traps (2 cases out of 12, or 17%) than did birds using another nesting strategy (Table 1).

DISCUSSION

To our knowledge, the overall number of studies on the topic of ecological traps is not large (see also Pärt et al. 2007), even though their significance for species protection is unquestionable. This is probably because ecological traps are very problematic to test (Robertson and Hutto 2006). Not only nesting preferences and the fitness of populations (i.e. nest density, fitness and reproductive success of individuals) but also the habitat quality (i.e. food resources, rate of nest predation and parasitization) must be investigated. Hence, there is also insufficiency of sample size in many studies (e.g. Remeš 2003, Machicote et al. 2004).

Although the papers we reviewed are also significantly biased toward North American studies, we found that the hypothesis of ecological traps was more frequently supported in Europe than in North America. This difference can be due to the higher human population density on the European continent (http://www.worldatlas.com) and, hence, possibly to more frequent habitat changes. However, this aspect merits further investigation.

We also show that ecological traps frequently occurred in relation to exotic species, because exotic predator and plant species may negatively affect the reproduction outputs of birds. For example, the preferred nesting habitat of Cory's Shearwater (*Calonectris diomedea*) is usually in cliff burrows at the Mediterranean Sea. In the Chafarinas Islands, however, rats (*Rattus rattus*) have been introduced by humans and their growing population has begun to depredate Cory's Shearwaters, and particularly their nestlings. The birds, however, did not interpret the presence of rats as an environmental cue by which to recognize an unsuitable environment, and they nested there in higher densities than at localities without rats (Igual et al. 2007).

Exotic plant species can also influence the reproductive success of birds (Misenhelter and Rotenbery 2000; Borgmann and Rodewald 2004; Nordby et al. 2008), because their presence causes changes in the structure of the vegetation which can negatively affect the abundance and diversity of food resources (Tallamy 2004), degree of cover, or nest availability (Schmidt and Whelan 1999). For instance, the Old World migratory species Blackcap (*Sylvia atricapilla*) had higher reproductive success in primary gallery forests in Moravia even though its nesting density is twice as high in secondary forests of Black Locust (*Robinia pseudacacia*; Remeš 2003). Birds preferred Black Locust growths probably because this tree produces its foliage earlier in spring than do native woody species, and therefore it offers

early cover and potential nesting places (so-called attractive sink biotopes; see Delibes et al. 2001 a, b; Aldridge and Boyce 2007).

The selection of a nesting place itself occurs on the basis of direct (amount of food resources, shelters, nesting opportunities, etc.) and/or indirect cues (e.g. the number of individuals of the same species or absence of a predator; Andrén 1990; Kokko and Sutherland 2001; Schlaepfer et al. 2002; Schlaepfer 2003; Roos and Pärt 2004; Eggers et al. 2005). The more complete information an individual has about a given biotope, the better is its judgement (Battin 2004; Kokko and Sutherland 2001). Simply speaking, good judgement of habitat quality requires sufficiency of time (Sol and Lefebvre 2000; Donovan and Thompson 2001; Robertson and Hutto 2007). Nevertheless, some migratory species can compensate their shortened time for habitat evaluation by copying the nesting strategies of sedentary species (heterospecific habitat copying hypothesis; see Parejo et al. 2006). Therefore, the risk of nesting failure associated with ecological traps did not differ between migratory and sedentary species in our data set.

We also found that the lowest occurrence of ecological traps was among ground nesting species. This can probably be affected by the fact that 8 of 12 papers studying ground nesters were from North America, where the appearance of the ecological trap phenomenon was also low.

Our findings show that ecological traps are more associated with open habitats. Most of the open habitats, such as fields, wastelands and meadows, are under greater pressure of human influence, in which cases ecological traps can appear more frequently. Nevertheless, since rapid habitat changes and exotic species usually occur in human settlements, we expected that the ecological trap hypothesis would be more supported in urban habitats. Although there exists a significant number of studies investigating nest success in urban zones (Vierling 2000; Blair 2004; Charter et al. 2007), surprisingly, only one work dealt with the ecological trap phenomenon in an urban environment (Ellison and Brush 2004). Also lacking are studies comparing the rate of nest predation between urban and undisturbed environments, which could thereby elucidate the mechanisms of ecological traps associated with human presence.

Nevertheless, it does seem that natural habitats also may play a significant role in creating ecological traps (Dwernychuk and Boag 1972; Kristan 2003), although works studying these in other than human-influenced environments are almost non-existent. It can be presumed that they can occur in environments stricken by larger natural changes of abiotic (windstorms, flooding, wildfires, volcanic activity) or biotic origin (e.g. Battin [2004] describes changes following invasion of a particular animal species). It is possible that birds which live in

rapidly changing environments are adapted to ongoing changes and that the ecological trap cannot damage them. If a rapid change occurs in a pristine habitat, on the other hand, this can cause more severe consequences due to low adaptability of the birds to such situations.

It is also possible that ecological traps exist in the landscape on a scale of much finer changes (e.g. a gradual change in the structure of a biotope due to changes in geology, or change in water regime caused by a beaver dam) than are those brought about by natural disasters (Ganter and Cooke 1998). In such cases, however, it would be very difficult to detect these and their evidence is very poor. The one example of an ecological trap within a natural environment that we found is seen in a study of Argentinian Burrowing Owls (*Athene cunicularia*), which prefer to nest in burrows with short vegetation cover (Machicote et al. 2004). In this study, the fates of 26 nests were determined. When nesting in burrows of the Plains Viscacha (*Lagostomus maximus*), the birds had a nesting success rate of 35%, but not a single nest survived in burrows of Big Hairy Armadillos (*Chaetophractus villosus*). Viscachas, unlike armadillos, regularly graze the surroundings of their burrows, so the soil there is usually without vegetation. However, a study from other localities showed that Burrowing Owls in burrows of armadillos can achieve higher nesting success rates if the soil around their burrows is bare (Harris 1998). Although the authors of that study had not tested habitat preferences and their sample size was low (n = 23), they suggested that burrows of armadillos could, in the case of Burrowing Owls, constitute a local ecological trap (Machicote et al. 2004).

In conclusion, our results indicate that the phenomenon of ecological trap occurs more frequently in Europe and can be driven by direct human influence and presence of exotic species. However, its appearance in pristine habitats should not be ignored. Migratory bird species are not under greater threat due to ecological traps than are sedentary species, which can be affected by their ability to copy the nesting strategies of sedentary species. Although our results have some limitation, mainly because of low sample size, our findings may have practical application in restoration plans for particular bird species groups and geographical regions.

ACKNOWLEDGEMENTS

REFERENCES

Albrecht, T. (2004). Edge effect in wetland – arable land boundary determines nesting success of Scarlet Rosefinch (*Carpodacus erythrinus*) in the Czech republic. *The Auk. 121* (2), 361-371.

Aldridge, C. L. & Boyce, M. S. (2007). Linking occurrence and fitness to persistence: Habitat-based approach for endangered Greater Sage-grouse. *Ecological Applications. 17* (2), 508-526.

Andrén, H. (1990). Despotic distribution, unequal reproductive success, and population regulation in the Jay *Garrulus glandarius* L. *Ecology. 71* (5), 1796-1803.

Andrén, H. (1992). Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology. 73* (3), 794-804.

Andrén, H. & Angelstam, P. (1988). Elevated predation rates as an edge effect in habitat islands: Experimental evidence. *Ecology. 60* (2), 544-547.

Arlt, D. & Pärt, T. (2007). Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology. 88*, 792-801.

Ball, J. R., Bayne, E. M. & Machtans, C. S. (2008). Energy sector edge effects on songbird nest fate and nest productivity in the boreal forest of Western Canada: a preliminary analysis. *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics,* 161-170.

Batáry, P., Winkler, H. & Báldi, A. (2004). Experiments with artificial nests on predation in reed habitats. *Journal of Ornithology. 145,* 59-63.

Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology. 18* (6), 1482-1491.

Bayne, E. M. & Hobson, K. A. (2001). Effects of habitat fragmentation on pairing success of Ovenbirds: importance of male age and floater behavior. *The Auk. 118* (2), 380-388.

Berg, Å. (2008). Habitat selection and reproductive success of Ortolan Buntings *Emberiza hortulana* on farmland in central Sweden – the importance of habitat heterogeneity. *Ibis. 150,* 565-573.

Best, L. B. (1986). Conservation tillage: ecological traps for nesting birds? *Wildlife Society Bulletin. 14,* 308-317.

Blair, R. (2004). *The effects of urban sprawl on birds at multiple levels of biological organization. Ecology and Society. 9* (5),
http://www.ecologyandsociety.org/vol9/iss5/art2/inline.html.

Borgmann, K. L. & Rodewald, A. D. (2004). Nest predation in an urbanizing landscape: the role of exotic shrubs. *Ecological Applications. 14* (6), 1757-1765.

Bosschieter, L. & Goedhart, P. W. (2005). Gap crossing decisions by Reed Warblers (*Acrocephalus scirpaceus*) in agricultural landscapes. *Landscape Ecology. 20,* 455-468.

Brotons, L. & Herrando, S. (2003). Effect of increased food abundance near forest edges on flocking patterns of Coal Tit *Parus ater* winter groups in mountain coniferous forests. *Bird Study. 50,* 106-111

Campomizzi, A. J., Morrison, M. L., Farrell, S. L., Wilkins, R. N., Drees, B. M. & Packard, J. M. (2009). Red Imported Fire Ants can decrease songbird nest survival. *The Condor. 111* (3), 534-537.

Carrete, M., Serrano, D., Illera, J. C., López, G., Vögeli, M., Delgado, A. & Tella, J. L. (2009). Goats, birds, and emergent diseases: apparent and hidden effects of exotic species in an island environment. *Ecological Applications. 19* (4), 840-853.

Chace, J. F. & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning. 74*, 46-69.

Chapa – Vargas, L. & Robinson, S. K. (2006). Nesting success of a songbird in a complex floodplain forest landscape in Illinois, USA: local fragmentation vs. vegetation structure. *Landscape Ecology. 21* (4), 525-537.

Charter, M., Izhaki, I., Bouskila, A. & Leshem, Y. (2007). Breeding Succes of the Eurasian Kestrel (*Falco tinnunculus*) nesting on buildings in Israel. *Journal of Raptor Research. 41* (2), 139-143.

del Hoyo, J., Elliott, A., Sargatal, J. & Christie, D. A. (1992 – 2011). *Handbook of the Birds of the World. 1 - 16*. Lynx Edicions.

Delibes, M., Gaona, P. & Ferreras, P. (2001) (a). Effects of an attractive sink leading into maladaptive habitat selection. *The American Naturalist. 158* (3), 277-285.

Delibes, M., Ferreras, P. and Gaona, P. (2001) (b). Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters. 4*, 401-403.

Deng, W.-H., Zheng, G.-M. & Gao, W. (2003). Nesting success of the meadow bunting along habitat edges in northeastern China. *Journal of Field Ornithology. 74* (1), 37-44.

Donovan, T. M. & Thompson, F. R. (2001). Modelling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications. 11,* 871–882.

Dwernychuk, L.W. &Boag, D.A. (1972). Ducks nesting in association with gulls – an ecological trap? *Canadian Journal of Zoology. 50*, 559-563.

Eggers, S., Griesser, M., Anderssen, T. & Ekman, J. (2005). Nest predation and habitat change interact to influence numbers. *Oikos. 111*, 150-158.

Ellison, K. & Brush, T. (2004). Hooded Oriole nest silure associated with a novel nest site. *Western Birds. 35*, 71-78.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics. 34,* 487-515.

Fernández – Juricic, E. & Jokimäki, J. (2001). A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation. 10*, 2023-2043.

Fernández – Juricic, E., Sanz, R. & Sallent, A. (2001). Frequency – dependent predation by birds at edges and interiors of woodland. *Biological Journal of the Linnean Society. 73* (1), 43-49.

Flaspohler, D. J., Temple, S. A. & Rosenfield, R. N. (2001). Species-specific edge effects on nest success and breeding density in a forested landscape. *Ecological Applications. 1,* 32-46.

Ganter, B. & Cooke, F. (1998). Colonial nesters in a deteriorating habitat: site fidelity and colony dynamics of Lesser Snow Geese. *The Auk. 115* (3), 642-652.

Gates, E. J. & Gysel, L. W. (1978). Avian nest dispersion and fledging success in field – forest ecotones. *Ecology. 59* (5), 871-883.

Gilroy, J. J. & Sutherland, W. J. (2007). Beyond ecological traps: Perceptual errors and undervalued resources. *Trends in Ecology and Evolution. 22* (7), 351-356.

Hansson, L. (1994). Vertebrate distributions relative to clear – cut edges in a boreal forest landscape. *Landscape Ecology. 9* (2), 105-115.

Harris, G. (1998). *A guide to the birds and mamals of coastal Patagonia*. Princeton University Press.

Hazler, K. R., Amacher, A. J., Lancia, R. A. & Gerwin, J. A. (2006). Factors influencing Acadian Flycatcher nesting success in an intensively managed forest landscape. *Journal of Wildlife Management. 70* (2), 532-538.

Igual, J. M., Forero, M. G., Gomez, T. & Oro, D. (2007). Can an introduced predator trigger an evolutional trap in a colonial seabird? *Biological Conservation. 137*, 189-196.

Jones, Z. F. & Bock, C. E. (2005). The Botteri´s Sparrow and exotic Arizona grasslands: an ecological trap or habitat regained. *Condor. 107* (4), 731-741.

Keeler, M. S. & Chew, F. S. (2008). Escaping an evolutionary trap: preference and performance of a native inscet on an exotic invasive host. *Oecologia. 156*, 559-568.

Kershner, E. L. & Bollinger, E. K. (1996). Reproductive success of grassland birds at east-central Illinois airports. *American Midland Naturalist 136.* (2), 358-366.

Klein, Á., Nagy, T., Csörgő, T. & Mátics, R. (2007). Exterior nest-boxes may negatively affect Barn Owls *Tyto alba* survival: An ecological trap. *Bird Conservation International. 17*, 273-281.

Kokko, H. & Sutherland, W. J. (2001). Ecological traps in changing environments: Ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research. 3*, 537-551.

Kragten, S. & de Snoo, G. (2007). Nest success of Lapwings *Vanellus vanellus* on organic and conventional arable farms in the Netherlands. *Ibis. 149*, 742-749.

Kriska, G., Malik, P., Szivák, I. & Horváth, G. (2008). Glass buildings on river banks as "polarized light traps" for mass-swarming polarotactic Caddis Flies. *Naturwissenschaften. 95*, 461-467.

Kristan, W. B. III (2003). The role of habitat selection behavior in population dynamics: source – sink systems and ecological traps. *Oikos. 103*, 457-468.

Leston, L. V. A. & Rodewald, A. D. (2006). Are urban forests ecological traps for understory birds? An examination using Northern Cardinals. *Biological Conservation. 131*, 566-574.

Lindell, C. A. (2008). The value of animal behavior in evaluations of restoration success. *Restoration Ecology. 16* (2), 197-203.

Machicote, M., Branch, L. C. & Villarreal, D. (2004). Burrowing Owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? *Oikos. 106*, 527-535.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. & Bazzaz, F. A. (2000). Biotic invasions: cause, epidemiology, global consequences, and control. *Ecological Applications. 10* (3), 689-710.

Mänd, R., Tilgar, V., Lõhmus, A. & Leivits, A. (2005). Providing nest boxes for hole-nesting birds – Does habitat matter? *Biodiversity and Conservation. 14,* 1823-1840.

Mannan, R. W., Steidl, R. J. & Boal, C. W. (2008). Identifying habitat sinks: a case study of Cooper´s Hawks in an urban environment. *Urban Ecosystem. 11*, 141-148.

Manu, S., Peach, W. & Cresswell, W. (2007). The effects of edge, fragment size and degree of isolation on avian species richness in highly fragmented forest in West Africa. *Ibis. 149*, 287-297.

Martínez-Abraín, A., Viedma, C., Bartolomé, M. A., Gómez, J. A. & Oro, D. (2007). Hunting sites as ecological traps for coots in southern Europe: Implications for the conservation of a threatened species. *Endangered Species Research. 3*, 69-76.

Marzluff, J. M. & Ewing, K. (2004). Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology. 9* (3), 280-292.

Marzluff, J. M. & Neatherlin, E. (2006). Corvid response to human settlements and campgrounds: causes, consequences and challenges for conservation. *Biological Conservation. 130,* 301-314.

McGowan, K. J. (2001). Demographic and behavioral comparisons of suburban and rural American Crows. Chapter 17 In J. M. Marzluff, R. Bowman & R. Donnelly (Eds.): *Avian Ecology and Conservation in an Urbanizing World* (pp 365-381). Kluwer Academic Press, Norwell, MA.

Miner, B. G., Sultan, S. E, Morgan, S. G., Padilla, D. K. & Relyea, R. A. (2005). Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution. 20* (12), 685-692.

Misenhelter, M. D. & Rotenberry, J. T. (2000). Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology. 81* (10), 2892-2901.

Newhouse, M. J., Marra, P. P. & Johnson, L. S. (2008). Reproductive success of House Wrens in suburban and rural landscapes. *Wilson Journal of Ornithology. 120* (1), 99-104.

Nordby, J. C., Cohen, A. N. & Beissinger, S. R. (2008). Effects of a habitat-altering invader on nesting sparrows: an ecological trap? *Biological Invasions. 11* (3), 565-575.

Parejo, D., Oro, D. & Danchin, E. (2006). Testing habitat copying in breeding habitat selection in a species adapted to variable environments. *Ibis*. 148, 146-154.

Pärt, T., Arlt, D. & Villard, M.-A. (2007). Empirical evidence for ecological traps: a two-step model focusing on individual decisions. *Journal of Ornithology. 148* (Suppl 2), S327-S332.

Paton, P. W. C. (1994). The effect of edge on avian nest success – how strong is the evidence. *Conservation Biology. 8* (1), 17-26.

Pelicice, F. M. & Agostinho, A. A. (2008). Fish-passage facilities as ecological traps in large neotropical rivers. *Conservation Biology. 22* (1), 180-188.

Pell, A. S. & Tidemann, C. R. (1997). The impact of two exotic hollow-nesting birds on two native parrots in savannah and woodland in Eastern Australia. *Biological Conservation. 79*, 145-153.

