Karlova Universita v Praze, Přírodovědecká fakulta,
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Distribuce predátorů, riziko predace a antipredační strategie vrubozobých

Disertační práce

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Prohlášení:

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Během posledních pěti let jsem potkal celou řadu lidí kteří mě poskytli radu a nezištnou pomoc při řešení konkrétních problémů, a nebo lidí jejichž existence mě jednoduše těší a tím mě poskytují zásadní oporu. Bohužel je zde nemohu všechny jmenovat a omezím se ty jejichž pomoc přispěla zcela zásadně k vypracování této práce.

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Obsah:

Úvod

Predace je jednou z hlavních příčin mortality u volně žijících populacích (Ricklefs 1969, Martin 1993 Caro 2005) a působí proto jako důležité selekční agens s hlubokými ekologickými a evolučními konsekvencemi (Martin & Li 1992, Bosque & Bosque 1995, Martin & Clobert 1996, Martin et al 2000a, Nosil & Crespi 2006). Práce, kterou předkládám je souborem publikací, zabývajících se různými aspekty predace, antipredačními adaptacemi (Kreisinger & Albrecht 2008) a rizikem predace v souvislosti s mikrohabitatovými preferencemi kořisti (Albrecht et al 2006) počínaje, a ekologickými příčinami a důsledky prostorové distribuce predátorů v elementech krajiny, fragmentované intenzivním zemědělstvím konče (Šálek et al. *in press*, Svobodová et al. *submitted*).

Většina těchto publikací v různé míře a různém úhlu naráží na problematiku predace ptačích hnízd, které jsou jedním z důležitých modelových systémů pro studium obecných aspektů predace. Důvodů pro zájem o tuto problematiku je několik. Hnízdní predace dosahuje u většiny druhů ptáků řádově desítek procent (Rickefs 1969, Martin 1993, Martin & Clober 1996), a patří tak k hlavním faktorům limitujícím jejich reprodukční úspěšnost. Z toho vyplývá i značný evoluční potenciál ovlivňující mnoho aspektů ptačí biologie. Například, mezidruhová variabilita v riziku hnízdní predace se přímo nebo nepřímo odráží v evoluci *life histories* a řadě aspektů reprodukční biologie s tím souvisejících (Arnold et al 1987, Martin et al. 2000a Martin & Li 1992, Bosque & Bosque 1995, Remeš & Martin 2002). Riziko hnízdní predace ovlivňuje i evoluci celé řady antipredačních adaptací (viz Montgomerie & Weatherhead 1988, Caro et al 2005 pro vyčerpávající review). Nezanedbatelné však nejsou ani důsledky problematiky hnízdní predace pro ochranu biodiversity. V souvislosti s antropogenními změnami v uspořádání krajiny (fragmentace biotopů, zvyšováni podílu okrajových biotopů, urbanizace a rozvoj suburbií) dochází ke kvantitativním a kvalitativním změnám ve složení fauny predátorů a ke změnám v jejich prostorové distribuci (Cooks & Soulé 1999, Ryall & Fahrig 2006, Didham et al 2007). To může mít dalekosáhlé důsledky na populace ptáků a přispívat tak spolu s dalšími faktory k populačním poklesům nebo dokonce lokálním extinkcím některých druhů (Robinson et al. 1995, Fahrig 2003, Schmidt 2003). Mechanistické pozadí těchto komplexních biotických interakcích však zůstává stále dosti nejasné (viz. Chalfoun et al. 2002, Ryall & Fahrig 2006).

V následujících odstavcích je šířeji diskutováno teoretické a empirické pozadí některých aspektů predace a antipredačních strategií, které souvisí s výsledky publikací obsažených v této práci. Jednotlivé části úvodu jsou členěny pseudoredukcionisticky, od popisu procesů determinujících pattern predace v měřítku krajiny, až po studie zabývající se vlivem konkrétních antipredačních strategií na hnízdní úspěšnost u jednotlivých druhů (Albrecht et al. 2006, Kreisinger & Albrecht

2008). Naproti tomu, řazení jednotlivých kapitol v hlavní části práce odpovídá subjektivnímu ohodnocení mého osobního vkladu do nich.

Jako apendix přikládám dvě práce (Albrecht, Kreisinger & Piálek 2006, Albrecht et al. 2007) zabývající se tématem, které je také objektem mého poměrně intenzivního zájmu, a to problematikou evoluce mimopárových paternit u ptáků.

1. Vliv struktury krajinny a krajiných elemetů na distribuci predátorů a riziko hnízdní predace

Složení krajiny prošlo v posledních několika desetiletích až století (v závislosti na geografické lokalizaci) dramatickými změnami díky zvýšené intenzitě a pozměněnému způsobu jejího využívání člověkem. Jedním z důsledků těchto změn je fragmentace původních typů habitatů na menší celky a snižování konektivity těchto fragmentů (Fahrig 2003). Současně s tím dochází ke zvětšování rozlohy habitatů, které jsou v důsledku intenzivního využívání pro některé druhy nevhodné (tzv. *matrix).* Populační úbytek v důsledku ztráty vhodných biotopů může být ještě zesílen díky emergentním procesům které jsou s fragmentací krajiny přímo spojeny. Například se snižováním konektivity jednotlivých subpopulací v důsledku fragmentace vhodných biotopů vzrůstá riziko ztráty genetické diversity a inbrední deprese (Frankham 2005). Malé subpopulace jsou navíc vystaveny vyššímu riziku lokání extinkce v důsledku stochastických procesů (Hilty et al. 2006). Ztráta konektivity může mít negativní důsledky i na menším měřítku než je měřítko (sub)populací. Udržení konektivity populací a potažmo i biotopů které tyto druhy využívají bývá proto považováno za jednu z priorit ochrany biodiversity (Hilty et al 2006).