Pérot, A. & Villard, M.-A. (2009). Putting density back into the habitat quality equation: case study of an open-nesting forest bird. *Conservation Biology. 23* (6), 1550-1557.

Pidgeon, A. M., Radeloff, V. C. & Matthews, N. E. (2003). Landscape-scale patterns of Black-throated Sparrow (*Amphispiza bilineata*) abundance and nest success. *Ecological Applications. 13*, 530-542.

Powell, L. L., Hodgman, T. P., Glanz, W. E., Osenton, J. D. & Fisher, C. M. (2010). Nest-site selection and nest survival of the Rusty Blackbird: does timber management adjacent to wetlands create ecological traps? *The Condor. 112* (4), 800-809.

Pöysä, H. & Pöysä, S. (2002). Nest-site limitation and density dependence of reproductive output in the Common Goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. *Journal of Applied Ecology. 39*, 502-510.

Purcell, K. L. & Verner, J. (1998). Density and reproductive success of California Towhees. *Conservation Biology. 12* (2), 442-450.

Rantanen, E. M., Buner, F., Riordan, P., Sotherton, N. & Macdonald, D. W. (2010). Habitat preference and survival in wildlife reintroductions: an ecological trap in reintroduced Grey Partridges. *Journal of Applied Ecology. 47,* 1357-1364.

Reed, J. M. (1999). The role of behavior in recent avian extinctions and endangerments. *Conservation Biology. 13* (2), 232-241.

Remeš, V. (2003). Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (*Sylvia atricapilla*). *Conservation Biology. 17* (4), 1127-1133.

Richkus, K. D. (2002). *Northern Pintail nest site selection, nest success, renesting ecology and survival in the intensively farmed prairies of Southern Saskatchewan: an evaluation of the ecological trap hypothesis.* A dissertation thesis. B. S., Virginia Polytechnic Institute and State University.

Ries, L. & Fagan, W. F. (2003). Habitat edges as potential ecological trap for an insect predator. *Ecological Entomology. 28*, 567-572.

Ries, L. & Sisk, T. D. (2004). A predictive model of edge effects. *Ecology. 85* (11), 2917-2926.

Robertson, B. A. & Hutto, R. L. (2006). A framework for understanding ecological traps and evaluation of existing evidence. *Ecology. 87,* 1075-1085.

Robertson, B. A. & Hutto, R. L. (2007). Is selectively harvested forest an ecological trap for Olive – sided Flycatchers? *The Condor. 109*, 109-121.

Rodewald, A. D., Shustack, D. P. & Hitchcock, L. E. (2010). Exotic shrubs as ephemeral ecological traps for nesting birds. *Biological Invasions. 12*, 33-39.

Rodriguez, J., Avilés, J. M. & Parejo, D. (2011). The value of nestboxes in the conservation of Eurasian Rollers *Coracias garrulus* in southern Spain. *Ibis. 153*, 735-745.

Roos, S. & Pärt, T. (2004). Nest predators and spatial dynamics of breeding Red-backed Shrikes (*Lanius collurio*). *Journal of Animal Ecology. 73*, 117-127.

Schlaepfer, M. A. (2003). Successful lizard eggs in a human-disturbed habitat. *Oecologia. 137*, 304-311.

Schlaepfer, M. A., Runge, M. C. & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in ecology and evolution. 17* (10), 474-480.

Schlaepfer, M. A., Sherman, P. W., Blossey, B. & Runge, M. C. (2005) Introduced species as evolutionary traps. *Ecology Letters. 8,* 241-246.

Schmidt, K. A. & Whelan, C. J. (1999). Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conservation Biology. 13* (6), 1502-1506.

Sekercioglu, C. H., Loarie, S. R., Oviedo Brenes, F., Ehrlich, P. R. & Daily, G. C. (2007). Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology. 21* (2), 482-494.

Shochat, E., Patten, M. A, Morris, D. W., Reinking, D. L., Wolfe, D. H. & Sherrod, S. K. (2005). Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos. 111,* 159-169.

Smith, L. A., Nol, E., Burke, D. M. & Elliott, K. A. (2007). Nest-site selection of Rose-breasted Grosbeaks in southern Ontario. *The Wilson Journal of Ornithology. 119* (2), 151-161.

Soderström, B, Pärt, T. & Ryden, J. (1998). Different predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia. 117*, 108-118.

Sol, D. & Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos. 90*, 599-605.

Steffens, K. E., Seddon, P. J., Mathieu, R. & Jamieson, I. G. (2005). Habitat selection by South Island Saddlebacks and Stewart Island Robins reintroduced to Ulva Island. *New Zealand Journal of Ecology. 29* (2), 221-229.

Stuart-Smith, A. K. & Hayes, J. P. (2003). Influence of residual tree density on predation of artificial and natural sonbird nests. *Forest Ecology and Management. 183* (1-3), 159-176.

Tallamy, D. W. (2004). Do alien plants reduce insect biomass? *Conservation Biology. 18* (6), 1689-1692.

Thyen, S. & Exo, K.-M. (2003). Wadden Sea saltmarshes: Ecological trap or hideway for breeding Redshanks *Tringa totanus*? *Wader Study Group Bulletin*. 100, 43-46.

Vergara, P. M. & Simonetti, J. A. (2003). Forest fragmentation and rhinocryptid nest predation in central Chile. *Acta Oecologica – International Journal of Ecology. 24* (5-6), 285-288.

Verhulst, S., Ooosterbeek, K., Rutten, A. L. & Ens, B. J. (2004). Shellfish fishery severely reduces condition and survival of Oystercatchers despite creation of large marine protected areas. *Ecology and Society. 9* (1), available online on: http://www.ecologyandsociety.org/vol9/iss1/art17/

Vierling, K. T. (2000). Source and sink habitats of Red-winged Blackbirds in a rural/suburban landscape. *Ecological Applications. 10* (4), 1211-1218.

Weidinger, K. (2000). The breeding performance of Blackcap *Sylvia atricapilla* in two types of forest habitat. *Ardea. 88* (2), 225-233.

Weldon, A. J. & Haddad, N. M. (2005). The effects of patch shape on Indigo Buntings: evidence for an ecological trap. *Ecology. 86,* 1422-1431.

Winter, M., Johnson, D. H., Shaffer, J. A., Donovan, T. M. & Svedarsky, W. D. (2006). Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management. 70* (1), 158-172.

Woodward, A. A., Fink, A. D. & Thompson, F. R. III. (2001). Edge effects and ecological traps: effects on shrubland birds in Missouri. *Journal of Wildlife Management. 65* (4), 668-675.

Yahner, R. H. & Piergallini, N. H. (1998). Effects of microsite selection on predation of artificial ground nests. *Wilson Bulletin. 110* (3), 439-442.

Table 1. List of all studies we identified.

Source	Cause of ecological trap	Geographic region + country	Species	Migratory (M) / Sedentary (S)	Habitat type	Natural (NH) / Anthropogenic (AH) type of habitat	Position of nest	Nests: natural (N) or nest box (B)
SUPPORTED								
Carrete et al. 2009	Exotic species	Fuerteventura (ES)	Lesser Short-toed Lark (*Calandrella rufescens*)	M	farmland	AH	ground	N
Dwernychuk and Boag 1972	Natural factors [1]	North America (CAN)	Lesser Scaup (*Aythya affinis*)	M	wetlands	NH	ground	N
			Gadwall (*Anas strepera*)	M	wetlands	NH	ground	N
			Northern Mallard (*Anas platyrhynchos*)	M	wetlands	NH	ground	N
			Northern Pintail (*Anas acuta*)	M	wetlands	NH	ground	N
			American Widgeon (*Anas americana*)	M	wetlands	NH	ground	N
			White-winged Scoter (*Melanitta deglandi*)	M	wetlands	NH	ground	N
Ellison and Brush 2004	Direct human influence	North America (USA)	Hooded Oriole (*Icterus cucullatus*)	M	urban and suburban zones	AH	tree	N
Igual et al. 2007	Exotic species	Southern Europe (ES)	Cory's Shearwater (*Calonectris diomedea*)	M	coastal zones and islands	NH	cavity in the ground	N
Klein et al. 2007	Direct human influence	Central Europe (HU)	Barn Owl (*Tyto alba*)	S	farmland	AH	cavity	B and church towers
Mänd et al. 2005	Direct human influence [2]	Southern Europe (EST)	Great Tit (*Parus major*)	S	forests	NH	cavity	B
Martínez-Abraín et al. 2007	Direct human influence	Southern Europe (ES)	Common Coot (*Fulica atra*), Red-knobbed Coot (*F. cristata*)	S	wetlands	NH	(---)*	(---)*

Misenhelter and Rottenbery 2000	Natural factors	North America (USA)	Sage Sparrow (*Amphispiza belli*)	M	coastal zones and islands	NH	shrub	N
Rantanen et al. 2010	Direct human influence	Western Europe (GB)	Grey Partridge (*Perdix perdix*)	S	farmland	AH	(---)*	(---)*
Remeš 2003	Exotic species	Central Europe (CZ)	Blackcap (*Sylvia atricapilla*)	M	forests	both	shrub	N
Robertson and Hutto 2007	Fragmentation of habitats and landscape management	North America (USA)	Olive-sided Flycatcher (*Contopus cooperi*)	M	forests	NH	tree	N
Rodewald et al. 2010	Exotic species	North America (USA)	Northern Cardinal (*Cardinalis cardinalis*)	M	forests	NH	shrub	N
Rodriguez et al. 2011	Direct human influence	Southern Europe (ES)	Eurasian Roller (*Coracias garrulus*)	M	semideserts	NH	cavity	B
Weldon and Haddad 2005	Fragmentation of habitats and landscape management	North America (USA)	Indigo Bunting (*Passerina cyanea*)	M	forests	NH	shrub	N

NOT SUPPORTED

Albrecht 2004	Fragmentation of habitats and landscape management	Central Europe (CZ)	Scarlet Rosefinch (*Carpodacus erythrinus*)	M	wetlands	NH	shrub	N
Aldridge and Boyce 2007	Natural factors	North America (USA)	Greater Sage-grouse (*Centrocercus urophasianus*)	S	grassland	NH	ground	N
Arlt and Pärt 2007	Natural factors [2]	Northern Europe (SWE)	Northern Wheatear (*Oenanthe oenanthe*)	M	farmland	AH	ground	N

Ball et al. 2008	Fragmentation of habitats and landscape management	North America (CAN)	forest birds	(---)	forests	NH	(---)	N
Best 1986	Direct human influence	North America (?)	farmland birds	(---)	farmland	AH	ground	N
Chapa - Vargas and Robinson 2007	Fragmentation of habitats and landscape management	North America (USA)	Acadian Flycatcher (*Empidonax virescens*)	M	forests	NH	tree / shrub	N
Flashpohler et al. 2001	Fragmentation of habitats and landscape management	North America (USA)	forest songbirds	M	forests	NH	ground and tree	N
Hazler et al. 2006	Fragmentation of habitats and landscape management	North America (USA)	Acadian Flycatcher (*Empidonax virescens*)	M	forests	NH	tree / shrub	N
Jones and Bock 2005	Exotic species	North America (USA)	Botteri's Sparrow (*Aimophila botterii*)	S	grassland	NH	ground	N
Kershner and Bollinger 1996	Direct human influence	North America (USA)	Eastern Meadowlark (*Sturnella magna*)	S	grassland	NH	ground	N
			Grasshopper Sparrow (*Ammodramus savannarum*)	M	grassland	NH	ground	N
			Savannah Sparrow (*Passerculus sandwichensis*)	M	grassland	NH	ground	N
			Red-winged Blackbird (*Agelaius phoeniceus*)	S	grassland	NH	shrub	N
			Song Sparrow (*Melospiza melodia*)	M	grassland	NH	shrub	N
			Horned Lark (*Eremophila alpestris*)	M	grassland	NH	ground	N

Leston and Rodewald 2006	Direct human influence	North America (USA)	Northern Cardinal (*Cardinalis cardinalis*)	M	forests	AH	shrub	N
McGowan 2001	Direct human influence	North America (USA)	American Crow (*Corvus brachyrhynchos*)	S	urban and suburban zones	AH	tree	N
Newhouse et al. 2008	Direct human influence	North America (USA)	House Wren (*Troglodytes aedon*)	M	urban and suburban zones	AH	cavity	B
Nordby et al. 2008	Natural factors	North America (USA)	Song Sparrow (*Melospiza melodia*)	M	wetlands	NH	shrub	N
Pärt et al. 2007	Natural factors	Northern Europe (SWE)	Northern Wheatear (*Oenanthe oenanthe*)	M	farmland	AH	ground	N
Pérot and Villard 2009	Fragmentation of habitats and landscape management	North America (CAN)	Ovenbird (*Seiurus aurocapilla*)	M	forests	NH	ground	N
Powell et al. 2010	Fragmentation of habitats and landscape management	North America (USA)	Rusty Blackbird (*Euphagus carolinus*)	M	wetlands	NH	tree	N
Pöysä et al. 1999	Fragmentation of habitats and landscape management	Northern Europe (FI)	Common Goldeneye (*Bucephala clangula*)	M	forests	NH	cavity	B
Richkus 2002	Fragmentation of habitats and landscape management	North America (USA)	Northern Pintail (*Anas acuta*)	M	farmland	AH	ground	N
Sekercioglu et al. 2007	Fragmentation of habitats and landscape management	South America (Costa Rica)	Orange-billed Nightingale-thrush (*Catharus aurantiirostris*)	S	forests	both	tree	N
			Silver-throated Tanager (*Tangara icterocephala*)	S	forests	both	tree	N

			White-throated Thrush (*Turdus assimilis*)	S	forests	both	tree	N
Steffens et al. 2005	Natural factors	New Zealand (NZ)	South Island Saddleback (*Philesturnus c. carunculatus*)	S	forests	NH	cavity	N
			Stewart Island Robin (*Petroica australis rakiura*)	S	forests	NH	cavity / tree	N
Stuart-Smith and Hayes 2003	Fragmentation of habitats and landscape management	North America (USA)	forest songbirds	(---)	forests	NH	ground and shrub	N
Weidinger 2000	Fragmentation of habitats and landscape management	Central Europe (CZ)	Blackcap (*Sylvia atricapilla*)	M	unclassified mosaic of different habitats	both	shrub	N
Woodward et al. 2001	Fragmentation of habitats and landscape management	North America (USA)	Indigo Bunting (*Passerina cyanea*)	M	unclassified mosaic of different habitats	both	shrub	N
			Northern Cardinal (*Cardinalis cardinalis*)	M	unclassified mosaic of different habitats	both	shrub	N
			Yellow-breasted Chat (*Icteria virens*)	M	unclassified mosaic of different habitats	both	tree / shrub	N
			Prairie Warbler (*Dendroica discolor*)	M	unclassified mosaic of different habitats	both	ground	N
			Field Sparrow (*Spizella pusilla*)	S	unclassified mosaic of different habitats	both	shrub / ground	N

STUDIES WHICH ONLY MENTION ECOLOGICAL TRAP IN THEIR PAPERS

Deng et al. 2003	Fragmentation of habitats and landscape management	Asia (CHI)	Meadow Bunting (*Emberiza cioides*)	S	unclassified mosaic of different habitats	both	shrub	N

Kragten and de Snoo 2007	Fragmentation of habitats and landscape management	Western Europe (NE)	Northern Lapwing (*Vanellus vanellus*)	M	farmland	AH	ground	N
Machicote et al. 2004	Natural factors	South America (ARG)	Burrowing Owl (*Athene cunicularia*)	M	grassland	NH	cavity in the ground	N
McGowan et al. 2005	Natural factors	North America (USA)	American Oystercatcher (*Haematopus palliatus*)	M	coastal zones and islands	NH	ground	N
Pidgeon et al. 2003	Natural factors	North America (USA)	Black-throated Sparrow (*Amphispiza bilineata*)	M	grassland	NH	shrub	N
Purcell and Verner 1998	Fragmentation of habitats and landscape management	North America (USA)	California Towhee (*Pipilo crissalis*)	S	forests	NH	shrub	N
Smith et al. 2007	Fragmentation of habitats and landscape management	North America (USA)	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	M	forests	NH	tree	N
Thyen and Exo 2003	Fragmentation of habitats and landscape management	Central Europe (DE)	Common Redshank (*Tringa totanus*)	M	wetlands	NH	ground	N
Verhulst et al. 2004	Direct human influence	Central Europe (DE)	Eurasian Oystercatcher (*Haematopus ostralegus*)	M	wetlands	NH	(---)*	(---)*

[1] i.e. non-human induced phenomenon such as inter- and intraspecific competition, natural habitat changes.

[2] i.e. human activities which directly affect bird populations, e.g. hanging nest boxes, direct disturbance of nesting birds by building constructions, bird hunting, eggs collection. On the other hand, human activities can affect bird populations also indirectly, i.e. by habitat fragmentation, habitat management, introduction of exotic species.

III.

Suvorov P. & Šálek M.: **Character of surrounding habitat determines nest predation in suburban wastelands.** *Submitted manuscript (Folia Zoologica)*

Character of surrounding habitat determines nest predation in suburban wastelands

Petr Suvorov and Miroslav Šálek

Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences, Kamýcká 129, 165 21 Prague 6, Czech Republic

E-mail: petr.suvorov@hotmail.com, salek@fzp.czu.cz

Phone to the corresponding author: +420604 924 214

ABSTRACT

Fragments of unmanaged wasteland in urbanized zones may attract threatened bird species to nest, but, at the same time, may be favoured by generalist nest predators attracted by food resources abundant in urban areas. Only few studies have analysed effects of nest predation risk in suburban habitat fragments while considering the character of the surrounding landscape. We used artificial nests to examine possible effects of patch size and shape, edge distance, extent of surrounding urbanization, habitat composition and heterogeneity on nest predation risk to ground-nesting birds in unmanaged wasteland patches within suburban areas. Nest predation risk varied regardless of internal patch attributes, whereas the character of surrounding landscape was strongly influential. In particular, predation risk was positively correlated with proportions of unstable disturbed sites nearby but negatively correlated with proportions of adjacent meadows and forests. From the standpoint of nature conservation and effective support to bird diversity in suburban areas, we point out the importance of diverse nature-like stands such as meadows or forests together with deliberate planning for construction and associated disturbances in proximity to the most valuable wastelands. This arrangement may reduce predation pressure on bird nests situated in these specific suburban habitats.

Keywords

Bird conservation, Generalist predator, Ground nests, Habitat fragmentation, Landscape heterogeneity Urbanization

1. Introduction

Worldwide destruction of natural habitats negatively affects animal life (Blair 2004, Fuller et al. 2007) and considerably reduces diversity of plant and animal communities (Noss 1991, Wilson & Peter 1988). Historically, new expansion of urban environment, which

includes building conglomerates and technical structures interspersed with gardens, parks, ornamental plantations and idle patches, has contributed to reducing original habitats. On the other hand, these extensive landscape changes may augment landscape heterogeneity (Blair 2004, Gering & Blair 1999). Consequently, modern habitats may partially compensate the loss of natural stands for at least some species that are tolerant of human-induced environments with disturbance effects. Fragments of unmanaged wasteland spread throughout urbanized zones and dominated by early successional vegetation may attract bird species, some of which are regionally threatened, such as, in Europe, Grey Partridge (*Perdix perdix*), Whinchat (*Saxicola rubetra*), Crested Lark (*Galerida cristata*), and Wheatear (*Oenanthe oenanthe*) (Blair 2004, Šálek et al. 2004, Šťastný et al. 2006). Despite their temporary character, and in contrast to the surrounding agricultural and urbanized lands, these habitats may function as refuges for the birds due to their reduced disturbance and the availability of nesting sites, plant seeds and insects that they provide (Evans et al. 2009, Kadlec et al. 2008, Šálek et al. 2004).

Urbanized areas can, however, be favoured also by generalist predators (Battin 2004, Hagan et al. 1996, Kokko & Sutherland 2001), which are attracted by such additional food resources as garbage, industrial products, and road-killed animals (Gooch et al. 1991, Jerzak 2001, Marzluff & Ewing 2001) and may also increase their densities there (Chace & Walsh 2006, Chiron & Julliard 2007, Howell et al. 2000, Jerzak 2001, Leston & Rodewald 2006). As the diets of many predators include bird eggs (Angelstam 1986, Hoove, et al. 2006, Roos 2002), one might expect suburban zones to be prone to increased incidental nest predation (Andrén et al. 1985, Vickery et al. 1992). Nevertheless, suburban areas and their surroundings have sometimes been found to be safe nesting zones for birds (e.g. Anderies et al. 2007, Antonov & Atanasova 2002, Gering & Blair 1999, Jokimäki et al. 2005). In light of these partially opposite trends, studies examining bird nest predation in suburban areas have not been consistent in their findings (Blair 2004, Chamberlain et al. 2009, Gering & Blair 1999). This inconsistency might reflect huge local variation worldwide in the richness of additional food resources for predators in urbanized areas. In some areas, the predators' needs can be more than supplied by foods from human sources while elsewhere food shortage leads to increased effort in searching for prey and higher incidental nest predation (Vickery et al. 1992). In general, this variation can be closely linked to urbanization rate, as urbanization influences the amount of additional secondary food and/or surrounding habitat heterogeneity. A diverse habitat mosaic should generally offer more sources than does a poor habitat mosaic. Only a few studies, however, have analysed the effects of characteristics attributable to the

surrounding landscape on nest predation risk in habitat fragments (e.g. Dunford & Freemark 2004, Marzluff & Ewing 2001, Saunders et al. 1991, Winter et al. 2006). Nest predation has been found to grow with an increasing proportion of surrounding farmland (Andrén 1992, Bayne & Hobson 1997, Chalfoun et al. 2002, Storch et al. 2005) as well as with the amount of urban habitat (Marzluff & Restani 1999, Wilcove 1985).

In addition, several studies investigating nest predation have revealed that decreasing size of habitat fragments may negatively affect nest survival (Pasinelli & Schiegg 2006, Weinberg & Roth 1998, Wilcove 1985, Winter et al. 2006). However, the results obtained from urbanized areas have been ambiguous and often have shown no significant effect of patch size (Huhta et al. 1996, Matthews et al. 1999, Zanette & Jenkins 2000). This inconsistency may stem from the different scales upon which the experiments have been designed. Paton (1994) reviewed previous studies and concluded that patches smaller than 10 ha usually suffer from higher predation rate. Therefore, only studies encompassing both small patches and sufficiently large patches (>> 10 ha) may reveal a significant size effect. As the ratio of edge length to interior area increases with decreasing fragment size (Brand & George 2001, Villard 1998), the explanation for increased predation risk in small fragments can be due to the edge effect (Andrén & Angelstam 1988, Batáry et al. 2004, Hoover et al. 2006, Schiegg et al. 2007, Storch et al. 2005). Many previous studies have shown that edge habitats are attractive for generalist predators (e.g. Andrén 1992, Chace & Walsh 2004, Paton 1994, Ries & Sisk 2004). Therefore, the size of habitat patches should be considered in predation studies.

While unmanaged wastelands embedded in urban zones may function as attractive nesting refuges for some bird species, they may, at the same time, provide only weak protection against nest predation. This may depend on the fragment area, nest position within it, as well as on urbanization rate or other habitat characteristics of the surroundings. The inconsistent findings to date, however, do not allow for predicting predation risks to bird nests in these specific habitats and for recommending conservation practices, such as what size and surrounding habitat structure might effectively support bird diversity in suburban zones. More detailed studies from various conditions and regions are thus needed to reveal the main factors driving nest predation risk in suburban zones worldwide.

In this study, we examined possible effects of patch size, shape, extent of surrounding urbanization, habitat structure and heterogeneity on predation risk to ground bird nests on unmanaged wasteland patches in suburban areas of Prague, Czech Republic. We predicted higher vulnerability to predation on the nests located (1) within small patches (up to 10 ha),

and (2) at the edges of large patches (> 10 ha) due to edge effect, as well as (3) in patches embedded within less diverse habitat mosaic, and (4) in patches with more urbanized surroundings due to reduced food resources at these stands.

2. Study area

The study was conducted around Prague, Czech Republic (50°1' – 50°6'N, 14°4' – 14°8'E; Fig. 1), in a transition zone between farmland-dominated landscape and urbanized areas of the capital city. We selected 103 unmanaged patches (51 in 2008 and 52 different ones in 2009) of various sizes (1 ha to 40 ha – see Fig. 2 for size distribution of the patches) using orthophotomaps and JanMap 2.3.0 software (www.janitor.cz). We established 1,000 m as the minimum distance between any two neighbouring patches to avoid overlaps of their habitat surroundings and minimize cumulative effect of individual predators. We selected only early successional sites (up to 10 years after initiation) dominated by pioneer herbs (*Urtica dioica, Apiaceae, Poaceae*), and sparsely broken by shrubs or tree seedlings (*Robinia pseudacacia, Rosa* sp.*, Malus* sp.*, Sambucus nigra*). The bird species inhabiting the area include common farmland species (e.g. Yellowhammer *Emberiza citrinella,* Eurasian Skylark *Alauda arvensis,* Whitethroat *Sylvia communis,* Common Pheasant *Phasianus colchicus*) but also scarcer species appearing in unmanaged wastelands where they are under the pressure of nest predation, such as Grey Partridge*,* Whinchat*,* Crested Lark*,* and Wheatear (Fuchs et al. 2002, Šálek et al., 2004, Šťastný et al. 2006). Wastelands around Prague are characterized by high diversity of weed plants and associated invertebrates which provide various types of food for the aforementioned species (Fuchs et al. 2002, Šálek et al., 2004).

approximate location for Figure 1

approximate location for Figure 2

We measured the area of each patch (m^2) and proportions of its surrounding habitats (specified in Table 1) in a circle up to 500 m distant from the patch margins by combining digitized photomap information with that from subsequent field inspection. In addition, the surrounding habitat heterogeneity was then calculated using the Shannon diversity index (Krebs 1989) where particular habitat attributes were included as proportions.

approximate location for Table 1

3. Material and methods

3. 1. Nest predation

During May–June 2008 and 2009, which corresponds to the main breeding period for the bird species in our climatic conditions (Hudec & Šťastný 2005, Šťastný et al. 2006), we placed two artificial ground nests in each patch in a manner to include possible variation in edge effect and nest position in the patch depending on patch size. One nest was placed at the immediate patch edge (up to 5 m in from the edge) while the second nest was put into a patch's interior (i.e. 50–60 m from the edge). The nests were constructed as small depressions in the ground strewn with dry grass (Angelstam 1986). Each nest was baited with a pair of hen eggs, one fresh and one filled with a wax–oil mixture. The wax–oil eggs were tied to the ground using a nail to prevent them from being carried away by a predator. Nest position was marked with short scraps of florist streamer 3 to 5 m apart. In order to minimize inadvertently attracting predators, nests were exposed for 14 d with no check in the interim period (Villard & Pärt 2004). Any nest was considered as depredated if at least one egg disappeared or had marks indicating a predator's visit. A similarly designed method using artificial nests has been previously applied in many nest predation studies (e.g. Martin & Joron 2003, Rangen et al. 2000, Yahner & Mahan 1996).

3. 2. Analyses

Prior to analysing nest predation, we used principal components analysis (PCA) to find the correlated explanatory variables representing the composition of habitat surroundings and reduced their numbers for further analysis. When PCA axes represented two or more explanatory variables, they were used as substitutional explanatory variables. A mixed-effects model was applied to analyse multiple effects of selected predictors on nest predation risk (Crawley 2005), which was expressed as a binomial response (a nest was either depredated or untouched). The predictors included (a) nest position (edge vs. interior), (b) scores of the main principal components (with eigenvalue $\lambda > 1$) as underlying factors of mutually intercorrelated environmental variables, and (c) other remaining (non-correlated) particular variables (see Table 2 for interrelationships among the variables and principal components). In addition, all first-order interactions of these variables with nest position (categorical variable) were included into the model. As two nests were treated at each patch, patch identity together with year were stated as random factors.

approximate location for Table 2

We removed all non-significant predictors ($p > 0.05$) in a stepwise backward selection procedure in order to simplify the model and achieve the minimum adequate model according to the rules recommended by Crawley (2005). Statistica 9.0 and R 2.8.0 were used in all

statistical analyses. To test the effect of patch shape, we selected seven patches with the most distinctly elongated shapes and 10 patches with regularly square or circular shapes. In a separate analysis, we applied a mixed-effects model to check the effect on nest predation risk of patch shape (expressed by the two well-defined extremes) in combination with nest position, patch area and their first-order interactions. In order to avoid over-parameterization of this model with reduced sample size, we did not consider including into this model such other variables as scores of principal components. Proportions of eggs predated by mammalian and avian predators were tested using a homogeneity test.

4. Results

Overall nest predation rate was 57.8% for the two years together (62.7% in 2008 and 52.9% in 2009). Whereas the eggs from 59.7% (n = 71) of all 119 depredated nests were removed by an unidentified predator, we detected marks of nest predators on egg remains in 48 nests (40.3%) and specified either avian or mammal predator at eggs in 45 nests (Table 3). We found that 70.0% of detected egg predations were exclusively due to avian predators (homogeneity test, $\chi^2 = 6.4$, df = 1, $p = 0.011$, total n = 40 eggs).

approximate location for Table 3

PCA reduced the set of 15 particular environmental variables representing patch surroundings to five principal components (PC1 to PC5) with eigenvalues $\lambda > 1$ for each. The sum of the eigenvalues for PC1–PC5 $\lambda_{sum} = 9.35$, and these variables together explained 62.4% of the total variance in relationships among the variables. Scores of the first four PC axes representing 11 particular variables (listed in Table 4) we used as predictors to the model. The variables "Roads", "Airports and playgrounds" and "Gardens and orchards" did not correlate with the considered principal components and were included as single predictors. Because "Patch area" correlated with only PC5 and then with lower eigenvalue ($\lambda = 1.1$), we decided to include this variable also as a single predictor instead of its PCA that was an ambiguous representative.

approximate location for Table 4

We revealed significant effects of two terms (PC2 and PC4) on nest predation risk (Table 5). PC2 (Fig. 3) positively correlated with the amount of early successional weed habitats around houses and other constructions while being negatively correlated with proportions of meadows and forests representing later successional (long-lasting and established) stands outside of urbanized segments. PC4 (Fig. 4) was most strongly correlated with the proportions of water bodies and railways. Neither the fixed effects of patch area and

nest position nor their interactions were significant (fixed effects: both $\chi^2 < 1.4$, df = 1, $p > 0.20$, interactions: all $\chi^2 < 3.0$, df = 1, $p > 0.07$, Table 5). In addition, comparison of the minimal adequate model and full model was also insignificant ($\chi^2 = 17.753$, df = 15, $p = 0.2$).

The analysis of patch shape revealed no significant effect on nest predation risk (all $p > 0.1$, Table 6).

approximate location for Figure 3

approximate location for Figure 4

5. Discussion

Wasteland patches represent an important part of the suburban habitat mosaic which creates opportunities for threatened openland bird species. Our findings on nest predation risk in these habitats may provide important information for landscape management with a view to supporting avian diversity in suburban zones.

Our results did not reveal significant effect of particular patch features (size, shape, edge effect) on the predation of our experimental nests. Therefore, we suggest that wasteland patches may create a convenient environment for birds independent of their internal characteristics. We expect that the predators use the entirety of patches equally when searching for food (Donovan et al. 1997, Thorington & Bowman 2003, Vickery et al. 1992). Thus, the conclusions of other, previous studies describing the effects of patch size or internal habitat structures may have resulted from correlativeness of these attributes with other factors or may have been derived on different scales than we investigated in this study. Nevertheless, we believe that at least the edge effect may still exist on an even coarser scale than we were able to detect (Laurance 2000, Storch et al. 2005).

approximate location for Table 5

On the other hand, the character of the surrounding landscape appeared to be the driving factor affecting the nest predation rate in our wasteland patches. Even though such mutually intercorrelated attributes as proportion of urbanized areas, farmland-to-city-centre gradient, and habitat heterogeneity indicated the highest variation among all treated variables, these did not contribute significantly to nest predation rate. Instead, we found that increasing proportion of early successional stages in the surroundings of the studied patches negatively influenced nest survival. Early successional stages with stronger human disturbances in urbanized areas and accompanied by higher nest predation contrasting with more stable ecosystems (meadows or forests) together with higher nest success extend the findings of

Jokimäki & Huhta (2000) and López-Flores et al. (2009), who had found that some components of urban environment negatively affected survival of their artificial nests. Medium-urbanized landscapes such as suburban zones at city borders usually produce highly heterogeneous environments attractive for generalist predators (Chiron & Julliard 2007, Donovan et al. 1997), which are sometimes termed "urban exploiters" (Chace & Walsh 2006). On the other hand, nest predation does not seem to increase more in highly urbanized areas closer to city centres (Donovan et al. 1997) because breeding and food opportunities for both birds and predators are not increasing more along this gradient.

approximate location for Table 6

Proportions of water bodies and railways also negatively influenced the survival of our experimental nests. Close surroundings of water bodies can be linked to occurrence of such nest predators as Marsh Harrier (*Circus aeruginosus*) or Grey Heron (*Ardea cinerea*) (Hansson et al. 2000, Opermanis et al. 2001, Teunissen et al. 2008), which might occasionally depredate the nests placed in nearby surroundings. Moreover, a railway constitutes a line structure that is often surrounded by wide belts of shrub which can attract mammal predators, using them as travel corridors while searching for prey (Wegner & Merriam 1979), as well as avian predators (corvids), using the stands for nesting (Wallander et al. 2006). All these predators may contribute to increased nest depletion near water bodies and railways. Nevertheless, as railway represented only a minor part of the landscape and the correlation with presence of water bodies may be only accidental, any generalizations are probably of minor importance.

Two-thirds of the eggs in depredated nests contained marks by avian predators. This result corresponds to other, similar studies which determined birds to be the principal nest predators in (sub)urban zones (Jokimäki & Huhta 2000, Matthews et al. 1999, Thorington & Bowman 2003). Mammals were also found to be regular nest predators, and this shows a diverse predation community and more complex predation pattern from site to site. The prevalence of bird nest predators in our sample can, however, be due to a methodological artefact that mammal predators might more often carry away large hen eggs. In addition, we would expect mammal predators to prefer habitats with shorter and sparser vegetation than occurs in wastelands, because dense and tall vegetation hinders movement and orientation (DeLong et al. 1995, Dion et al. 2000). Finally, we cannot exclude that our human-installed artificial nests without concealment by an incubating parent were more easily detectable by visually oriented avian predators (Burke et al. 2004, Söderström et al. 1998, Villard & Pärt 2004, Yahner & Piergallini 1998).

6. Conclusion

Nest predation risk in unmanaged wasteland patches spread out across suburban zones of cities varies regardless of those patches' shape, size or position within the farmland-to-city-centre gradient, and with unimportant edge effect. From the general standpoint of nature conservation in suburban areas, we nevertheless highlight the importance of diverse nature-like stands such as meadows or forest fragments together with deliberate planning of human-made structures in proximity to the most valuable patches (e.g. where scarce birds are known to breed). We suggest that this arrangement may increase and spread out the general food supply for nest predators and, consequently, reduce the predation pressure specifically on nests situated in the target patches. Although the early successional stands themselves would generally be prone to increased nest predation by avian predators in particular, they play an important role as reproduction habitats for several uncommon or endangered bird species and should therefore be of interest to conservationists.

References

Anderies J. M., Katti, M. & Shochat E. 2007: Living in the city - Resource availability, predation and bird population dynamics in urban areas. *J Theor Biol, 247, 36 – 49*.

Andrén H. 1992: Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology, 73 (3), 794 – 804*.

Andrén H., Angelstam P., Lindström E. & Widén P. 1985: Differences in predation pressure in relation to habitat fragmentation - An experiment. *Oikos, 45, 273 – 277*.

Andrén H. & Angelstam P. 1988: Elevated predation rates as anedge effect in habitat islands: experimental evidence. *Ecology, 60 (2), 544 – 547*.

Angelstam P. 1986: Predation on ground – nesting birds´ nests in relation to predator densities and habitat edge. *Oikos. 47, 365 – 373*.