Častou praktickou aplikací konceptu konektivity je budování koridorů které umožňují efektivnější a bezpečnější disperzi jedinců do okolních fragmentů oddělených matrix. Rozsah těchto projektů je různý, od lokálního měřítka, až po snahy o udržení konektivity v rámci celého kontinentu (Passeo Pantera Project; www.afn.org/~wcsfl/pp.htm, Y2Y project; www.y2y.net). Přes přímočarost teorií které stojí v pozadí těchto snah (Brown & Kordic-Brown 1977) je jejich efektivita, vzhledem k vynaloženým finančním nákladům, často zpochybňována. Relevantní data, která by dokládala vliv koridorů na životaschopnost populací většinou chybí. V určitých případech mohou mít koridory i negativní důsledky na populace, které by měly být předmětem jejich ochrany (detailní diskuse viz Hilty et al. 2006). To jsou také asi dva hlavní důvody proč zájem o problematiku koridorů neustále stoupá (lineární korelace mezi počtem článků podle Web of Science obsahujících slova „corridor(s)“ a „ecology“ v názvu, abstraktu nebo klíčových slovech a rokem publikace (od roku 1991 do 2008); $F_{(2,16)} = 46.20$, $p < 0.0001$, $R^2 = 0.743$)

Naše práce "*Corridor versus hayfield matrix use by mammalian predators in an agricultural landscape*" (Šálek et al.: Agriculture, Ecosystems and Environment *in press*) ukazuje, že savčí mezopredátoři silně preferují lineární pásy vzrostlé vegetace před pravidelně kosenými loukami. Tento krajiný prvek tak může v lokálním měřítku zvyšovat konektivitu habitatů využívaných některými středoevropskými druhy šelem v krajině, kde převládá zemědělská matrix, a poskytovat pro ně vhodný biotop. Na rozdíl od jiných studií (Laurance and Laurance 1999, Hilty and Merenlender 2004) ale nebyl na základě našich dat prokázán vliv charakteru vegetace v koridoru (pokryvnost keřového a stromového patra a šířka koridoru) na výskyt cílových druhů.

Životaschopnost populace nemusí být ovlivněna pouze faktory které přímo vyplývají z úbytku vhodných habitatů a jejich fragmentace biotopů (tzv "*single species model*", Ryall & Fahrig 2006, viz výše). Nesrovnatelně obtížněji predikovatelné důsledky na životaschopnost populací může mít změna mezidruhových interakcí v důsledku fragmentace krajiny (Didham et al. 1996, Ryall & Fahrig 2006). Konkrétní populace může například profitovat z lokální extinkce predátora v důsledku fragmetace, který je habitatový specialista a vyžaduje větší home range než jeho kořist (Ryall & Fahrig 2006). Na druhou stranu extinkce specializovaných predátorů může uvolnit niku mesopredátorům s oportunističtějšími habitatovými a potravními preferencemi, a tím pádem i výraznějším efektem na populace kořisti (tzv. "*mesopredator realase hypothesis*", Crooks & Soule 1999, Smith 2003).

Jedním z důsledků těchto mezidruhových interakcí může být tzv. okrajový efekt. V kontextu hnízdní predace to znamená zvýšení rizika predace snůšky v okrajových partiích biotopů v porovnání s jejich interiorem (Andren & Angelstam 1988). Přes jistou nekonzistenci výsledků byl vliv okrajového efektu potvrzen celou řadou studií provedených v různých geografických oblastech (Chalfoun et al. 2002). Okrajový efekt může negativně ovlivňovat reprodukční úspěšnost řady druhů žijících ve fragmentované krajině (Schmidt 2003). Mechanistické pozadí zvýšeného rizika predace v biotopových rozhraních je poměrně nejasné, ale předpokládá se, že vzniká důsledkem prostorové distribuce zdrojů využívaných predátory (Ries et al. 2004, Ries & Sisk 2004).

Ve studii "*The test of mechanistics explanation for mammalian predator responses to habitat edges*" (Svobodová et al.) je testován předpoklad, že distribuce savčích mezopredátorů podél okraje mezi loukou a sekundárním lesem je ovlivněna distribucí drobných hlodavců, kteří představují významnou složku jejich diety (Goszczyński 1986, Lanszki and Heltai 2007). Data presentovná v této práci však nepřináší přesvědčivou podporu pro toto hypotézu. Distribuce savčích predárů podél okraje těchto biotopů vykazovala značnou mezisezónní variabilitu. Zatímco v prvním roce studia nebyly zaznamenány žádné preference pro okrajové struktury, v roce následujícím byla distribuce predátorů v habitatovém rozhraní několikanásobně vyšší než v interioru lesa nebo louky. Abundance drobných hlodavců byla pětinásobně vyšší v druhém roce než prvním, avšak prostorový gradient jejich distribucí nevykazoval konzistentní *pattern* s gradientem v distribuci šelem. V interioru lesa a lesních okrajích byly zaznamenány dvakrát vyšší početnosti hlodavců než v interoru a okraji louky. Okraj lesa přitom vykazoval marginálně nesignifikantně vyšší abundance než zbylé tři typy biotopů (okraj louky a interor lesa a louky). I když poněkud vyšší počty hlodavců na lesních okrajích mohou do jisté míry ovlivnit preference šelem pro tyto biotopy, hlavně v letech s vysokými populačními hustotami myší, distribuce hlodavců podél okraje louka/les neposkytuje v středoevropských podmínkách dostatečné vysvětlení pro vznik okrajového efektu.

2. Vliv antipredačních strategií na riziko hnizdní predace

Následující text se bude vhledem k šířce tématu zabývat poměrně těsně pouze těmi aspekty hnízdní predace a antipredačních strategií, které tématicky souvisí s předkládanými pracemi (Kreisinger & Albrecht 2008, Albrecht et al. 2006). Pokus o vyčerpávající review této problematiky by pouze suploval již existující excelentní práce na dané téma (například Ruxton et al 2004, Caro 2005).