Antonov A. & Atanasova D. 2002: Nest-site selection in the Magpie *Pica pica* in a high-density urban population of Sofia (Bulgaria). *Acta Omithol, 37, 55 – 66.*

Batáry P., Winkler H. & Báldi A. 2004: Experiments with artificial nests on predation in reed habitats. *J Ornithol, 145, 59 – 63.*

Battin J. 2004: When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv Biol, 18 (6), 1482 – 1491.*

Bayne E. M. & Hobson K.A. 1997: Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conserv Biol, 11, 1418 - 1429.*

Blair R. 2004: The effects of urban sprawl on birds at multiple levels of biological organization. *Ecol Soc, 9 (5), available online*:
http://www.ecologyandsociety.org/vol9/iss5/art2/inline.html

Brand L.A. & George T.L. 2001: Response of passerine birds to forest edge in coast redwood forest fragments. *Auk, 118 (3), 678 – 686.*

Burke D.M., Elliott K., Moore L., Dunford W., Nol E., Phillips J., Holmes S. & Freemark K. 2004: Patterns of nest predation on artificial and natural nests in forests. *Conserv Ecol, 18 (2), 381 – 388.*

Chace J. F. & Walsh J. J. 2006: Urban effects on native avifauna - A review. *Landscape Urban Plan, 74, 46 – 69.*

Chalfoun A.D., Thompson F.R. & Ratnaswamy M.J. 2002: Nest predators and fragmentation - A review and meta-analysis. *Conserv Biol, 16, 306 - 318.*

Chamberlain D. E., Cannon A. R., Toms M. P., Leech D. I., Hatchwell B. J. & Gaston K. J. 2009: Avian productivity in urban landscapes - A review and meta-analysis. *Ibis, 151, 1 – 18.*

Chiron F. & Julliard R. 2007: Responses of songbirds to magpie reduction in an urban habitat. *J Wildlife Manage,71 (8), 2624 – 2631.*

Crawley M.J. 2005: Statistics - An Introduction using R. *John Wiley and Sons Ltd.*

DeLong A.K., Crawford A. & DeLong Jr. D.C. 1995: Relationship between vegetational structure and predation of artificial Sage Grouse nests. *J Wildlife Manage, 59 (1), 88 – 92.*

Dion N., Hobson K A. & Larivière S. 2000: Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. *The Condor, 102, 629 – 634.*

Donovan T.M., Jones P.W., Annand E.M. & Thompson F.R. 1997: Variation in local-scale edge effects - Mechanisms and landscape context. *Ecology, 78 (7), 2064 – 2075.*

Dunford W. & Freemark K. 2004: Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. *Landscape Ecol, 20, 497 – 511.*

Evans K.L., Newson S.E., Gaston K.J. 2009: Habitat influence on urban avian assemblages. *Ibis, 151, 19 – 39.*

Fuchs R., Škopek J., Formánek J. & Exnerová A. 2002 : Atlas hnízdního rozšíření ptáků Prahy. (Atlas of breeding birds in Prague) [in Czech].*Consult Praha.*

Fuller R. J., Smith K.W., Grice P.V., Currie F.A. & Quine C.P. 2007: Habitat change and woodland birds in Britain - Implications for management and future research. *Ibis, 149 (Suppl. 2), 261 – 268.*

Gering J.C & Blair R.B. 1999: Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? *Ecography, 22, 532–541.*

Gooch S., Baillie S.R. & Birkhead T.R. 1991: Magpie *Pica pica* and songbird populations - Retrospective investigations of trends in population density and breeding success. *J Appl Ecol, 28 (3), 1068-1086.*

Hagan J.M., Vander Haegen M. & McKinley P.S. 1996: The early development of forest fragmentation effects on birds. *Conserv Biol, 10 (1), 188 – 202.*

Hansson B., Bensch S. & Hasselquist D. 2000: Patterns of nest predation contribute to polygyny in the Great Reed Warbler. *Ecology, 81, 319 – 328.*

Hoover J.P., Tear T.H. & Baltz M.E. 2006: Edge effect reduce the nesting success of Acadian Flycatchers in a moderately fragmented forest. *J Field Ornithol, 77 (4), 425 – 436.*

Howell C.A., Latta S.C., Donovan T.M., Porneluzi P.A., Parks G.R. & Faaborg J. 2000: Landscape effects mediate breeding bird abundance in midwestern forests. *Landscape Ecol, 15, 547 – 562.*

Hudec K. & Šťastný K. 2005: Fauna ČR: Ptáci 2/I a II (Fauna of the CR. Birds 2/I and II) [in Czech]. *Academia Praha.*

Huhta E., Mappes T. & Jokimaki J. 1996: Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. *Ecography, 19, 85 - 91.*

Jerzak L. 2001: Synurbanization of the magie in the Paleartic. In: Marzluff J.M., Bowman R. & Donnelly R. (eds.), Avian ecology and conservation in an urbanizing world. *Kluwer Academic, Norwell, MA: 403 - 425.*

Jokimäki J. & Huhta E. 2000: Artificial nest predation and abundance of birds along an urban gradient. *The Condor, 102 (4), 838 – 847.*

Jokimäki J., Kaisanlahti-Jokimäki M.-L., Sorace A., Fernández-Juricic E., Rodriguez-Prieto I. & Jimenez, M D. 2005: Evaluation of the "safe nesting zone" hypothesis across an urban gradient - A multi-scale study. *Ecography, 25, 59 – 70.*

Kadlec T., Beneš J., Jarošík V. & Konvička M. 2008: Revisiting urban refuges - Changes of butterfly and burnet fauna in Prague reserves over three decade. *Landscape Urban Plan, 85, 1 - 11.*

Kokko H. & Sutherland W.J. 2001: Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evol Ecol Res, 3, 537 – 551.*

Krebs C. 1989: Ecological Methodology. *Harper Collins. New York.*

Laurance W. 2000: Do edge effects occur over large spatial scales? *Tree, 15 (4): 134 – 135.*

Leston L.F.V. & Rodewald A.D. 2006: Are urban forests ecological traps for understory birds? An examination using Northern Cardinals. *Biol Conserv, 131, 566 – 574.*

López-Flores V., MacGregor-Fors I. & Schondube J.E. 2009: Artificial nest predation along a Neotropical urban gradient. *Landscape Urban Plan, 92, 90 – 95.*

Martin J.-L. & Joron M. 2003: Nest predation in forest birds - influence of predator type and predator´s habitat quality. *Oikos, 102, 641 – 653.*

Marzluff J. M. & Ewing K. 2001: Restoration of fragmented landscapes for the conservation of birds - A general framework and specific recommendations for urbanizing landscape. *Restor Ecol, 9 (3), 280 – 292.*

Marzluff J. M. & Restani M. 1999: The effect of forest fragmentation on avian nest predation. In: Rochelle J.A., Lehmann L.A. & Wisniewski J. (eds.). Forest fragmentation: Wildlife and management implications. *Leiden, Boston, Köln: Brill Academic Publishers: 155 – 170.*

Matthews A., Dickman C.R. & Major R.E. 1999: The influence of fragment size and edge on nest predation in urban bushland. *Ecography, 22, 349 – 356.*

Noss R. F. 1991: Do we really want diversity? In: Willers W.B. (ed.): Listen to the land. *Island Press: 41 – 45.*

Opermanis O., Mednis A. & Bauga I. 2001: Duck nest predators: interaction, specialisation and possible management. *Wildlife Biol, 7, 87 – 96.*

Pasinelli G. & Schiegg K. 2006: Fragmentation within and between wetland reserves: the importance of spatial scales for nest predation in Reed Buntings. *Ecography, 29, 721 – 732.*

Paton P.W.C. 1994: The effect of edge on avian nest success – how strong is the evidence. *Conserv Biol, 8 (1), 17 – 26.*

Rangen S.A., Clark R.G. & Hobson K.A. 2000: Visual and olfactory attributes of artificial nests. *Auk, 117 (1), 136 – 146.*

Ries L. & Sisk T.D. 2004: A predictive model of edge effects. *Ecology, 85 (11), 2917 – 2926.*

Roos S. 2002: Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia, 133, 608 – 615.*

Šálek M., Marhoul P., Pintíř J., Kopecký T. & Slabý L. 2004: Importance of unmanaged wasteland patches for the Grey Partridge *Perdix perdix* in suburban habitats. *Acta Oecol, 25, 23 – 33.*

Saunders D.A., Hobbs R.J. & Margules C.R. 1991: Biological consequence of ecosystem fragmentation: a review. *Conserv Biol, 5 (1), 18 – 32.*

Schiegg K., Eger M. & Pasinelli G. 2007: Nest predation in Reed Buntings (*Emberiza schoeniclus*) - an experimental study. *Ibis, 149, 365 – 373.*

Šťastný K., Bejček V. & Hudec K. 2006: Atlas hnízdního rozšíření ptáků v České Republice (Atlas of nesting birds in the Czech Republic) [in Czech]. *Aventinum.*

Soderström B, Pärt T. & Ryden J. 1998: Different predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia 117, 108-118.*

Storch I., Woitke E. & Krieger S. 2005: Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe. *Landscape Ecol, 20, 927 – 940.*

Teunissen W., Schekkerman H., Willmes F. & Majoor F. 2008: Indentifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis, 150 (Suppl. 1), 74 – 85.*

Thorington K. K. & Bowman R. 2003: Predation rate on artificial nests increases with human housing density in suburban habitats. *Ecography, 26, 188 – 196.*

Vickery P.D., Hunter M.L. Jr. & Wells J.V. 1992: Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos, 63, 281-288.*

Villard M.-A. 1998: On forest – interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *Auk, 115 (3), 801 – 805.*

Villard M.-A. & Pärt T. 2004: Don´t put all your eggs in real nests - a sequel to Faaborg. *Conserv Biol, 18 (2), 371 – 372.*

Wallander J., Isaksson D. & Lenberg T. 2006: Wader nest distribution and predation in relation to man – made structures on coastal pastures. *Biol Conserv, 132, 343 – 350.*

Wegner J.F. & Merriam G. 1979: Movements by birds and small mammals between a wood and adjoining farmland habitats. *J Appl Ecol, 16 (2), 349 – 357.*

Weinberg H.J. & Roth R.R. 1998: Forest area and habitat quality for nesting Wood Thrushes. *Auk, 115 (4), 879 – 889.*

Wilcove D S. 1985: Nest predation in forest tracts and the decline of migratory songbirds. *Ecology, 66, 1211 - 1214.*

Wilson E O. & Peter F.M. 1988: Biodiversity. *National Academy Press. Washington D. C.*

Winter M., Johnson D.H., Shaffer J.A., Donovan T.M. & Svedarsky W.D. 2006: Patch size and landscape effects on density and nesting success of grassland birds. *J Wildlife Manage*, *70 (1), 158 – 172.*

Yahner R.H. & Mahan C.G. 1996: Effects of egg type on depredation of artificial ground nests. *Wilson Bull, 108 (1), 129 – 136.*

Yahner R.H. & Piergallini N.H. 1998: Effects of microsite selection on predation of artificial ground nests. *Wilson Bull, 110 (3), 439 – 442.*

Zanette L. & Jenkins B. 2000: Nesting success and nest predators in forest fragments - A study using real and artificial nests. *Auk, 117 (2), 445 – 454.*

Table 1. Habitat types.

Description of measured habitat attributes

Fields ("field")

Forests ("forest")

Other wastelands ("weed")

Orchards and gardens ("gard")

Meadows ("mead")

Baulks and field paths ("path")

Water bodies and flows ("wat")

Roads outside urbanized zones ("road")

Railways outside of cities and villages ("rail")

Buildings and structures, including integrated roads and railway ("hous")

Bare fallow, sand and gravel grounds and newly established building sites ("bare")

Managed lawn areas such as playgrounds, stadiums or airports ("airp")

Table 2. Correlation coefficients between particular environmental variables and principal components PC1–PC5 (with $\lambda \geq 1$). Variables strongly associated with a particular principal component ($r > 0.6$) are in bold.

Variable	Particular axes of principal components				
	PC1	PC2	PC3	PC4	PC5
Patch area	0.40	0.08	-0.13	-0.05	**0.61**
Distance to city centre	**-0.65**	-0.11	0.27	-0.09	0.35
Fields	**-0.91**	-0.10	>> - 0.01	0.03	-0.02
Forests	0.43	**-0.59**	-0.06	0.01	0.31
Buildings and structures	**0.71**	0.39	-0.23	-0.27	-0.02
Roads	0.15	0.45	0.47	-0.15	0.11
Weeds	0.51	**0.61**	0.13	0.06	-0.01
Airports and playgrounds	0.14	<< 0.01	0.34	0.29	0.44
Gardens and orchards	0.37	-0.41	0.33	0.06	-0.43
Meadows	0.36	**-0.64**	0.21	-0.14	-0.09
Water bodies	0.35	-0.21	-0.07	**0.65**	0.08
Paths	**-0.61**	0.03	0.27	0.20	0.16
Bare soil	-0.02	0.21	**0.67**	0.13	-0.19
Railway	0.04	0.23	-0.22	**0.74**	-0.15
Surrounding habitat heterogeneity	**0.82**	-0.15	0.30	0.02	0.06

Table 3. Predator prints of nests with depredated eggs and total counts of nests with removed eggs.

Type of nest depredation		Count of depredated nests	% in overall count of depredated nests
nests with eggs marked by predator prints	bird	28	23.5
	mammal	12	10.1
	combined	5	4.2
	undetermined	3	2.5
nests with eggs totally removed with no marks		71	59.7
Total		119	100

Table 4. Eigenvalues of correlation matrix, and related statistical values.

Value number	Eigenvalue (λ)	% of total variance	Cumulative eigenvalue	Cumulative %
PC1	3.84	25.59	3.84	25.59
PC2	1.86	12.39	5.70	37.98
PC3	1.33	8.89	7.03	46.87
PC4	1.23	8.23	8.27	55.10
PC5	1.09	7.24	9.35	62.34

Table 5. Results of the mixed-effects model (n = 103). Df includes values for both numerator and denominator. Effects of two significant predictors were tested as controlled for the effect of one another.

Factor	Estimate	SE	χ^2	df	p
PC4	0.06	0.05	11.55	1, 5	< 0.001
PC2	0.12	0.06	9.89	1, 5	0.002
Nest position : proportion of gardens	- 0.02	0.01	2.93	1, 7	0.08
Proportion of roads	0.03	0.02	2.63	1, 6	0.11
Nest position : PC4	0.10	0.06	2.37	1, 8	0.12
Proportion of gardens	0.02	0.01	1.58	1, 12	0.21
Nest position	0.77	0.73	1.36	1, 9	0.24
Nest position : PC1	0.10	0.07	1.39	1, 16	0.24
Nest position : PC2	- 0.07	0.07	1.17	1, 15	0.28
PC3	- 0.08	0.06	1.15	1, 10	0.28
Proportion of airports	0.02	0.01	1.05	1, 8	0.31
PC1	- 0.14	0.06	0.96	1, 7	0.33
Patch area	0.02	0.11	0.47	1, 11	0.49
Nest position : patch area	- 0.11	0.14	0.22	1, 19	0.64
Nest position : proportion of airports	- 0.004	0.02	0.08	1, 18	0.78
Nest position : PC3	0.02	0.08	0.05	1, 20	0.81
Nest position : proportion of roads	- 0.001	0.02	0.05	1, 17	0.82

Table 6. Results of the mixed-effects model analysing effect of patch shape on predation risk (n = 17). Df includes both numerator and denominator values.

| Factor	Estimate	SE	χ^2	df	p
Nest position : patch area	>> - 0.001	<< 0.001	2.58	1, 7	0.11
Nest position	0.16	0.23	1.92	1, 4	0.17
Patch shape	0.04	0.36	1.19	1, 5	0.28
Patch shape : nest position	- 0.23	0.25	0.97	1, 8	0.33
Patch shape : patch area	>> - 0.001	<< 0.001	0.49	1, 9	0.49
Patch size	<< 0.001	<< 0.001	0.40	1, 6	0.53

Captions for figures

Fig. 1. All 103 study sites around Prague (large map) and position of Prague within the Czech Republic (small map). Legend: black triangles = study sites. Source: GIS.
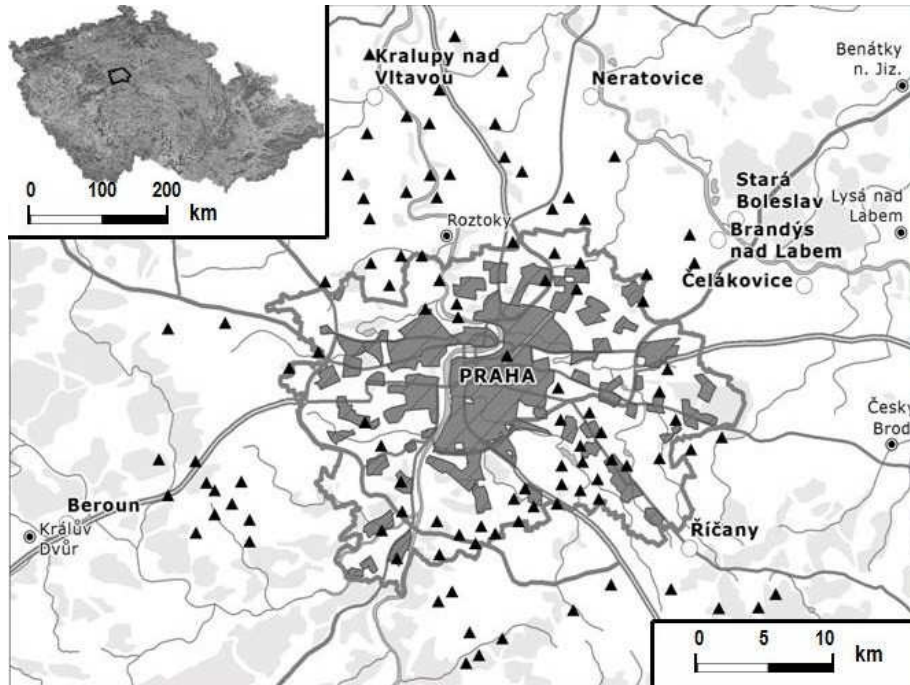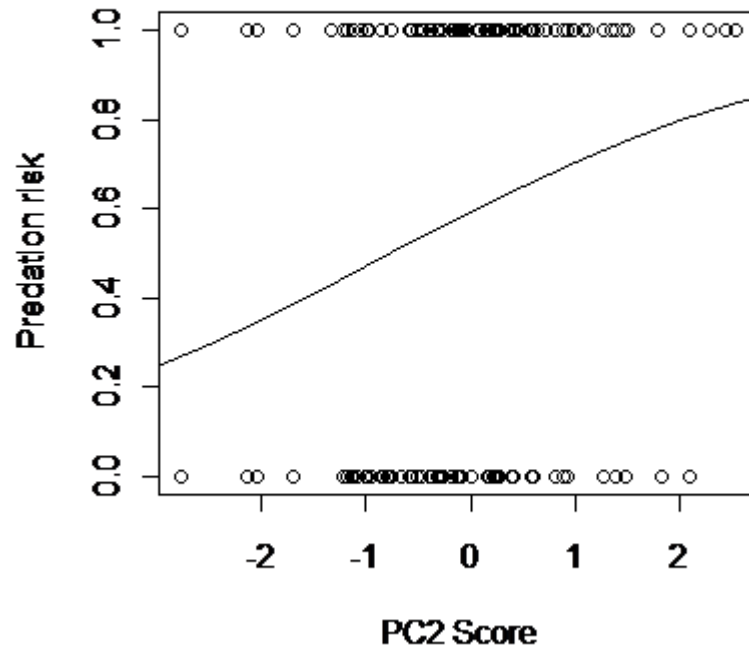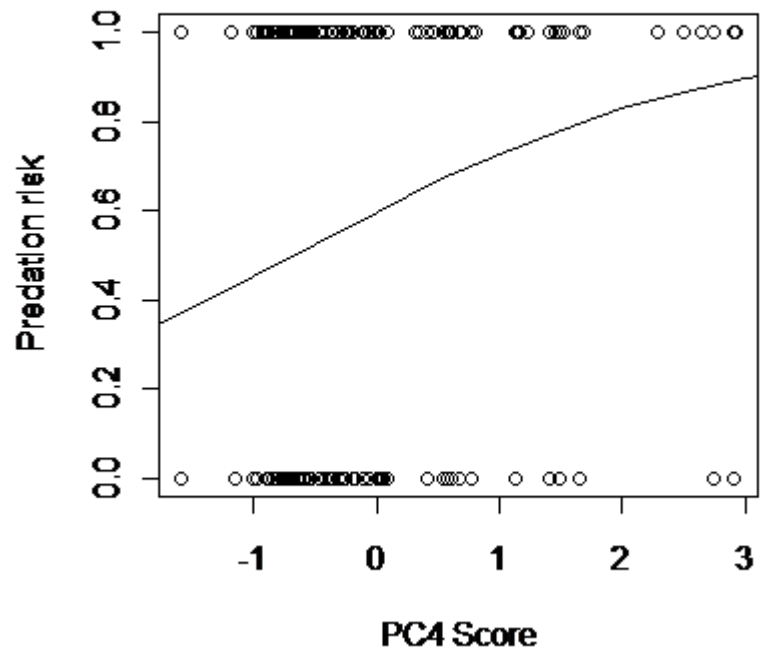
Fig. 2. Distribution of patch sizes.
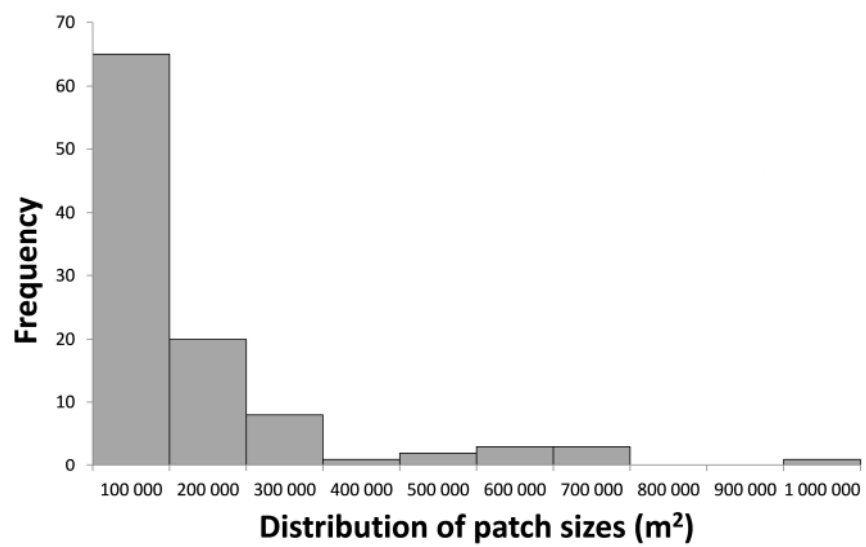
Fig. 3. Probability of predation risk according to PC2 score (see Table 2 for interpretation).

Fig. 4. Probability of predation risk according to PC4 score (see Table 2 for interpretation).

IV.

Suvorov P., Svobodová J. & Albrecht T.: **Predation of artificial nests in wetland habitat: Evidence of the edge effect.** *In preparation.*

Predation of artificial nests in wetland habitat: Evidence of the edge effect

PETR SUVOROV[1], JANA SVOBODOVÁ[1] AND TOMÁŠ ALBRECHT[2,3]

[1] Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences, Kamýcká 129, 165 21 Prague 6, Czech Republic

[2] Institute of Vertebrate Biology, Academy of Sciences of the Czech republic, v. v. i., Květná 8, 603 65 Brno

[3] Charles University in Prague, Faculty of Science, Department of Zoology, Viničná 7, 128 44 Prague

E-mail and phone to the corresponding author: petr.suvorov@hotmail.com, +420604 924 214

ABSTRACT

In Central Europe, edge effect has been demonstrated mostly in reed wetlands. However, a little is known about its appearance in pristine grass-dominated wetlands. During three breeding periods we conducted an experiment with aritificial ground nests to test the edge effect along two gradients between wetland and meadow, and wetland and forest. In addition, we also tested the edge effect using artificial shrub nests which simulated real nests of Scarlet Rosefinch (*Carpodacus erythrinus*). Since rosefinch usually breeds in wetland habitats in our study area, the artificial nest were installed only in two habitats, i.e. wetland edge and wetland interior. Predation rates on the ground nests reached up to 31.2% and on the shrub nests 57.1% and 6.5% for particular years. The edge effect appeared in all of our experiments, but with various patterns of distribution and irregularly over particular years. Our data in the transition to the forest indicate three different patterns – *ecotonal effect* for the first year, *negative edge effect* in the wetland and no edge effect in the forest for the second year and no edge effect in the last season. Nest predation on the transition to the meadow showed significant effect of the edge, i.e. *ecotonal effect* over all three studied years. Edge effect also appeared in the shrub nests in one of studied years which indicates similar nest predation pattern as reported before in the study using real nests of Scarlet Rosefinch. Differences in the nest predation pattern over particular seasons, habitats and nest types may be caused by differences in the predator foraging preferences. Our results extend the evidence of the edge effect.

INTRODUCTION

Nest predation is the main factor driving nesting failure in birds (Ricklefs 1969). Temporal and spatial variation in nest predation rates is well documented (Andrén 1992, Martin 1993, Sieving and Willson 1999, Lahti 2001, Fisher and Wiebe 2006, Suvorov et al. 2011) though is not well understood and explained (Gustafson 2005, Donovan et al. 1997, Koubová et al. 2011). For example, nest predation can be higher in habitat edges compare to habitat interior (edge effect; Gates and Gysel 1978). So far, five mechanistic explanations for higher nest predation in edge habitats have been proposed based on causal links between predator occurrence and habitat-specific resource (Ries and Sisk 2004, more in Koubová et al. 2011). Basically, there are two models linking predator movements with elevated nest predation rates in habitat edges: *(1) matrix effect* model supposes that predators penetrate from the habitat of higher predator density to the habitat of lower predator density and cause a transition between two habitat patches (also the *spillover model*, *sensu* Lidicker 1999) and/or *(2)* edges may contain complementary resources from both adjacent habitats and/or can contain specific resources which can be specifically used by nest predators (*ecotonal effect*; Lidicker l. c.).

The existence of edge effect on bird nesting success is very well documented mostly in hard edges, where two distinct habitats meet (Batáry and Báldi 2004). Typically, predation rate is documented in North American and Scandinavian studies (arable land-forest border), but it is less apparent in mosaic European landscapes (see Batáry et al. 2004). Nevertheless, increased nest predation rate in the interior habitats comparing to edge zones (*negative edge effect*) and a neutral response of nest predator to habitat edges (Angelstam 1986, Ratti and Reese 1988, Santos and Tellería 1992) have also been demonstrated in some experiments (Storch 1991, Marini et al. 1995). In addition, it is evident that the edge effect on nest predation is a dynamic process with temporal variation (Svobodová et al. 2012).

Whereas many studies investigated the edge effect mainly in agricultural landscape with hard edges (Wilcove et al. 1986, Andrén 1992, 1995, Huhta et al. 1996, Major and Kendal 1996, Bayne et al. 1997, Donovan et al. 1997, Lahti 2001, Conner and Perkins 2003, Batáry and Báldi 2004), data from opened habitats with soft edges such as transition zone between wetland and meadow are less available (e.g. Pasinelli and Schiegg 2006, Wallander et al.

2006) despite the fact that wetland habitats belong to the most endangered ecosystems in the world (Zedler and Kercher 2005). In Central Europe, studies on the edge effect are mostly restricted to reed habitats (e.g. Batáry et al. 2004, Batáry and Báldi 2004, 2005, Báldi and Batáry 2005, Schiegg et al. 2007, Trnka et al. 2009). Although opened bogs and inundated meadows of Central Europe provide important breeding sites for particular threatened species such as waders, Corn Crake (*Crex crex*), Hen Harrier (*Circus cyaneus*) or Black Grouse (*Tetrao tetrix*) (Hagemeijer and Blair 1997) studies from grass-dominated wetlands are rare (Albrecht 2004).

The aim of our study was to analyse distribution of nest predation in grass-dominated wetland, in Central Europe fragmented by production forest and meadow. In our study area, Albrecht (2004) already demonstrated higher breeding productivity of a small shrub- and open-cup nesting passerine, the Scarlet Rosefinch (*Carpodacus erythrinus*) in the interior wetland habitat than in its edge towards arable land. However, the mechanisms of the edge effect have not been tested because rosefinch nests usually occurred only in wetland habitat habitats, i.e. not in whole transition zone between wetland and meadow. Using artificial ground nests distributed in seven habitat elements (i.e. edge and interior of wetland, forest and production meadow respective) we were able to test the two mechanisms of the edge effect, i.e. the *matrix* and *ecotonal effect* model. We furthermore used artificial shrub nests to test whether the spatial distribution of predation of artificial shrub nests resemble predation of real rosefinch nests.

MATERIAL AND METHODS

Study site

The study locality was situated in the Vltava River Valley of the Šumava Mts. National Park (48°47'- 48°53'N, 13°57' - 13°51'E, 800 a. s. l.), Czech Republic, which belongs to one of very few areas of primary non-forested habitats in Central Europe (Sádlo and Bufková 2002). The area was mainly composed by periodically inundated wetlands (25%) surrounded by coniferous or mixed forest (15%) or extensively used meadow (60%). For the purpose of this study, we distinguished six habitat types: The wetland interior *(1)* was mostly created by mosaic of shrub and humid herbal vegetation with dominating species such as Bridewort (*Spiraea salicifolia*) and *Phalaroides sp., Glyceria sp., Carex sp., Eriophorum sp.,* Meadowsweet (*Filipendula ulmaria*), respectively. This area is also regularly flooded. The extensively mowed meadow interior *(2)* was dominated by grasses. The canopy of the forest

interior *(3)* was mainly composed by soft-wood species (*Betula pendula, Salix sp., Alnus sp.*) and by spruces (*Picea* sp.). The shrub and herbal undergrowth were usually sparsely develop (>30 %). The next three habitat types were edges habitats that consist of very narrow strips of vegetation (up to 10 m wide). Wetland edge with meadow *(4)* and with forest *(5)* was dominated by wetland herbs mixed either with forest or meadow species. Meadow edges with wetland *(6)* and forest edges with wetland *(7)* were composed by either grasses or forest vegetation supplemented by wetland herbs. The shrub layer in these forest edges was usually dense (> 25%), consisting mainly of Bridewort, European Black Elder and saplings of canopy trees.

Experimental design

To test if the nest predation is influenced by the distance of nest from the habitat edge we used two types of artificial nests, i.e. ground and shrub nests. The ground nest was constructed as small depression in the ground lining with small amount of dry grass. The cup of shrub nest was created from a half of cut tennis ball covering by soil and plant material which were fixed by wire to shrub branch. Since rubber scent of tennis ball can discourage potential predators the shrub nests were aired for 14 days (Davison and Bollinger 2000). Both types of nests would resemble the nests of bird species such as Corn Crake (*Crex crex*), Black Grouse (*Tetrao tetrix*), Common Quail (*Coturnix coturnix*), Whinchat (*Saxicola rubetra*) as ground nesting birds, and the Scarlet Rosenfinch (*Carpodacus erythrinus*) and Whitethroat (*Sylvia communis*) as open-cup shrub nesting birds that regularly occur in our study area (Hora et al. 1997). The experiment was conducted from mid-April till mid-May, which is the average period of clutch laying for these species in the Czech Republic (Šťastný and Hudec 2011). The ground nests were installed during three breeding periods (2005 – 2007), the shrub nest in two periods (2006 - 2007). Each nest was baited with two quail eggs, one of them was filled by wax for predator identification (Thompson a Burhans 2004, Storch et al. 2005). In both nest types, wax eggs were anchored in the nest pits with a string and nail in order to prevent predators from carrying them away (Söderström et al. 1998). We expected Red Fox (*Vulpes vulpes*), mustelids, Wild Boar (*Sus scrofa*) and corvid birds to appear as nest predators. These animal groups are able to keep all the quail egg by their bills or mouths, so they can be considered to appear as the potential nest predators (Montevecchi 1976, Larivière 1999). On the other hand, animals like rodents cannot be considered as valid nest predators of our artificial nests because they usually are not able to bite the thick shell of quail egg (DeGraaf et al. 1999, Pärt and Wretenberg 2002).

In total, we installed 720 ground nests during three years along two different gradients – *(1)* from the interior wetland across the boundary line to the interior meadow and *(2)* from the interior wetland to the interior forest, i.e. to the wetland interior, meadow interior, forest interior, wetland-meadow edge, wetland-forest edge, meadow edge and forest edge with wetland.

Shrub nests were installed only in two habitats, 31 nests in wetland interior and 31 nests in wetland-meadow edge (i.e. 124 in total during two years). Whereas interior nests were installed at least 100 m away from habitat border (also see Albrecht 2004 for edge effect on real rosefinch nests in the study area), edge nests were placed at distance up to 20 m from habitat edge. To avoid pseudoreplication, the minimum distance between neighbouring nests was 100 m (Pärt and Wretenberg 2002).

All nests were checked only once after ten-day exposure to reduce the observer effect and to preserve nest concealment (Martin and Joron 2003, Villard and Pärt 2004). The nest was considered as depredated if at least one of the eggs was damaged or completely missing in the nest bowl. Nest predators were identified by beak or tooth marks left on the wax eggs and were divided in three categories: bird predator, mammalian predator, and unidentified. The nests that were not retrospectively discovered mainly due to regularly spring flood were not included to our further analysis.

Statistical analysis

We evaluated the *ecotonal* and *matrix effect* models of nest predation along two transition zones, (i.e. between wetland and meadow habitats, and between wetland and forest habitats) therefore two generalized linear models (GLM) were performed. Since the procedure was explained elsewhere in detail (Svobodová et al. 2011, 2012) here is described only briefly. First, 2 explanatory variables were assessed to code the spatial position of individual nests: each nest was placed *(1)* on the edge or in the interior and at the same time *(2)* in one of the habitat type. According to the *ecotonal effect* model, nest predation risk is predicted to be higher in edge habitats compared to the interior of either habitat, hence the effect of edge position should be significant. On the other hand, under the *matrix effect* model, predation risk is predicted to be higher at the edge of one habitat, yet lower in the edge of the second one, i.e. an interactive effect of both edge and habitat type should be significant (Ries and Sisk 2004). Since shrub nests were placed only in two habitat types (wetland interior and edge) only edge position variable was included in a generalized linear model. Finally, the effect of

year, and all two-way interactions between main effects were included in our statistical models.

The probability of nest predation was analysed by generalized linear models, where nest fate was the binary dependent variable with binomial distribution (predated = 1, vs. successful = 0). The significance ($p < 0.05$) of a particular term in the models was based on the change in deviance between the full and reduced / null models, with degrees of freedom equal to the difference in the degrees of freedom between the models with and without the term in question. All non-significant terms were removed using backward stepwise procedure to reach the minimal adequate models, i.e. models with all terms significant (Crawley 2002). All GLM models were performed in software R.2.12.1 (R Development Core team 2008).

RESULTS

Due to regular strong floods we were not able to localize position of some of our artificial nests (7.5% of ground nests and 4.8% of shrub nests placed in wetlands, 13.3% ground nests in forests, and 1.7% ground nests and 4.8% of shrub nests in arable land-meadows). Therefore, 666 nests were included in the next analysis. Nest predation rate of ground nests in all studied years reached up to 31.2 % (n = 666). In total, we found only two reliable imprints – one caused by a small carnivore in 2006 and one caused by a bird in 2007. Both of them were found in the interior wetland.

Transition zones between wetland and forest

The minimal adequate model (n = 312) included the effect of habitat type and nest position and the interactive effect of the year and nest position (Table 1). Since probability of nest predation significantly changed among years next analysis were performed separately for particular years. In 2005, only the effect of nest position was significant in the model suggesting *ecotonal effect* model. In 2006, the interactive effect of habitat type and nest position appeared to be significant. In 2007, all the effects were insignificant (see Table 2 and Fig. 1).

Transition zones between wetland and grassland

In the model for transition zones between wetland and meadow (n = 356) only nest position was a significant variable. Nest predation was higher in both edge habitats, i.e. in wetland edge and meadow edge (Tab. 3, Fig. 2).