Výběr hnízdního habitatu a riziko predace snůšky: Umístění hnízda a charakter mikrohabitatu v jeho okolí často determinuje pravděpodobnost jeho predace (Kuehl & Clark 2002, Zanette & Jenkins 2000, Martin 1993, Martin & Roper 1988, Clark & Shutler 1999). U řady druhů proto existují mechanismy které vedou k nenáhodnému umístění hnízda vzhledem k charakteru okolního habitatu, čímž je riziko jeho predace sníženo (Martin & Roper 1988, Martin 1993, Badyaev 1995, Clark & Shurler 1999, Wiebe & Martin 1998, Smith et al. 2007, Lloyd et al 2000).

Výběr umístění hnízda však není vždy vyladěn tak, aby bylo riziko predace snůšky minimalizováno (Clark & Shutler 1999, Remeš 2003). Na rozhodnutí o umístění hnízda se může podílet i řada dalších selekčních faktorů, které nemusí působit konzistentně s enviromentálním gradientem v riziku predace snůšky. Mikrohabitat, kde je riziko predace snůšky malé, může být například spojen se zvýšeným rizikem predace inkubujícího rodiče (Wiebe & Martin 1998, Miller et al. 2007) a nebo suboptimálními teplotními parametry pro inkubaci snůšky (Shutler et al. 1998, Amat & Masero 2004).

Riziko predace je navíc poměrně dynamický proces ovlivněný krátkodobými změnami v abundancích hnízdních predátorů a distribuci a abundanci alternativních typů kořisti (Ackerman 2002, Schmidt et al. 2008). Lze tedy očekávat poměrně omezenou odpověď na krátkodobé fluktuace v predačním tlaku způsobené těmito faktory (ale viz např Fontaine & Martin 2006). Navíc výběr umístění hnízda může reflektovat spíše selekční tlaky které jej optimalizovaly v evoluční historii, avšak které úplně neodpovídají aktuálnímu směru selekce (Clak & Shutler 1999). S tímto souvisí i koncepce ekologické pasti (“*ecological trap*“, Ratti and Reese 1988, Schlaepfer et al 2002), tj. v kontextu hnízdní predace maladaptivní preference nových nebo nepůvodních, často antropogenně vzniklých biotopů, kterými se daný druh ve své evoluční historii neměl možnost setkat. Preference těchto biotopů vyplývá ze skutečnosti, že jejich charakter, jako například struktura vegetace, vykazuje určité znaky, které v původních biotopech poskytovaly relevantní informaci o pravděpodobnosti hnízdní predace, a proto sloužily na proximátní úrovni k adaptivnímu výběr umístění hnízda. Avšak v nových typech biotopů tyto znaky relevantní informaci o riziku predace neposkytují (např. Remeš 2003).

Hnízdící jedinci se spoléhají na několik obecných a poměrně častých mechanismů, jimiž lze vhodnou volbou umístění hnízda riziko jeho predace snížit: (i) Některé druhy umisťují svá hnízda do blízkosti agresivních obratlovců nebo hmyzu a využívají tak jejich antipredačního potenciálu k obraně vlastní snůšky (Quinn & Ueta 2008). (ii) Hnízda mohou být umisťována na místech, kde je výskyt predátorů málo pravděpodobný a nebo na místech pro ně obtížně dostupných (Collias & Collias 1984, Schmidt 2003). (iii) Častá je také preference mikrohabitatů, které detekci hnízda znesnadňují.

Umístění hnízda v korunách stromů (Schmidt 2003), dutinách (Martin & Li 1992), na koncových větvích (Collias & Collias 1984), v litorálních porostech a nebo na ostrovech obklopených vodní plochou (Hines & Mitchell 1983, Hill 1984, Kellet et al. 2003) představuje účinnou bariéru pro některé druhy predátorů. Data presentovaná v práci „Factors determining pochard nest predation along a wetland gradient“ (Albecht et al. 2006: Journal of Wildlife Management 70: 784-791) demonstrují, že vodní plocha eliminuje riziko predace snůšky některými druhy terestrických predátorů. U umělých hnízd umístěných v litorálu a na ostrovech sledovaných rybníků nebyla zaznamenána predace savčími predátory, na rozdíl od hnízd umístěných na břehu. Konzistentně s tím bylo riziko predace hnízd poláka velkého (*Aythya ferina*) umístěných na břehu vodních nádrží vyšší než riziko predace hnízd umístěných v litorálních porostech nebo ostrovech, přičemž ostrovy představovaly nejbezpečnější hnízdní habitat. Tento gradient v riziku predace pravděpodobně ovlivňuje i výběr umístění hnízda. Na ostrovech byly zaznamenány vyšší hnízdní denzity než v břehových a nebo litorálních porostech (Albrecht et al. 2006, Kreisinger et al. *unpubl data*).

Řada druhů ptáků preferuje místa s vysokou hustotou vegetace zakrývající hnízdo (Holway 1991, Martin 1993, Braden 1999, Clark & Shutler 1999, Dearborn & Sanchez 2001). Shrnující metaanalýza (Clark & Nudds 1991) prokázala, že tato strategie je efektivní hlavně proti vizuálně se orientujícím predátorům. Na druhou stranu hustá vegetace může do určité míry zamezit šíření pachů, které jsou klíčové pro nalezení hnízda olfaktoricky se orientujícími predátory (Lariviere & Messier 2001). Dvě zde presentované publikace prokázaly negativní korelaci mezi zakrytostí hnízda vegetací a pravděpodobností jeho predace u dvou druhů kachen; kachny divoké (*Anas platyrhynchos*, Kreisinger & Albrecht 2008) a poláka velkého (Albrecht et al. 2006). Tento výsledek je poměrně předvídatelný, vzhledem k dominantnímu zastoupení vizuálně se orientujících predátorů, převážně pak krkavcovitý ptáků (*Corvidae*) a motáka pochopa (*Circus aeruginosus*), na sledovaných lokalitách (Albrecht et al. 2006).