Shrub nests

Nest predation rate on shrub nests reached up to 57.1% in 2006 and 6.5% in 2007. Further analysis using GLM (n = 118) showed significant effects of the year (χ^2 = 42.54, P << 0.001, Df = 1) and nest position (χ^2 = 8.56, P = 0.003, Df = 1) (Fig. 3). Since their interaction was significant (χ^2 = 19.08, P << 0.001, Df = 1). In addition, the nest predation was higher in the wetland edge. However, the difference between habitat type was not evident only in 2006.

DISCUSSION

Our results show the influence of the edge effect on predation rate of artificial nests in the landscape of the Vltava River Valley. Edge effect appeared in two of studied years in the transition from interior wetland to its border with adjacent forests. Forest edges in our study site may have, appeared as irregular travel lines (Wegner a Merriam 1979, Andrén 1994, Pangau et al. 2006) and, as a consequence, nest predation rate in such sites increased. However, in according to our results, appearance of edge effect is probably inconsistent between the years. Whereas first year the predator response corresponds to *ecotonal effect* hypothesis, second year seems to copy *negative edge effect* in the wetland part and no edge effect in the forest part of the habitat. Last year, no edge effect was detected.

Trend of temporal variation in predator responds to artificial nests is in accordance with our previous results from Czech Republic in different habitats (Svobodová et al. 2011) and with some other studies (Chiarello et al. 2008). Differences may be caused by switching in foraging preferences of nest predators (Marcström et al. 1988, Lindström et al. 1994) or by fluctuations of their main prey (Angelstam et al. 1984, Small et al. 1993, Moss and Watson 2001, Korpimäki et al. 2005) because bird nest predation tends to be more influenced by predator foraging behaviour than by its abundance (Vickery et al. 1992). Absence of the edge effect on nest predation can appear also in case when main nest predator community comprises of highly mobile predators such as Wild Boars which equally scan the landscape during their search for food (Einarsen et al. 2008).

We also detected *ecotonal effect* on the gradual meadow – wetland transition but its pattern seems to be equal for all studied seasons. It is possible that main resources in highly contrast transition from wetland to forest can change more frequently than in less contrast (and more stable) transition to meadow. Alternatively, maybe that our study was carried for too short period to detect the variability between years in all possible habitats.

Results on artificial shrub nests showed also the temporal variation – whereas in 2006 edge effect did appear, in 2007 no effect was detected. Edge effect on nest predation in the Vltava

River Valley has been already demonstrated by Albrecht (2004) using real nests of Scarlet Rosefinch. Artificial nests are used in cases where the sufficient amount of real nests is difficult to find (Burke et al. 2004). However, reliability of such experiments has been criticised in the past (Bayne et al. 1997, Pärt and Wretenberg 2002, Faaborg 2004). Method of artificial nests does not enable to simulate parental activity (Matthews et al. 1999, Pärt a Wretenberg 2002, Burke et al. 2004) or natural scent (Githiru et al. 2004, but see King et al. 1999 or Pärt and Wretenberg 2002), yet, placing of the nest in the biotope may differ from that selected by a bird (Yahner a Piergallini 1998). Predation rate of real and artificial nests may, then, differ each to other (Pärt a Wretenberg 2002, Thompson a Burhans 2004, Gustafson 2005). However, despite we did not install the artificial shrub nests to all available habitats, our results show that the pattern of their predation may be similar as in the real nests (Martin 1987, Bayne et al. 1997, Söderström et al. 1998, Trnka et al. 2009). Interestingly, the overall nest predation rate reported by Albrecht (2004) for real nests based on nest survival (29.7% estimated destroyed in total, 13.5% in wetland interior habitats and 49.4% in edges) fits well to our own figures based on artificial nests.

We cannot unambiguously say which group depredated our artificial nests the most. In many cases we were not able to identify the predator species (see also Larivière 1999) or the egg missed. Teunissen et al. (2008) showed that similarly looking eggs of waders were depleted in 93% by mammals than by Carrion Crows (*Corvus corone*). In Svobodová et al. (2012), 41% of the experimental nests were depleted by Wild Boars. Despite we did not systematically search for the potential nest predators, but Wild Boars were frequently observed in particular parts of the study site, independently to the habitat type.

CONCLUSION

In conclusion we found that artificial nests of both types in the pristine landscape of Vltava River Valley are exposed to the edge effect but this effect appears irregularly, probably in according to the predator preferences or distribution of its main prey. Pattern of nest predation seems to be different in according to particular habitats. Our results may contribute to the overall common knowledge of the edge effect and extend its body of evidence mainly in opened habitats, i.e. wetlands. In addition, they can be also applied in the practical protection of the landscape and bird populations in Vltava River Valley but, however, it needs further research.

ACKNOWLEDGES

REFERENCES

Albrecht T., 2004: Edge effect in wetland – arable land boundary determines nesting success of Scarlet Rosefinch (*Carpodacus erythrinus*) in the Czech republic. *The Auk 121 (2):* 361 – 371.

Andrén H., 1992: Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology 73:* 794 - 804.

Andrén H., 1994: Effects of habitat fragmentation on birds and mammals in landscapes with different portions of suitable habitat – a review. *Oikos 71 (3):* 355 – 366.

Andrén H., 1995: Effects of landscape composition on predation rates at habitat edges. Pp 225 - 255 In: Hansson L., Fahrig L. & Merriam G. (eds): *Mosaic landscapes and ecological processes.* Iale Studies in Landscape Ecology, Chapman & Hall

Angelstam P., 1986: Predation on ground – nesting birds´ nests in relation to predator densities and habitat edge. *Oikos 47:* 365 – 373.

Angelstam P., Lindström E. & Widen P., 1984: Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia 62:* 199-208.

Batáry P. & Báldi A., 2004: Evidence of an edge effect on avian nest success. *Conservation Biology 18 (2):* 389 – 400.

Batáry P., Winkler H. & Báldi A., 2004: Experiments with artificial nests on predation in reed habitats. *Journal of Ornithology 145:* 59 – 63.

Batáry P. & Báldi A., 2005: Factors affecting the survival of real and artificial Great Reed Warbler´s nests. *Biologia Bratislava 60 (2):* 215 – 219.

Báldi A. & Batáry P., 2005: Nest predation in European reedbeds: different losses in edges but similar losses in interiors. *Folia Zoologica 54:* 285 - 292.

Bayne E. M., Hobson K. A. & Fargey P., 1997: Predation on artificial nests in relation to forest type: Contrasting the use of quail and plasticine eggs. *Ecography 20 (3):* 233 – 239.

Burke D. M., Elliott K., Moore L., Dunford W., Nol E., Phillips J., Holmes S. & Freemark K. 2004: Patterns of nest predation on artificial and natural nests in forests. *Conservation Ecology 18 (2):* 381 – 388.

Chiarello A. G., Srbek-Araujo A. C., Del Duque Jr. H. J. & de Rodrigues Coelho E., 2008: Ground nest predation might not be higher along edges of Neotropical forest remnants

surrounded by pastures: evidence from the Brazilian Atlantic forest. *Biodiversity Conservation 17:* 3209 – 3221.

Conner L. M. & Perkins M. W., 2003: Nest predator use of food plots within a forest matrix: an experiment using artificial nests. *Forest Ecology and Management 179 (1 – 3):* 223 – 229.

Crawley M. J., 2002: Statistical computing: an introduction to data analysis using S-Plus.

Davison W. B. & Bollinger E., 2000: Predation rates on real and artificial nests of grassland birds. *The Auk 117 (1):* 147 – 153.

DeGraaf R. M., Maier T. J. & Fuller T. K., 1999: Predation of small eggs in artificial nests: effects of nest position, edge and potential predator abundance in extensive forest. *Wilson Bulletin 111 (2):* 236 – 242.

Donovan T. M., Jones P. W., Annand E. M. & Thompson F. R., 1997: Variation in local-scale edge effects: mechanisms and landscape context. *Ecology 78 (7):* 2064 – 2075.

Einarsen G., Hausner V. H., Yoccoz N. G. & Ims R. A., 2008: Predation on artificial ground nests in birch forests fragmented by spruce plantations. *Ecoscience 15 (2):* 141 – 149.

Faaborg J., 2004: Truly artificial nest studies. *Conservation Biology 18 (2):* 369 – 370.

Fisher R. J. & Wiebe K. L., 2006: Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. *Oecologia 147 (4):* 744 – 753.

Gates E. J. & Gysel L. W., 1978: Avian nest dispersion and fledging success in field – forest ecotones. *Ecology 59 (5):* 871 – 883.

Githiru M., Lens L. & Creswell W., 2004: Nest predation in a fragmented Afrotropical forest: evidence from natural and artificial nests. *Biological Conservation 123:* 189 – 196.

Gustafson T., 2005: *Nest predation in birds – important concepts and methodological problems.* Introductory Research Essay 22. Department of Conservation Biology SLU

Hagemeijer W. J. M. & Blair M. J., 1997: *The EBCC atlas of european breeding birds: Their distribution and abundance.* T & AD Poyser London.

Hora J., Bürger P. & Pykal J., 1997: Ptactvo Vltavského luhu (Šumava, jižní Čechy): výsledky síťového mapování v hnízdním období 1993 a 1994. *Sylvia 33 (1 – 2):* 113 – 140.

Huhta E., Mappes T. & Jokimaki J., 1996. Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. *Ecography 19:* 85-91

King D. I., DeGraaf R. M., Griffin C. R. a Maier T. J., 1999: Do predation rates on artificial nests accurately reflect predation rates on natural bird nests? *Journal of Field Ornithology 70 (2):* 257 – 262.

Korpimäki, E., Norrdahl, K., Huitu, O. & Klemola, T. 2005: Predator-induced synchrony in population oscillations of coexisting small mammal species. *Procceedings of the Royal Society B 272:* 193 - 202.

Koubová M., Suvorov P., Svobodová J., Albrecht T. & Kreisinger J., 2011: Fragmentation and loss of natural habitats. Chapter 7 in: Daniels J. A. (eds.): *Advances in Environmental Research 14.* Nova Science Publishers Inc.

Lahti D. C., 2001: The „edge effect on nest predation" hypothesis after twenty years. *Biological Conservation 99:* 365 – 374.

Larivière S., 1999: Reasons why predators cannot be inferred from nest remains. *The Condor 101:* 718 – 721

Lidicker W. Z. Jr., 1999: Responses of mammals to habitat edges: an overview. *Landscape Ecology 14:* 333 - 343.

Lindström E. R., Andrén H., Angelstam P., Cederlund G., Hörnfeldt B., Jöderberg L., Lemnell P. A., Martinsson B., Sköld K. & Swenson J. E., 1994: Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. *Ecology 75(4):* 1042 – 1049.

Major R. E. & Kendal C. E. 1996: The contribution of artificial nests experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis 138:* 298 - 307.

Marcström V., Kenward R.E. & Engren E. 1988: The impact of predation on boreal tetraonids during vole cycles: an experimental study. *Journal of Animal Ecology 57:* 859 - 872.

Marini M. A., Robinson S. K. & Heske E. J., 1995: Edge effects on nest predation in the Shawnee – national – forest, Southern Illinois. *Biological Conservation 74 (3):* 203 – 213.

Martin T. E., 1987: Artificial nest experiments: effects of nest appearance and type of predator. *The Condor 89:* 925 – 928.

Martin T. E., 1993: Nest predation and nest sites: new perspectives on old patterns. BioScience 43: 523 - 532.

Martin J. – L. & Joron M, 2003.: Nest predation in forest birds: Influence of predator type and predator´s habitat quality. *Oikos 102:* 641 – 653.

Matthews A., Dickman C. R. & Major R. E., 1999: The influence of fragment size and edge on nest predation in urban bushland. *Ecography 22:* 349 – 356.

Montevecchi W. A., 1976: Egg size and the egg predatory behaviour of crows. *Behaviour 57:* 307 - 320.

Moss R. & Watson A., 2001: Population cycles of the grouse family (*Tetraonidae*). *Ecologhical Research 32:* 53 - 111.

Pangau-Adam M. Z., Waltert M. & Muhlenberg M., 2006: Nest predation risk on ground and shrub nests in forest margin areas of Sulawesi, Indonesia. *Biodiversity and Conservation 15 (13):* 4143 – 4158.

Pärt T. & Wretenberg J., 2002: Do artificial nests reveal relative nest predation risk for real nests? *Journal of Avian Biology 33:* 39 – 46.

Pasinelli G. & Schiegg K., 2006: Fragmentation within and between wetland reserves: the importance of spatial scales for nest predation in reed buntings. *Ecography 29:* 721 – 732.

Ratti J. T. & Reese K. P., 1988: Preliminary test of the ecological trap hypothesis. *Journal of Wildlife Management 52:* 484 - 491.

Ries L. & Sisk T. D., 2004: A predictive model of edge effects. *Ecology 85 (11):* 2917 – 2926.

Ricklefs R. E., 1969: An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology 9:* 1 - 48.

Sádlo J. & Bufková I., 2002: Vegetace Vltavského luhu na Šumavě a problém reliktních praluk. *Preslia Praha 74:* 67 – 83.

Santos T. & Telleria J. L., 1992: Edge effects on nest predation in Mediterranean fragmented forest. *Biological Conservation 60:* 1 - 5.

Schiegg K., Eger M. & Pasinelli G. 2007: Nest predation in Reed Buntings (*Emberiza schoeniclus*): an experimental study. *Ibis 149:* 365 – 373.

Sieving K. E., Willson M. F., 1999: A temporal shift in Steller's Jay predation on bird eggs. *Canadian Journal of Zoology 77:* 1829 - 1834.

Small R. J., Marcström V. & Willebrand T., 1993: Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography 16:* 360 – 364.

Soderström B., Pärt T. & Ryden J., 1998: Different predator faunas and nest predation risk on

ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia 117:* 108 - 118.

Šťastný K. & Hudec K., 2011: *Fauna ČR. Aves III/2.* pp 1189. Academia Praha.

Storch I., 1991: Habitat fragmentation, nest site selection, and nest predation risk in Capercaillie. *Ornis Scandinavica 22:* 213 - 217.

Storch I., Woitke E. & Krieger S., 2005: Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe. *Landscape Ecology 20:* 927 – 940.

Suvorov P., Svobodová J., Koubová M. & Dohnalová L., 2012: Ground nest depredation by European Black-billed Magpies *Pica pica*: an experimental study with artificial nests. *Acta Ornithologica 47 (1):* 55 - 61.

Svobodová J., Kreisinger J., Šálek M., Koubová M. & Albrecht T., 2011: Testing mechanistic explanations for mammalian predator responses to habitat edges. *European Journal of Wildlife Research. 57 (3):* 467 – 474.

Svobodová J., Koubová M., Mrštný L., Albrecht T. & Kreisinger J., 2012: Temporal variation in nest predation risk along habitat edges between grassland and secondary forest in Central Europe. *European Journal of Wildlife Research 58:* 315 – 323.

Teunissen W., Schekkerman H., Willmes F. & Majoor F., 2008: Indentifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis, 150 (Suppl. 1):* 74 – 85.

Thompson F. R. & Burhans D. E., 2004: Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. *Conservation Biology 18 (2):* 373 – 380.

Trnka A., Batáry P. & Prokop P., 2009: Interacting effects of vegetation structure and breeding patterns on the survival of Great Reed Warbler *Acrocephalus arundinaceus* nests. *Ardea 97 (1):* 109 – 116.

Vickery P. D., Hunter M. L. Jr. & Wells J. V., 1992: Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos 63:* 281 - 288.

Villard M.-A. & Pärt T., 2004: Don´t put all your eggs in real nests: a sequel to Faaborg. *Conservation Biology 18 (2):* 371 – 372.

Wallander J., Isaksson D. & Lenberg T., 2006: Wader nest distribution and predation in relation to man – made structures on coastal pastures. *Biological conservation 132:* 343 – 350.

Wegner J. F. & Merriam G., 1979: Movements by birds and small mammals between a wood and adjoining farmland habitats. *Journal of Applied Ecology 16 (2):* 349 – 357.

Weidinger K., 2001: How well do predation rates on artificial nests estimate predation on natural passerine nests? *Ibis 143:* 632 – 641.

Wilcove D. W., McLellan C. H. & Dobson A. P., 1986: Habitat fragmentation in the temperate zone. pp 237 - 256 In: Soulé, M. E (ed.): *Conservation biology: the science of scarcity and diversity.* Sinauer Associates, Sunderland, Massachusetts.

Yahner R. H. & Piergallini N. H., 1998: Effects of microsite selection on predation of artificial ground nests. *Wilson Bulletin 110 (3):* 439 – 442.

Zedler J. B. & Kercher S., 2005: Wetland resources: Status, trends, ecosystem services and restorability. *Annual Review of Environment and Resources 30:* 39 – 74.