Závěrem nutno poznamenat, že tyto dvě práce (Albrecht et al. 2006, Kreisinger & Albrecht 2008) jsou založeny na datech nashromážděných během let 1999 – 2005. Od té doby však došlo k výrazným posunům v některých aspektech hnízdní predace, které do značné míry souvisejí s šířením norka amerického (*Neovison vison*) na studovaných lokalitách. Během let 2006 - 2009 došlo k výraznému vzestupu predace samic inkubujících hnízdo, což byl jev do té doby poměrně ojedinělý. Například v letech 2006-2009 byla zaznamenána predace inkubujících samice u 10-15 %

nalezených hnízd (Benešová et al. 2007). Riziko predace hnízdících samic může vzhledem k relativní dlouhověkosti kachnovitých (Forbes et al. 1994) a poměrně vysoké pravděpodobnosti náhradního hnízdění po predaci první snůšky (u kachny divoké bylo za pomoci genetické analýzy peří odebraného z hnízdní výstelky [Munclinger et al. 2006] zaznamenáno náhradní hnízdění po prvním neúspěšném hnízdním pokusu u 15 - 35 % jedinců [Kreisinger et al. 2008]) představovat silnější selekční tlak na umístění hnízda, než samotné riziko predace snůšky. Ostrovy které do roku 2005 představovaly bezpečné refugium proti většině druhů terestrických predátorů (Albrecht et al 2006), mohu za současné situace představovat suboptimální biotop. Konzistentně s tímto předpokladem byl v letech 2006-2009 zaznamenán výrazný pokles hnízdních denzit na ostrovech sledovaných lokalit (Benešová, diplomová práce *in prep*). Nelze samozřejmě vyloučit, že se na tomto poklesu podílí i jiné faktory, jako například celkový pokles populace či nižší podíl hnízdících jedinců v těchto letech.

Vliv krypse na riziko hnízdní predace: Krypse je široce rozšířenou antipredační strategií, znesnadňující detekci kořisti pomocí nevýrazného či korespondujícího zbarvení (Ruxton et al 2004, Caro 2005). Tradičně je krypse pojímána jako "*backgroud matching*" (Endler 1978), t.j. shoda ve zbarvení těla a náhodného vzorku pozadí. I následující text bude vycházet převážně z tohoto pojetí, i když teorie krypse nabízí daleko pestřejší škálu strategií, které znesnadňují pomocí zbarvení detekci a/nebo predaci kořisti (Thayer 1909, Cott 1940). Není bez zajímavosti, že sofistikovanější empirické testy těchto hypotéz, starých mnohdy téměř 100 let , jsou prováděny až velmi recentně, ovšem povětšinou na modelových systémech dosti abstrahovaných od reálné přírody (viz např. Cuthill et al 2005, Stevens et al 2008).

Během hnízdění může krytické zbarvení vajec (Westmoreland & Kiltie 1996), těla inkubujících rodičů (Martin & Badyaev 1996) a nebo kryptická konstrukce hnízda (Moller 1987) snižovat pravděpodobnost detekce snůšky hnízdními predátory. Vliv krypse na riziko predace hnízd je v některých z těchto aspektů překvapivě málo studovaný a výsledky empirických studií jsou často rozporuplné. Práce zabývající se touto problematikou navíc často trpí určitými metodickými nedostatky.

Antipredační efekt kryptického zbarvení u ptáků je poměrně silně podpořen několika studiemi, demonstrujícími na mezidruhové úrovni zvýšenou míru predace, v důsledku nápadného zbarvení těla (Huhta et al. 2003, Moller & Nielsen 2006). Naproti tomu jiné práce ukazují, že nápadné zbarvení nemusí být vždy nutně spojené s vyšším rizikem predace (Gotmark 1993, Gotmark & Unger 1994). Na vnitrodruhové úrovni může nápadné zbarvení například indikovat kvalitu daného jedince, a tím i malou pravděpodobnost jeho predace ("*unprofitability prey hypothesis*", Gotmark & Unger 1994).

Zbarvení inkubujícího rodiče může hypoteticky ovlivnit i pravděpodobnost detekce a potažmo i riziko predace hnízda. V takové případě by evoluce kyptického zbarvení mohla být přímo podmíněna rizikem hnízdní predace. Této možnosti však byla věnována překvapivě malá pozornost. Martin & Badyaev (1996) prokázali ve své komparativní práci na mezidruhové úrovni slabý positivní vztah mezi barevností samic a rizikem predace hnízda, ale tento výsledek nemusí být, vzhledem ke korelativnímu typu dat, nutně interpretován jako přímá kauzalita. Jednoznačný vliv zbarvení rodičů na osud hnízda nebyl prokázána ani u dvou případových studií experimentálního charakteru, ve kterých bylo porovnáváno přežívání snůšek inkubovaných rodičem a nebo modelem rodiče s přirozeným zbarvením a zbarvením jehož nápadnost byla experimentálně zvýšena (Miller 1999, Stutchbury & Howlett 1995). Přestože tyto práce naznačují, že riziko predace snůšky nemusí být důležitou selekční silou ovlivňující zbarvení těla inkubujícího rodiče, zasloužila by si tato hypotéza do budoucna více pozornosti jak experimentálních, tak i komparativních studií.

Přírodním výběrem by rovněž měla být preferovaná hnízda s méně nápadnou konstrukcí. V případě konstrukce hnízda však riziko predace není zdaleka jediným faktorem determinujícím jeho vzhled. Výsledný design hnízda vzniká obvykle jako kompromis stabilizovaný spolupůsobením řady dalších selekčních tlaků, jako např. izolace snůšky od vlivů klimatu (Winkler 1993, Lombardo et al. 1995, Mayer et al 2009) a minimalizace energie spojené s úsilím do stavby hnízda. Kryptická funkce je připisována také řadě materiálů jako jsou lišejníky nebo pavoučí kokony, používané pro vnější konstrukci hnízda (Hansell 1996). Ale tyto materiály mohou plnit i jiné funkce (Hilton et al. 2004) a jejich přímý vliv na riziko predace snůšky byl testován jen zřídka (ale viz Martin 1987). Moller (1990) na experimentálních datech ukazuje, že velikost může být stabilizována dvěma protichůdnými selekčními tlaky, a to selekcí na nenápadnost hnízda, která vede k zmenšování velikosti, a na termoizolační vlastnosti hnízda, která působí opačně (Slagsvold 1982, Kern 1984). Přestože některé pozdější studie hypotézu, že zmenšování hnízda je účinná antipredační strategie poporují (Lent 1992, Hatchwell et al. 1996, Willson & Gende 2000), lze nalézt i řadu prací přinášejících opačné výsledky (Weidinger 2004).

Jedním ze znaků snižujících riziko predace hnízda může být i zbarvení a kresba snůšky. Tato hypotéza byla postulována samotným průkopníkem teorie přírodního výběru (Wallace 1989), na základě skutečnosti, že vejce bez kryptické pigmentace skořápy se vyskytují převážně u druhů které buďto hnízdí na bezpečných místech či jsou schopny účinné obrany proti predátorům, a nebo u těch, kteří kryjí snůšku po většinu inkubačního období svým tělem. Stejně jako ve výše zmiňovaných případech je predace pouze jedním z možných selekčních tlaků, který pigmentaci skořápky podmiňuje. Depozice pigmentů do skořápky může například zvyšovat její pevnost při nedostatku zdrojů kalcia (Gosler et al. 2005), ovlivňovat reflektanci, a tím eliminovat riziko přehřívání embrya (Montevecchi 1976, Bakken et al. 1978), nebo také být signálem kvality sociálního partnera (Moreno & Osorno 2003). Walaceova hypotéza byla testována celou řadou empirických studií, jejichž počet přesahuje počty ostatních prací, zabývajících se vlivem krypse na riziko hnízdní predace. Výsledky těchto prací však neposkytují jednoznačnou podporu testované hypotézy. To může být z části dané nedostatky experimentálního designu. Většina autorů používala umělá hnízda, která mohou přitahovat pozornost predátorů víc než hnízda přirozená a tak mohou být pro nalezení snůšky důležitějším vodítkem než zbarvení snůšky. Navíc krypse snůšky byla často hodnocena na základě subjektivních kritérií, která neberou ohled na světelný režim v hnízdech a která vzhledem k výrazným odlišnostem ve vizuální percepci mezi ptáky a člověkem mohou být zdrojem chyb (Bennett et al. 1994, Eaton Lanyon 2003, viz též Kilner 2006 pro podrobnější diskusi). Recentní komparativní práce R. M. Kilner (2006) v souladu s původní formulací Walaceovy hypotézy nicméně naznačuje asociaci mezi kryptickým zbarvením (hnědá barva skořápky a skvrnitý vzor) a umístěním hnízda, které může být spojeno s vyšším rizikem predace (t.j. hnízda umístěná na zemi), a to i po statistické kontrole na nezávislost dat díky fylogenetické příbuznosti.

Vliv rodičovského chování na riziko hnízdní predace: Aktivní inkubace snůšky je u naprosté většiny ptáků nezbytná k úspěšnému vyvedení snůšky (Deeming 2002). Kromě zajištění optimálních podmínek pro vývoj embrya (Webb 1980, Haftorn 1988) ovlivňuje ale přítomnost a aktivita rodičů na hnízdě i riziko jeho predace. Pro predátory může být hlasová a pohybová aktivita rodičů a mláďat na hnízdě důležitým klíčem k jeho nalezení (Skutch 1949, Martin et al 2000a, Muchai & du Plessis 2005, Smith et al. 2007). Naproti tomu, většina druhů ptáků disponuje širokým spektrem antipredačních strategií (Montgomeie & Weatherhead 1988, Caro et al 2005), které mohou riziko predace snůšky redukovat.

Práce pokoušející se odseparovat vliv antipredační kapacity inkubujících rodičů a jejich aktivity na pravděpodobnost predace snůšky vycházejí observačních dat (korelace mezi přežíváním snůšky, časem stráveným na hnízdě a frekvencí návštěv hnízda Andersson & Waldeck 2006) nebo jsou založeny na kontrolovaném experimentu. Experimentálně je obvykle porovnáno přežívání aktivních snůšek daného druhu s přežíváním umělých snůšek jejichž osud není přítomností rodičů ovlivněn (Cresswell 1997, Remeš 2005, Weidinger 2002, Kreisinger & Albrecht 2008). Výsledky těchto prací poukazují na značnou mezidruhovou variability ve vlivu rodičovského chování na hnízdní úspěšnost. U řady druhů přežívají lépe neaktivní umělá hnízda (Smith et al. 2007) v některých případech není mezi aktivním a neaktivními snůškami rozdíl (Schaefet et al. 2005, Cresswell 1997, Remeš 2005, Weidinger 2002) a u některých druhů antipredační kapacita rodičů vede k výrazně lepšímu přežívání aktivních snůšek (Weidinger 2002, Andersson & Waldeck 2006).

Jednotlivé druhy často využívají více než jednu z výše uvedených antipredační strategii. V takovém případě ale nemusí jednotlivé antipredační strategie vystupovat jako nezávislé prediktory hnízdní úspěšnosti, ale jejich vliv na pravděpodobnost predace může být kombinován v komplexních neaditivních interakcích. Největší pozornosti se dostalo interaktivního efektu rodičovského chování a zakrytí hnízda vegetací. Řada prací dokládá, že zakrytí hnízda vegetací ovlivňuje riziko predace snůšky více u umělých snůšek, jejichž osud není ovlivněn aktivitou rodičů, než u snůšek aktivních, jejichž osud je ovlivněn inkubačním chováním rodičů (Gotmark et al. 1995, Cresswell 1997, Weidinger 2002, Remeš 2005). Pro kompenzaci vlivu vegetace rodičovským chováním existuje několik možných, avšak málo kdy testovaných hypotéz. Nedostatečné zakrytí hnízda může být aktivně kompenzováno behaviorální plasticitou v inkubačním a antipredačním chování. Rodiče mohou například snižovat svou aktivitu u hnízd umístěných na místech s vysokým předpokládaným rizikem predace (Martin et al 2000b), a nebo jedinci s vyšším antipredačním potenciálem mohou hnízdit na málo bezpečných místech (Mclean et al. 1986). Vysoké zakrytí hnízda může zabraňovat dostatečnému výhledu do okolí a znesnadňovat tak detekci predátora. Tím je omezena možnost adekvátní reakce za strany rodičů na jeho přítomnost (jako například redukce počtu návštěv, Gotmark et al 1995, Martin & Wiebe 1998).