Table 1. Analysis of transition zones between wetland and forest for all three seasons (n = 312).

| Variable	DF	χ^2	P
Habitat type	1	7.07	**0.01**
Year	2	14.77	**< 0.001**
Nest position	1	1.83	0.18
Habitat type : year	2	1.66	0.44
Habitat type : nest position	1	7.61	**0.01**
Nest position: year	2	14.48	**< 0.001**
Nest position: habitat type : year	2	4.51	0.11

Table 2. Analysis of transition zones between wetland and forest for particular years

Variable	DF	χ^2	P	DF	χ^2	P	DF	χ^2	P
		2005			**2006**			**2007**	
Habitat type	1	1.48	0.22	1	6.94	0.008	1	0.22	0.64
Nest position	1	13.36	**< 0.001**	1	2.65	0.10	1	0.03	0.85
Habitat type : nest position	1	0.55	0.46	1	10.84	**0.001**	1	0.15	0.70

**Table 3.** Analysis of transition zones between wetland and meadow for all three seasons (n = 354).

| Variable	DF	χ^2	P
Habitat type	1	2.33	0.13
Year of the installation	2	4.4	0.13
Nest position	1	10.00	**0.002**
Habitat type : year of the installation	2	2.13	0.34
Habitat type : nest position	1	2.6	0.15
Nest position: year of the installation	2	4.72	0.09

Figure 1. Predation rate of artificial ground nests in the forest group in particular years.
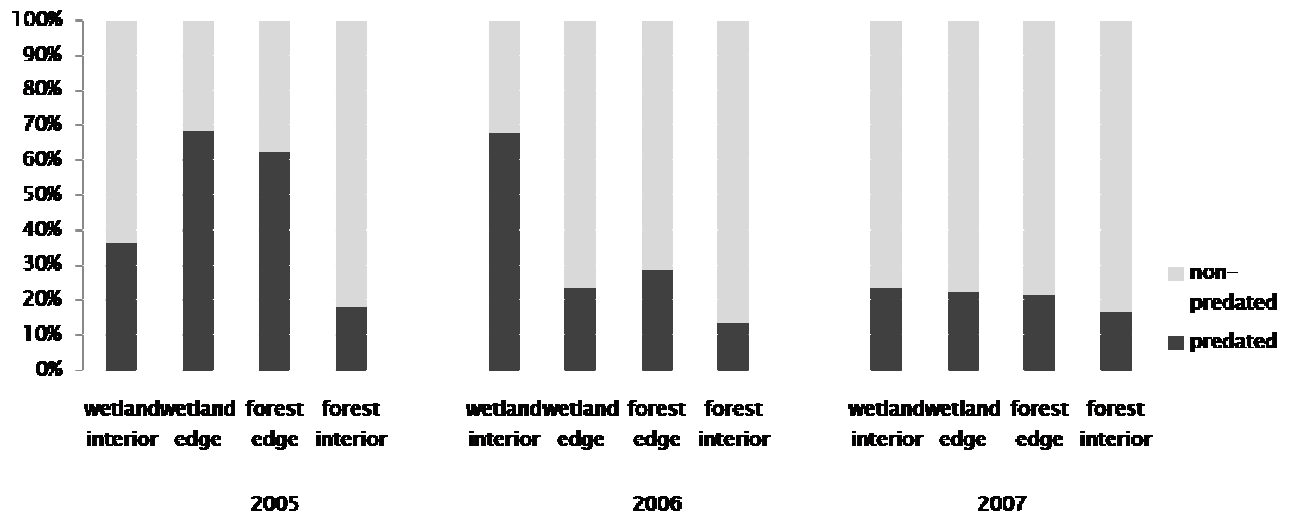
Figure 2. Predation rate of artificial ground nests in the meadow group in all studied years.
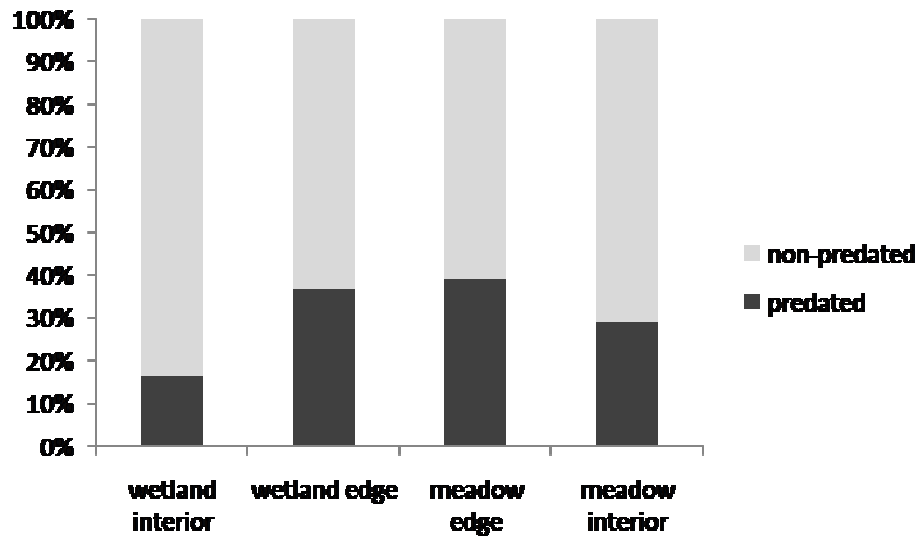
Figure 3. Predation rate of the artificial shrub nests on the transition from interior wetland to its border with adjacent meadows.

V.
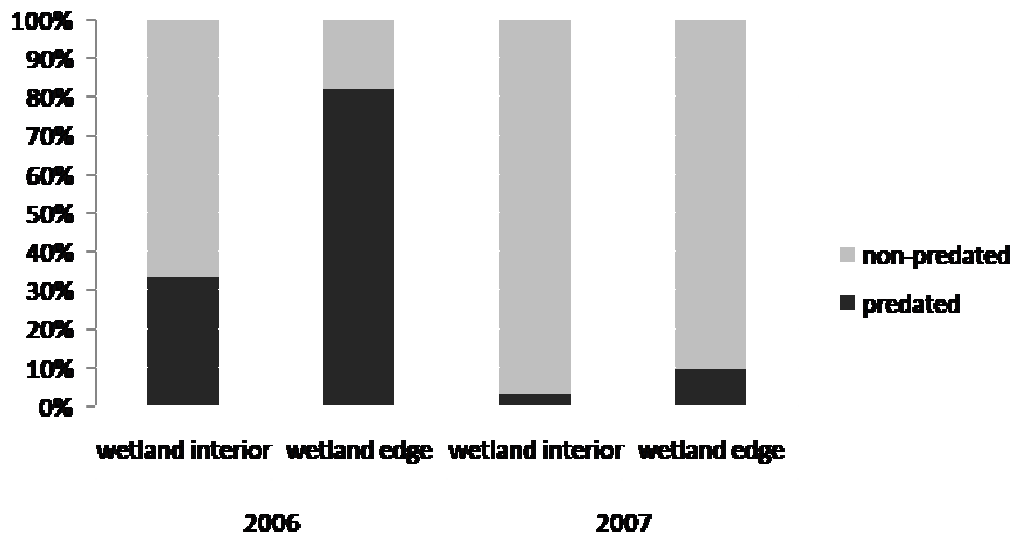
Suvorov P., Svobodová J., Koubová M. & Dohnalová L., 2012: **Effect of quail and chicken eggs on predation by European Black-billed Magpie** *Pica pica.* *Acta Ornithologica 47 (1): 55 - 61.*

Ground nest depredation by European Black-billed Magpies *Pica pica*: an experimental study with artificial nests

Petr SUVOROV, Jana SVOBODOVÁ, Martina KOUBOVÁ & Lucie DOHNALOVÁ

Department of Ecology, Faculty of Environmental Science, Czech University of Life Sciences, Kamýcká 129, 165 21 Prague 6, CZECH REPUBLIC, e-mail: svobodovajana@fzp.czu.cz

Abstract. Nest characteristics can significantly affect specific behaviour of predators during nest depredation, such as relating to nest searching, manipulating and eating eggs. However, the effect of egg size and coloration on behaviour of avian predators rarely has been quantified. Since the European Black-billed Magpie *Pica pica* is regarded as an important nest predator in suburban areas, we studied the effect of different types of artificial ground nests — baited with chicken and quail eggs — on predation probability by magpie. In addition, to compare temporal changes in magpie predation, experimental clutches were installed at 39 active magpie nests in two breeding stages: incubation stage and stage of nestling feeding. In our experiment, magpies detected almost all artificial nests at both breeding stages. However in contrast to our prediction, nests were preferentially depredated at the first stage. This probably was due to the change of magpie foraging preference to invertebrates as a main food of nestlings. Furthermore, we found that predation rate did not differ between real and wax eggs, suggesting that magpies are not able to discriminate between them. Whereas quail eggs were carried away, chicken eggs were consumed in the nest where remnants of egg shell and egg content were left. Obviously, the possibility to immediately carry the egg away increases food attractiveness for magpies. Therefore, we conclude that chicken eggs are more suitable for identification of middle-sized avian predators than quail eggs.

Key words: artificial nest, bird predator, predator-generalist, suburban area

Received — Jan. 2012, accepted — June 2012

INTRODUCTION

In Europe, corvids comprise an important group of nest predators in anthropogenic landscapes (Jokimäki & Huhta 2000, Albrecht 2004). Their densities usually increase near human settlements due to such additional food resources as garbage, waste materials or animal cadavers along roads (Jerzak 2001, Anton & Atanasova 2002, Marzluff & Neatherlin 2006). Although many studies have suggested that corvids negatively impact on bird populations in urban areas (e.g. Møller 1988, Groom 1993, Roos 2002, Šálek 2004), no direct link has been shown between the dynamics of corvid populations and the rate of nest predation (Gooch et al. 1991). This is probably due to the fact that most studies have failed to reliably determine species of nest predators. Therefore, they have not been able to evaluate the effect of particular species on nest predation (Danielson et al. 1997, Maier & DeGraaf 2000, Šálek 2004, Thompson &

Burhans 2004). Moreover, if predators completely remove particular eggs or whole clutches without leaving evidence of predation events (i.e. egg remains, predator's footprints, hair and feathers), a possibility of reliable estimation of total predation risk is precluded. In the case of crows, for instance, it has been found that they are able to remove up to 75% of both natural and artificial eggs while leaving no traces (Fjeld & Sonerud 1984, Schaefer 2004). Though such behaviour has been recorded in many other species (Maier & DeGraaf 2000, Rangen et al. 2000, Mazgajski & Rejt 2005, Weidinger 2010), it has not been quantified in particular predators.

Artificial nests are frequently used in various types of studies (e.g. behavioural, Olsen & Schmidt 2004; landscape, Andrén & Angelstam 1988, Yahner & Mahan 1996, Davison & Bollinger 2000), even though some researchers have doubts about their applicability, mainly due to their insufficiency in simulating predation rate on natural

nests (Jobin & Picman 2002, Pärt & Wretenberg 2002). Nevertheless, this approach is still accepted as a useful tool for relative comparison of nest predation (Grégoire et al. 2003), predator identification (Gustaffson 2005, Purger et al. 2008), and behaviour (Maier & DeGraaf 2000, Purger et al. 2004a) because analogous experiments on natural nests are time-consuming and, in particular, methodologically difficult (Burke et al. 2004). Predation risk usually differs interspecifically due to nest visibility caused by different nest position, parental behaviour, clutch size, and eggs coloration (Jokimäki & Huhta 2000, Martin et al. 2000, King & DeGraaf 2006, Castilla et al. 2007). Hence, the use of artificial nests containing eggs of similar size and colour makes it possible to separate these effects.

The main aim of our study was to evaluate effects of different experimental clutches (quail and chicken) on the rate of predation and predation behaviour of Eurasian Black-billed Magpie *Pica pica* (thereafter magpie). Since carrying away chicken eggs is more complicated than smaller quail eggs, we assumed that magpies would more frequently depredate quail clutches. We also tested whether predation rate changes between different nesting stages (the incubation stage and stage of nestling feeding) of the predator. We assumed that breeding birds could find artificial nests within a shorter time during the stage of nestling feeding than in the incubation stage because they would search for food more intensively (Ottvall et al. 2005). In addition, they can memorize the place of easily accessible food (clutch position) (e.g. Angelstam 1986, Sonerud & Fjeld 1987, Danielson et al. 1997, Roos 2004) and thus they would arrive to the experimental clutches within a shorter time in the stage of feeding the nestlings if a previous predation attempt was successful (Willebrand & Marcström 1988, Weidinger & Kočvara 2010).

MATERIALS AND METHODS

Study area
Magpie observation was conducted in suburban areas of Prague, Czech Republic (50°4′–50°7′N, 14°19′–14°42′E; ca 400 km^2; average altitude 200–250 m a.s.l.). The study areas were composed of residential buildings with gardens and solitary trees (50%), farmland (35%), and park forests (15%). The farmland mostly consisted of cultivated fields that were segmented by forest patches

and line habitats along roads and draining channels. The forest growths of suburban parks were typically dominated by oaks *Quercus* ssp., lindens *Tilia* ssp., Norway Spruce *Picea abies* and Scots Pine *Pinus sylvestris*. Tree canopy of line habitats usually consisted of fruit trees *Malus* sp. and *Pyrus* sp., as well as such broadleaved tree species as poplars *Populus* ssp., birches *Betula* ssp., and ashes *Fraxinus* ssp.

Magpie observation
Magpie nest depredation behaviour was examined using artificial nests. In April 2008 and 2009, we searched for active magpie nests, i.e. nests occupied by breeding pairs. To compare magpie behaviour toward different types of clutches, one pair of experimental nests (one with quail and one with chicken clutch) was installed at a distance of approximately 50 m from each magpie nest. The distance between experimental clutches was ca 1 m, which enabled simultaneously observing magpie behaviour at each experimental nest.

Each artificial nest was constructed by digging a small ground depression and then lining it with a small amount of dry grass. One nest in each pair was baited with two uniformly brown chicken eggs (chicken nest) and the other with four darkly speckled Japanese quail eggs (quail nest) to adjust for the difference in visibility between chicken and quail eggs. Half of eggs in each experimental nest were filled with wax and anchored in the nest pits with a string and nail. This is a common technique for predator identification which prevents predators from carrying eggs away (e.g. Pasitschniak-Arts & Messier 1995, Söderström et al. 1998). Hereafter, eggs unfilled by wax we will call "real eggs".

To evaluate the effect of nest type on predation by magpie at different breeding stages, pairs of artificial nests were installed twice at each magpie nest, i.e. at the incubation stage (April) and the stage of nestling feeding (May; Hudec et al. 1983, Prokop 2004). Since grass in a suburban area is frequently mowed during the growing season, the nest visibility remains similar during both these breeding stages. To minimize the observer effect on magpie behaviour, experimental nests were installed before daylight. In addition, observation was conducted using binoculars and Cuddeback Digital Capture tree cameras (producer: Non Typical Inc., USA) from concealed places near the experimental nests. We measured the time at which magpies arrived to artificial nests from the beginning of observation, i.e. from the start of

daylight. After a magpie flew away, we checked the artificial nests and magpie behaviour was classified as follows: (i) arrived or did not arrive within five monitored hours (nest detection by magpie), (ii) approached quail or chicken nest first, (iii) chicken and/or quail nest was or was not depredated, and (iv) real chicken and/or quail egg was carried away or depredated at the experimental nest and in its vicinity. A nest was considered depredated if at least one (i.e. real or wax) egg was damaged, removed from the nest bowl, or missing.

Data analysis
Generalized linear mixed models (GLMM; package lme4) were used to analyse magpie behaviour. The time within which magpies arrived to experimental nests was analysed as a response variable with Gaussian error distribution and was log transformed before calculation. Such magpie behaviour as (i) arrived/did not arrive, (ii) approached/did not approach first, (iii) predated/did not predate, (vi) carried away/did not carry away were fitted as dependent variables with binomial distribution. In all models, nest type (quail vs. chicken), year, nesting stage (incubation vs. feeding of nestlings) and interactions between these effects were included as fixed effects. Since two pairs of experimental nests were installed within two nesting stages at each magpie nest (locality), the factor locality was included as a random effect.

In all analyses, the significance of particular explanatory variables and their two-way interactions was calculated by change of deviance between the model containing the particular term and the reduced model (deletion tests; Crawley

2007). The best minimal adequate model (MAM; i.e. that model with lowest parsimony and all variables being significant) was achieved by backward elimination of non-significant effects (p>0.05). All analyses were performed in R 2.12.1. software (R Development Core Team 2008).

RESULTS

In total during two nesting stages, 78 pairs of experimental nests were placed at 39 different magpie nests (34 and 44 pairs in 2008 and 2009 respectively). In nine cases (11.5%; 5x in the incubating stage, 4x in the stage of feeding nestlings) magpies did not find artificial nests. Detection (i.e. found or did not find) of experimental nests by magpies did not differ between years and nesting stages.

The mean time in which magpies arrived to the experimental nests was 21.41 ± 6.22 min, and this did not change between years and nesting stages. The birds preferentially approached the quail nests before they did the chicken nests (66.7% vs. 33.3%; Table 1), and their behaviour in this respect did not differ between years and breeding stages (Table 1).

Overall nest predation (i.e. quail plus chicken nests) was 32.4% and 42.1% in 2008 and 2009, respectively. In seven cases (18.0%), the magpie only arrived to the nests and robbed neither real nor wax eggs (1x in the incubating stage, 6x in the stage of feeding nestlings). Although predation occurrence by magpies did not differ between years, artificial nests were depredated more frequently during the incubation stage (32.7%) than in the stage of feeding nestlings (24.4%; Table 1).

Table 1. Effects of nest type and breeding stage on the preference (approached first), probability if egg was carried away or depredated at the experimental nest and predation of artificial ground nests by magpie respectively. Models are based on GLMM modelling with magpie nest (locality) treated as random effect (n = 39).

Model parameters	estimate	SE	z	p
Approached first				
Intercept	0.103	0.227	0.454	0.651
Nest type = chicken	-1.307	0.352	-3.716	< 0.001
Nest type = quail	0			
Nest predation				
Intercept	0.636	0.238	2.672	0.008
Breeding stage = feeding	-0.687	0.329	-2.092	0.036
Breeding stage = incubation	0			
Carry out of the eggs				
Intercept	0.154	0.227	0.679	0.497
Egg type = chicken	-4.498	1.032	-4.359	< 0.001
Egg type = quail	0			

Magpies depredated quail nests more frequently (n = 50) than chicken nests (n = 39), but the factor nest type was nevertheless non-significant. Since wax eggs are not edible, we also tested the effect of egg type in the sense of its edibility. However, no difference was found in predation between real and wax eggs ($\chi^2 = 1.44$, $\Delta DF = 1$, p = 0.229).

The probability of magpies carrying away eggs from the experimental nest did not differ between years and nesting stages. Egg type was the single significant factor in the model (Table 1). From all depredated real eggs, all chicken eggs were eaten near the experimental nest, whereas most quail eggs (84.0%) were carried away without any trace.

DISCUSSION

The magpie is usually regarded as an important nest predator in urban and suburban areas (Møller 1988, Groom 1993, Chiron & Julliard 2007, Newson et al. 2010). Though previous studies have failed to reliably identify nest predators, they have revealed that shrub passerine nests and artificial ground nests had lower survival rates in the vicinity of magpie nests than in areas where magpies were absent (Møller 1988, Šálek 2004). In our experiment, magpies detected almost all artificial nests at both breeding stages (nest incubation and nestling feeding). This is not a surprising result, because both nest types were well-visible for such visually oriented predators as corvids (Huhta et al. 1996). Cases when magpies arrived to artificial nests but did not eat the eggs were probably caused by the birds being disrupted rather than due to the inedibility of wax eggs, because in the urban area where our experiment was conducted human activities are frequent. In addition, a magpie is not able to discriminate between a real and wax egg because predation rate did not differ between them.