Podobný neaditivní efekt na hnízdní úspěšnost jaký byl pozorován u kombinace rodičovského chování a umístění hnízda může existovat i mezi jinými typy antipredačních strategií, i když empirické testy této hypotézy téměř neexistují. Cott (1940) upozornil, že kryptické zbarvení může mít nižší vliv na riziko predace na místech krytých vegetací, než na nekrytých místech. Přímé testy této hypotéz doposud chyběly, i když některé práce poskytují výsledky konzistentní s predikcemi této hypotézy (Stuart-Fox. & Ord 2004).

Vrubozobí (*Anseriformes*) jsou typickým příkladem skupin ptáků, u nichž je riziko hnízdní predace ovlivněno řadou antipredačních mechanismů. Výběr umístění hnízda má často značný vliv na reprodukční úspěšnost (Albrecht et al. 2006). Řada druhů je schopná účinné aktivní obrany hnízda, čímž dokáže redukovat riziko jeho predace (Opremanis 2004, Anderson & Waldeck 2006). Zbarvení inkubující samice je často kryptické, i když přímý vliv na hnízdní predaci nemá silnou empirickou podporu (viz např. Figuerola & Green 2000). Avšak snůška vrubozobých je nekrypticky zbarvená, bez výrazné kresby s mezidruhovou variabilitou ve zbarvení od bílé až po odstíny zelenomodré. Samice ji však během přestávek v inkubaci zakrývá nestrukturovanou hnízdní výstelkou, která většinou obsahuje výrazný podíl prachového peří. Tomuto typu chování je připisována termoizolační role (Caldwell & Cornwell 1975), i když zásadní experimenty, které by umožnily hodnotit termoizolační efekt zakrývání na hnízdní úspěšnost nebyly doposud provedeny. Na druhou stranu zakrývání snůšky může redukovat riziko její predace jak u vrubozobých (Götmark & Ahlund 1984, Oprermanis 2005), tak i u jiných skupin ptáků, kde se tento typ chování vyskytuje (Salonen & Penttinen 1988, White & Kennedy 1997).

Cílem práce "*Nest protection in mallards (Anas plathyrhynchos): Untangling the role of crypsis and parental behaviour*" (Kreisinger & Albrecht 2008: Functional Ecology. 22: 872-879) bylo určit vliv jednotlivých komponent antipredačních strategií (rodičovské chování, krypse v důsledku zakrývání snůšky tělem inkubující samice a krypse v důsledku zakrývání hnízdním materiálem a vegetací) a možné neaditivní interakce mezi těmito antipredačními adaptacemi u kachny divoké.

Práce ukazuje, že přítomnost inkubující samice, zakrývání snůšky hnízdním materiálem po dobu její nepřítomnosti a umístění hnízda v husté vegetaci snižuje riziko predace snůšky. Tyto faktory ale přispívají k hnízdní úspěšnosti aditivně. Naproti tomu naše práce nepotvrdila signifikantní vliv kryptického zbarvení těla samice na riziko predace snůšky.

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Nest protection in mallards *Anas platyrhynchos*: untangling the role of crypsis and parental behaviour

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Summary

1. The covering of clutches with nest material is generally considered to improve the thermal environment of developing embryos. Here we tested an alternative hypothesis: that this behaviour reduces the risk of clutch detection by predators and hence, fulfils a cryptic anti-predation function in a ground-nesting non-passerine bird, the mallard. In addition, we assess the anti-predation function of the direct presence of an incubating parent on the nest for the first time in a ground-nesting non-passerine bird.

2. We compared predation rates of real mallard nests with two types of artificial clutches: (i) covered with nest material and (ii) uncovered. In addition, the cryptic effectiveness of nest material, female body presence, and uncovered clutch were assessed using a simulated search for nests on photographs by human volunteers. This allowed us to evaluate separately the impact of overall crypsis (covering of the clutch by nest material and colouration of the female feather) and the direct protective capacity of the incubating female.

3. Our data demonstrate that in mallards, concealment of the clutch with nest material reduces the risk of nest predation. Although the incubating female seems to provide less effective crypsis to the nest than nest material alone, the presence of the female on the clutch enhanced nest survival, suggesting a significant anti-predation capacity of the incubating parent in this species.

4. Contrary to some previous studies, the relative effects of crypsis and parental anti-predation behaviour on nest survival did not differ with respect to nest concealment by surrounding vegetation.

Key-words: anti-predation behaviour, nest construction, parental compensation hypothesis, waterfowl

Introduction

Investments in parental care are expected to maximize the fitness of parents by optimizing the trade-off between the survivorship and quality of their offspring on one hand and parental reproductive output during future breeding attempts on the other (Williams 1966). Variable (and sometimes opposing) selective pressures drive the evolution of parental care, such as maintaining conditions for development of embryos (Haftorn 1988), diminishing the risk of nest predation (Montgomerie & Weatherhead 1988) or provisioning for young. Particular behavioural adaptations associated with parental care may enhance parental fitness by various mechanisms, but direct fitness consequences often remain poorly understood.

The covering of clutches with nest material during parental absence occurs in a wide variety of animals, including both invertebrates (Shimoda, Shinkaji & Amano 1994) and vertebrates, such as fish (Fleming *et al.* 1996), amphibians (Orizaola & Brana 2003), reptiles (Burger 1976) and birds (Summers & Hockey 1981; Götmark & Ahlund 1984; Salonen & Penttinen 1988). However, direct evidence for fitness benefits resulting from this behaviour is limited. Traditionally, clutch covering is believed to increase hatching success by improving the thermal isolation of the clutch (Caldwell & Cornwell 1975). Nevertheless, the few studies that have attempted to test this hypothesis directly have produced mixed results (e.g. see Burger 1976 and Shimoda *et al.* 1994). Various alternative hypotheses have been suggested to explain the adaptive function of clutch covering; for instance, parents may bury eggs under the nest material as an anti-parasitic strategy (Clark & Robertson 1981). In addition, clutch covering is also believed to be involved in sexual conflict: a female may use clutch covering to hide her eggs thereby camouflaging the stage of her fertile period from a social partner or extra pair intruders (Valera, Hoi & Schleicher 1997; Low

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2004). Moreover, clutch covering by various animal taxa is thought to reduce the risk of clutch detection by predators (Götmark & Ahlund 1984; Shimoda *et al.* 1994; Orizaola & Brana 2003) in a similar way to the cryptic colouration of eggshells (Haskell 1996) or of adults incubating the clutch (Martin & Badayaev 1996).

Nest crypsis (cryptic colouration of parents or eggshells, or a specific type of nest construction) may affect nest survival in combination with other factors. Parents often place nests in sites concealed by the surrounding vegetation, which may diminish the risk of nest detection by predators (Clark & Shutler 1999). In addition, parental incubation behaviour (such as parental presence at the nest) may reduce the risk of nest predation by directly defending the clutch (sensu Montgomerie & Weatherhead 1988); alternatively, parental presence itself may deter predators from approaching the nest (i.e. Opermanis 2004). At the same time parental incubation behaviour (such as moving on or around the nest during incubation breaks) may enhance the risk of the nest disclosure to predators (Skutch 1949). These mechanisms may act simultaneously to affect the probability of nest predation, and their relative contribution to reproductive success may combine in a complex, non-additive way. For example, the effect of parental incubation behaviour may be crucial for survival of nests that are poorly concealed by vegetation, but not for nests that are exposed to low predator detection risk due to sufficient vegetation concealment (Cresswell 1997; Weidinger 2002). Similarly, the anti-predation effect of crypsis provided by parents or nest structures (eggs, feathers) is believed to be lower when vegetation concealment is high (Cott 1940; Stuart-Fox & Ord 2004).

The aim of this study was to test whether incubation behaviours and clutch covering by females reduces nest predation risk in the mallard, a ground-nesting non-passerine bird for which the incubating female has cryptic body colouration. Since nest concealment by surrounding vegetation may affect nest success (Albrecht & Klvaňa 2004; Albrecht *et al.* 2006), we tested for an interaction between vegetation concealment and the influence of parental presence (called the 'parental compensation hypothesis'; Cresswell 1997; Remeš 2005). In addition, our experimental approach allowed us to test whether the protective effect of vegetation concealment nullifies the anti-predation effect of nest crypsis (covering of the clutch by nest material and/or the cryptic incubating female; e.g. Cott 1940; Stuart-Fox & Ord 2004).

Parental body colouration may affect the risk of nest predation (Martin & Badayaev 1996); however, previous experiments examining the effect of parental behaviour on nest predation have often implicitly assumed that active nests incubated by parents and artificial nests, which are not affected by parental behaviour, are equally cryptic (e.g. Cresswell 1997; Weidinger 2002; Remeš 2005; Fontaine *et al.* 2007). Our study evaluates separately, to the best of our knowledge for the first time, the contribution of crypsis and parental incubation behaviour to nest success, by comparing the survival of naturally incubated mallard clutches (affected by parental activity, *sensu* Cresswell 1997) with that of two types of artificial clutch whose fate is not affected by parental incubation behaviour; that is, clutches either (i) covered or (ii) uncovered by nest material. Second, the cryptic effectiveness of nests covered by either nest material or the cryptic female, and uncovered nests, are compared using simulated nest searches of visually oriented predators (humans) as a proxy of crypsis (i.e. Cuadrado, Martin & Lopez 2001).

If clutch covering performs an anti-predation function, then covered clutches should have lower detection by human predators than uncovered clutches (i.e. they should suffer a lower predation risk by visually oriented predators). The evaluation of crypsis, using human volunteers, may help to roughly separate the effect of protective parental behaviour and crypsis. For instance, parental incubation behaviour could be said to be predominantly protective if survival of both types of artificial clutches is lower than survival of incubated nests and if these nest types do not differ in crypsis (or incubated nests are even less cryptic than artificial nests). The opposite pattern, that is, a higher survival rate for artificial clutches compared to natural nests, would indicate that nest disclosure due to parental movements around the incubated nest prevails over the protective effect of parental presence (i.e. Skutch 1949). On the other hand, our approach does not allow us to directly separate the effect of crypsis and parental incubation behaviour in the situation where one clutch type would be both more cryptic and more successful against real predators than the other. To test the hypothesis that the anti-predation effect of the vegetation concealment compensates the effect of parental activity (i.e. Cresswell 1997) and cypsis (i.e. Cott 1940), in both experiments, we further examined the significance of the interaction between nest type (clutches covered by nest material, incubating female or uncovered clutches) and vegetation cover.

Material and methods

STUDY SITE

Field work was conducted from mid-April through mid-July of 2003 and 2004 on seven-selected fishponds (total study area; 40 km^2) in the Třeboň Biosphere Reservoir, Doudlebia, Czech Republic (49°9′N, 14°43′E). We searched for nests on small artificial islands (5–30-m wide, 50–300-m long), where visually oriented avian predators (marsh harriers *Circus aeruginosus* and crows *Corvus corone*) cause the majority of nest losses (Albrecht *et al.* 2006). The vegetation around mallard nests included the common reed (*Phragmites communis*, 53% of all nests included in the experiment), stinging nettle (*Urtica dioica*, 16%) and sedge grass (*Calamagrostis epigeos*, 31%); see Albrecht & Klvaňa (2004) for details.