We also found no difference between breeding stages in magpie arrivals to artificial nests, although corvids can memorize the position of a nest and return to the same place to repeat its depredation (Danielson et al. 1997, Roos 2004, Weidinger & Kočvara 2010). Moreover, in contrast to our prediction, the rate of nest predation was higher during the incubation stage than in the stage of feeding nestlings. This discrepancy is probably associated with changes in magpie food preferences during the breeding stage rather than with its ability to memorize (Tatner 1983), because, whereas magpie adults are typically omnivorous

predators (Andrén 1992), invertebrates predominate in the diet of magpie nestlings (up to 80%; mainly Orthoptera, Colleoptera, Lepidoptera, and Diptera; Ponz et al. 1999, Jerzak 2001). Thus, breeding birds feeding their nestlings may preferentially search for invertebrates at this stage (Martínez et al. 1992).

Intensity of nest predation can be associated mainly with nest visibility, predator activity and prey availability (e.g. Nisbet 1975, Yahner & Cypher 1987, Sieving & Willson 1999, Roos 2004), and according to these factors predation can significantly vary during the breeding season (Bátary et al. 2004). As in other studies, we found higher nest predation by magpies early in the incubation stage than in the nestling stage which is usually attributed to lower vegetation cover and thus to poorer nest concealment against predators (Beauchamp et al. 1996, Bátary et al. 2004). Visibility of our artificial nests was similar in both breeding stages, however, because grass plots in residential areas are regularly mowed during the growing season. We believe that the difference in nest predation is mainly related to food availability. Although we did not investigate food availability in our study, density of insects for magpie nestlings can be limited in suburban areas due to a lack of suitable habitats, i.e., of grass plots (Robinson 2005, Chace & Walsh 2006, Ahrné 2008). Adults may thus spend more time in searching for invertebrates at different localities, such as nearby surrounding farmlands, and may ignore different kind of food (e.g. bird eggs) which is difficult to transport to the nest.

Our results explicitly confirmed an effect of different nest type on magpie behaviour in predating nests. Whereas chicken eggs were consumed at the nest or in its immediate vicinity, quail eggs were carried away. In addition, magpies preferentially approached first to the quail nest versus the chicken nest. Obviously, the possibility of the immediate carrying of the egg away increases food attractiveness in magpies and in other corvid species (Montevecchi 1976, Olsen & Schmidt 2004, Schaefer 2004). This predation behaviour apparently enables the birds to avoid conflict with the incubating parents (Purger et al. 2004a), food loss due to other competitors (e.g. harriers or buzzards), and being killed by other predators (Fjeld & Sonerud 1988).

In many species of nest predators (mammals, birds, reptiles), it has been documented that the animals can completely remove an entire clutch from the nest while leaving no evidence of their

identity (Larivière 1999). That impedes the reliability of predation rate estimation and predator species determination (Burke et al. 2004). Despite this fact, predator behaviour toward different types of clutches in particular has been studied mainly in small rodents (DeGraaf & Maier 1996, Maier & DeGraaf 2000, Purger et al. 2004b). In contrast to small passerine eggs, small rodents are not able to bite through quail shell (DeGraaf et al. 1999, Pärt & Wretenberg 2002). This indicates that quail eggs are not applicable for such studies in areas with prevalence of rodent predators. On the other hand, our data show that eggs of larger size (chicken eggs) may be useful for determination of middle-sized bird predators (Jays *Garrulus glandarius* and magpies) because they mostly forage chicken eggs in the nest and egg remnants are used for predator detection (Marini & Melo 1998, but see Söderström et al. 1998). In our previous experiments from a different locality, for example, we found that from 174 depredated quail nests, predators were determined in only two events (one was ascribed to a bird), yet eggs were regularly fixed to the ground by nail and string. Within 119 depredated chicken clutches, however, 33 events were ascribed to birds and 17 to mammalian predators (P. Suvorov — unpublished data).

Among corvids and other bird species, it has been observed that they are able to remove eggs large in comparison to their body size by pecking a hole into the egg shell (Montevecchi 1976, Moksnes et al. 1991). Although we did not observe this behaviour in magpies, we have no reason to assume that magpies have not evolved it. Probably, the frequent possibility of intrusion by human activities into our study area may have lead birds to avoid food objects of larger size because manipulation with larger food objects is more time-demanding. Although manipulating with chicken eggs must be more difficult than with quail eggs, we nevertheless found only marginally significant difference in predation risk between chicken and quail clutches. Moreover, a similar pattern was revealed also in our previous experiment (Svobodová et al. 2012). We believe, therefore, that chicken clutches comprise a convenient experimental tool for relative comparison of nest predation in areas with prevalence of middle-sized predators, but further research is needed using an experimental design different than that in our study.

In conclusion, we found that Black-billed Magpies depredated artificial nests more intensively early in the breeding season. This can be attributed to change of magpie foraging preference. Whereas chicken eggs were consumed in the vicinity of experimental clutches, quail eggs were carried away. Since remnants of depredated chicken eggs usually were left near experimental nests, chicken clutches appear to be more suitable for identifying middle-sized avian predators than are quail nests.

REFERENCES

Ahrné K. 2008. Local management and landscape effects on diversity of bees, wasps and birds in urban green areas. Doctoral Thesis. Acta Universitatis Agriculturae Sueciae. Sweedish University of Agricultural Sciences.

Albrecht T. 2004. Edge effect in wetland — arable land boundary determines nesting success of Scarlet Rosefinch (*Carpodacus erythrinus*) in the Czech republic. Auk 121: 361–371.

Andrén H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73: 794–804.

Andrén H., Angelstam P. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 60: 544–547.

Angelstam P. 1986. Predation on ground-nesting birds´ nests in relation to predator densities and habitat edge. Oikos 47: 365–373.

Antonov A., Atanasova D. 2002. Nest-site selection in the Magpie *Pica pica* in a high-density urban population of Sofia (Bulgaria). Acta Ornithol. 37: 55–66.

Batáry P., Winkler H., Báldi A. 2004. Experiments with artificial nests on predation in reed habitats. J. Ornithol. 145: 59–63.

Beauchamp W. D., Koford R. R., Nudds T. D., Clark R. G., Johnson D. H. 1996. Long-term declines in nest success of prairie ducks. J. Wild. Manage. 60: 247–257.

Burke D. M., Elliott K., Moore L., Dunford W., Nol E., Phillips J., Holmes S., Freemark K. 2004. Patterns of nest predation on artificial and natural nests in forests. Conserv. Biol. 18 (2): 381–388.

Castilla A. M., Dhondt A. A., Uriarte R. D., Westmoreland D. 2007. Predation in ground-nesting birds: An experimental study using natural egg — color variation. Avian Conserv. Ecol. 2: 2, http://www.ace-eco.org/vol2/iss1/art2

Chace J. F., Walsh J. J. 2006. Urban effects on native avifauna: A review. Landscape Urban Plan. 74: 46–69.

Chiron F., Julliard R. 2007. Responses of songbirds to magpie reduction in an urban habitat. J. Wildl. Manage. 71: 2624–2631.

Crawley M. J. 2007. The R Book. Wiley & Sons, Chichester, UK.

Danielson W. R., DeGraaf R. M., Fuller T. K. 1997. Rural and suburban forest edges: Effect on egg predators and nest predation rates. Landscape Urban Plan. 38: 25–36.

Davison W. B., Bollinger E. 2000. Predation rates on real and artificial nests of grassland birds. Auk 117: 147–153.

DeGraaf R. M., Maier T. J. 1996. Effect of egg size on predation by White–footed Mice. Wilson Bull. 108: 535–539.

DeGraaf R. M., Maier T. J., Fuller T. K. 1999. Predation of small eggs in artificial nests: effects of nest position, edge and potential predator abundance in extensive forest. Wilson Bull. 111: 236–242.

Fjeld P. E., Sonerud G. A. 1984. [Identification of predators of tetraonid nests — the experiment with artificial nests]. Nord. Viltforskerkongress: 32–35. Kalo, Denmark.

Fjeld P. E., Sonerud G. A. 1988. Food caching, cache recovery, and the use of an egg shell dump in Hooded Crows Corvus corone cornix. Ornis Scand. 19: 268–274.

Gooch S., Baillie S. R., Birkhead T. R. 1991. Magpie *Pica pica* and songbird populations. Retrospective investigations of trends in population density and breeding success. J. Appl. Ecol. 28: 1068–1086.

Grégoire A., Garnier S., Dréano N., Faivre B. 2003. Nest predation in Blackbirds (*Turdus merula*) and the influence of nest characteristics. Ornis Fennica 80: 1–10.

Groom D. W. 1993. Magpie *Pica pica* predation on Blackbird *Turdus merula* nests in urban areas. Bird Study 40: 55–62.

Gustafson T. 2005. Nest predation in birds — important concepts and methodological problems. Introductory Research Essay 22. Department of Conservation Biology SLU Uppsala.

Hudec K. (ed.). 1983. [Fauna ČSSR vol. 24, Ptáci — Aves, III/2]. Akademia, Praha.

Huhta E., Mappes T., Jokimaki J. 1996. Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. Ecography 19: 85–91.

Jerzak L. 2001. Synurbanization of the Magpie in the Palearctic. In: Marzluff J. M., Bowman R., Donnelly R. (eds.). Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publishers. pp. 403–425.

Jobin B., Picman J. 2002. Predation on artificial nests in upland habitats adjacent to freshwater marshes. Am. Midl. Nat. 147: 305–314.

Jokimäki J., Huhta E. 2000. Artificial nest predation and abundance of birds along an urban gradient. Condor 102: 838–847.

King D. I., DeGraaf R. M. 2006. Predators at bird nests in a northern hardwood forest in New Hampshire. J. Field Ornithol. 77: 239–243.

Larivière S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101: 718–721.

Maier T. J., DeGraaf R. M. 2000. Predation on Japanese Quail vs. House Sparrow eggs in artificial nests: Small eggs reveal small predators. Condor 102: 325–332.

Marini M. A., Melo C. 1998. Predators of quail eggs, and the evidence of the remains: Implications for nest predation studies. Condor 100: 395–399.

Martin T. E., Scott J., Menge C. 2000. Nest predation increases with parental activity: Separating nest site and parental activity effects. Procceedings: Biol. Sci. 267: 2287–2293.

Martínez J. G., Soler M. Soler J. J., Paracuellos M., Sánchez J. 1992. [Alimentation of the nestlings of Black-billed Magpie (*Pica pica*) in relation to the age and availability of the prey]. Ardeola 39: 35–48.

Marzluff J. M., Neatherlin E. 2006. Corvid response to human settlements and campgrounds: Causes, consequences and challenges for conservation. Biol. Conserv. 130: 301–314.

Mazgajski T. D., Rejt Ł. 2005. Forest fragment size affects edge effect in nest predation — experiment with artificial nests. Pol. J. Ecol. 53: 233–242.

Moksnes A., Røskaft E., Braa T. A. 1991. Rejection behavior by Common Cuckoo hosts towards artificial brood parasite eggs. Auk 108: 348–354.

Møller A. P. 1988. Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of Magpies and Blackbirds. Oikos 53: 215–221.

Montevecchi W. A. 1976. Egg size and the egg predatory behaviour of crows. Behaviour 57: 307–320.

Newson S. E., Rexstad E. A., Baillie S. R., Buckland S. T., Aebischer N. J. 2010: Population change of avian predators and grey squirrels in England: Is there evidence for an impact on avian prey populations? J. Appl. Ecol. 47: 244–252.

Nisbet I. C. T. 1975. Selective effects of predation in a tern colony. Condor 77: 221–226.

Olsen H., Schmidt N. M. 2004. Response of Hooded Crow *Corvus corone cornix* and Magpie *Pica pica* to exposure to artificial nest. Bird Study 51: 87–90.

Ottvall R., Larsson K., Smith H. G. 2005. Nesting success in Redshank *Tringa totanus* breeding on coastal meadows and the importance of habitat features used as perches by avian predators. Bird Study 52: 289–296.

Pärt T., Wretenberg J. 2002. Do artificial nests reveal relative nest predation risk for real nests? J. Avian Biol. 33: 39–46.

Pasitschniak-Arts M., Messier F. 1995. Risk of predation on waterfowl nests in the Canadian prairies: Effects of habitat edges and agricultural practices. Oikos 73: 347–355.

Ponz A., Gil-Delgado J. A., Barba E. 1999. Factors affecting prey preparation by adult magpies feeding nestlings. Condor 101: 818–823.

Prokop P. 2004. The effect of nest usurpation on breeding success of the Black-billed Magpie *Pica pica*. Biologia (Bratislava) 59: 213–217.

Purger J. J., Csuka S., Kurucz K. 2008. Predation survival of ground nesting birds in grass and wheat fields: Experiment with plasticine eggs and artificial nests. Pol. J. Ecol. 56: 481–486.

Purger J. J., Mészáros L. A., Purger D. 2004a. Predation on artificial nests in post-mining recultivated area and forest edge: Contrasting the use of plasticine and quail eggs. Ecol. Eng. 22: 209–212.

Purger J. J., Mészáros L. A., Purger D. 2004b. Ground-nesting in recultivated forest habitats — a study with artificial nests. Acta Ornithol. 39: 141–145.

R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/

Rangen S. A., Clark R. G., Hobson K. A. 2000. Visual and olfactory attributes of artificial nests. Auk 117: 136–146.

Robinson W. H. 2005. Urban insects and arachnids. A handbook of urban entomology. Cambridge University Press.

Roos S. 2002. Functional response, seasonal decline and landscape differences in nest predation risk. Oecologia 133: 608–615.

Roos S. 2004. Nest predation processes and farmland birds. Habitat selection and population dynamics of predators and prey. PhD thesis, Swedish University of Agricultural Sciences.

Schaefer T. 2004. Video monitoring of shrub-nests reveals nest predators. Bird Study 51: 170–177.

Sieving K. E., Willson M. F. 1999. A temporal shift in Steller's Jay predation on bird eggs. Can. J. Zool. 77: 1829–1834.

Söderström B., Pärt T., Ryden J. 1998. Different predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. Oecologia 117: 108–118.

Sonerud G. A., Fjeld P. E. 1987. Long-term memory in egg predators: an experiment with a Hooded Crow. Ornis Scand. 18: 323–325.

Svobodová J., Koubová M., Mrštný L., Albrecht T., Kreisinger J. 2012. Temporal variation in nest predation risk along habitat edges between grassland and secondary forest in Central Europe. Eur. J. Wildlife Res. 58: 315–323.

Šálek M. 2004. The spatial pattern of the Black-billed Magpie, *Pica pica* to predation risk on dummy nests. Folia Zool. 53: 57–64.

Tatner P. 1983. The diet of urban Magpies *Pica pica*. Ibis 125: 90–107.

Thompson F. R., Burhans D. E. 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. Conserv. Biol. 18: 373–380.

Weidinger K. 2010. Foraging behaviour of nest predators at open-cup nests of woodland passerines. J. Ornithol. 151: 729–735.

Weidinger K., Kočvara R. 2010. Repeatability of nest predation in passerines depends on predator species and time scale. Oikos 119: 138–146.

Willebrand T., Marcström V. 1988. On the danger of using dummy nests to study predation. Auk 105: 378–379.

Yahner R. H., Cypher B. L. 1987. Effects of nest location on depredation of artificial arboreal nests. J. Wildl. Manage. 51: 178–181.

Yahner R. H., Mahan C. G. 1996. Effects of egg type on depredation of artificial ground nests. Wilson Bull. 108: 129–136.

STRESZCZENIE

[Drapieżnictwo sroki na sztucznych gniazdach zawierających jaja kurze i przepiórcze]

Charakterystyka gniazd ptaków może w istotny sposób wpływać na zachowanie drapieżników rabujących gniazda — na wyszukiwanie przez nie gniazd i sposób ich rabowania. Natomiast jak dotąd związek wielkości i kolorystyki jaj znajdujących się w gnieździe z drapieżnictwem jest słabo poznany. W pracy badano wpływ dwóch rodzajów sztucznych gniazd — z jajami kurzymi i przepiórczymi — na prawdopodobieństwo drapież-nictwa ze strony sroki. Sroka jest uznawana za ważnego drapieżnika gniazd ptasich, szczególnie na terenach podmiejskich. Sztuczne gniazda były umieszczone w parach: gniazdo z czterema jajami przepiórki oraz gniazdo z dwoma jajami kurzymi, w pobliżu 39 gniazd zajętych przez sroki w czasie dwóch okresów sezonu lęgowego tego drapieżni-ka — wysiadywania jaj i karmienia piskląt. Autorzy wykorzystali m.in. bezpośrednie obserwacje zachowań drapieżników w pobliżu sztucznych gniazd. Połowa jaj w sztucznych gniazdach była wypełniona woskiem i przymocowana na stałe do gniazda, celem ułatwienia późniejszej identyfikacji drapieżnika.

W czasie eksperymentu sroki odnalazły prawie wszystkie sztuczne gniazda, choć szybciej odnajdywały gniazda z jajami przepiórczymi (Tab. 1). Gniazda penetrowane były zarówno w okresi, kiedy sroki wysiadywały jaja, jak i gdy karmiły pisklęta, niemniej jednak — w przeciwieństwie do założeń autorów — sroki rabowały sztuczne gniazda częściej w pierwszym z tych okresów (Tab. 1). Wynikało to prawdopodobnie z faktu zmiany diety sroki w okresie karmienia młodych, polegającej na wzroście udziału bezkręgowców. Ponadto stwierdzono, że drapieżnictwo na jajach prawdziwych i jajach wypełnionych woskiem było podobne, co sugeruje, że ptaki nie potrafiły odróżniać tych dwóch typów jaj. Jaja przepiórcze były przez sroki wynoszone z gniazda i konsumowane z dala od niego, podczas gdy jaja kurze były częściej zjedane na miejscu (Tab. 1). Z tego względu wydaje się, że jaja kurze są lepsze do badań drapieżnictwa z wykorzystaniem sztucznych gniazd, ponieważ — ze względu na swoją wielkość — są konsumowane w gnieździe, co daje możliwość identyfikacji drapieżnika w oparciu o resztki jaj i ślady jego obecności.