EXPRIMENT 1: THE EFFECT OF CLUTCH COVERING AND PARENTAL PRESENCE ON NEST FATE

Artificial nest experiment

Experiments using artificial clutches enable the separation of the contributions of crypsis (Haskell 1996) and parental incubation behaviour (Cresswell 1997) to nest success. For each real nest (hereafter called ‘incubated nest’), we assigned a pair of artificial nests (not incubated, and therefore not affected by parental activity; Cresswell 1997) 7·5 ± 2·7 m (mean ± SE, range 5·5–15 m) from the incubated nest. For each pair of artificial clutches, one was covered by nest material taken from the spatially associated incubated nests, and the second was left uncovered (although we added some nest material around this clutch to mimic the scent and appearance of a real mallard nest (Guyn & Clark 1997). This experimental design enabled us to test the anti-predation function of clutch covering (survival of covered vs. uncovered artificial nests), as well as the contribution of parental incubation behaviour to the nest success (survival of incubated vs. covered artificial clutches; we assumed that an equivalent or lower quality of clutch crypsis is provided by the female feather colouration compared to nest material [see below]).

Artificial nests were constructed from dead vegetation shaped into a cup closely resembling natural mallard nests. Real inactive nests baited with an artificial clutch have previously been used to assess the effect of parental activity on nest survival in open cup shrub-nesting birds (Cresswell 1997; Komdeur & Kats 1999; Weidinger 2002). In the case of ground-nesting birds, clutch colouration rather than nest design is expected to be a crucial clue for predator nest disclosure (i.e. Weidinger 2001). Thus, we assume that the use of human-made artificial nests does not seriously affect the results of this experiment.

Clutches of artificial nests consisted of four brown chicken eggs. In the additional experiment performed in year 2006 on the same study plots (data not included in the results), artificial clutches baited with chicken eggs had a survival rate comparable to those baited with mallard eggs (28 artificial nest couples $\chi^2 = 0{\cdot}65$, d.f. = 1, $P > 0{\cdot}40$; in fact mallard eggs were slightly more predated than chicken eggs, 19 vs. 16 nests predated, Kreisinger & Albrecht unpublished data). Hence, the difference in eggshell colouration between chicken and greenish mallard eggs is unlikely to bias our results.

Nest sites for artificial clutches were chosen to approximate the nest site of the associated incubated clutch in features that could affect the probability of predation (e.g. vegetation structure, height and density, proportion of dead vegetation, distance to the closest tree, shrub and water). We took special care not to manipulate or damage the vegetation around all nests. To control for possible bias in this aspect, vegetation concealment was measured for each clutch at the beginning of each experiment. A 20 × 20-cm grid composed of eight white 5 × 5-cm squares was placed directly on the nest bowl, and the percentage of white squares obscured by vegetation when viewed from 1 m directly overhead was scored. The mean vegetation concealment of all nests was 50·7 ± 24·0% (mean ± SE) with no differences in vegetation concealment between incubated and artificial clutches in each triplet (6·3 ± 8·7% [mean ± SE], Repeated Measures ANOVA, $F_{2,173} = 0{\cdot}658$, $P > 0{\cdot}5$).

The relative proportion of time that a female spends on the nest differs noticeably between the pre-incubation and incubation stages (Afton & Paulus 1992). Therefore, in this experiment, we only included real nests that survived to day 3–5 of incubation (based on the floating test of Westerkov 1950). Clutches found during pre-incubation or very early incubation (< 3 days) are often abandoned (e.g. Johnson, Nichols & Schwartz 1992), and therefore, were not included in our experiment since the influence of parental behaviour cannot be assessed for abandoned nests. Incubated nests included in this experiment were a random sub-sample of all mallard clutches found in our localities which fulfilled the criteria mentioned above.

Nests triplets were checked twice, the first time after 5·7 ± 0·8 (mean ± SE) and a second time after 11·4 ± 1·1 (mean ± SE) days from the start of the experiment. When we approached the nest, the female duck usually left the nest suddenly without covering eggs with nest material. When this happened, we covered clutches with nest material after the nest check to mimic the behaviour of an undisturbed female leaving the nest during incubation recesses (Caldwell & Cornwell 1975). During the second check, successful artificial clutches were removed.

Nests were defined as predated if the clutch was damaged or at least one egg was missing. This criterion makes our results rather conservative, because incubated nests with partial clutch loss, where the female continued the incubation were classified as predated (two incubated nests, one and three eggs missing, respectively). Nevertheless, in these cases we could not distinguish between partial clutch predation (i.e. Ackerman *et al.* 2003) and other causes of eggs loss (such as the ejection of an egg with a broken shell by the female). We excluded two nest triplets for which the incubated nest was abandoned by the female during the experiment and the clutch was found intact during a subsequent visit. The final analysis included 60 nest triplets.

Experiments using artificial nests increase natural nest densities, which may draw predators and lead to an artificial increase of predation rates. However, mallards already breed in high densities in our locality. As only a small proportion of incubated nests were included in the experiment (15–18% mallard nests found), nest densities were only increased by the experimental setup by 30–35%. Similarly, the mean distance between neighbouring natural nests (10–20 m) was only increased slightly by our experiment. We assumed that this modest increase in nest densities did not alter natural predator densities or predation rates, since experiments based on much larger differences in duck nest densities show no consistent effect of nest densities on predation rates (see Ackerman, Blackmer & Eadie 2004 for review).

EXPERIMENT 2: CRYPTIC QUALITIES OF EGGSHELLS, NEST MATERIAL AND THE FEMALE BODY

To compare the cryptic quality of nest material, the female feather colouration and uncovered eggs, 15 groups of photographs of mallard nests were taken during the breeding season. Each group contained three pictures: (i) a clutch covered by a stuffed female mallard; (ii) a clutch covered by nest material, and (iii) an uncovered clutch. In addition, 150 photographs containing no nest were included in the experiment (i.e. Cuadrado *et al.* 2001). Fifteen of these control pictures featured the vegetation microhabitat close to nests included into this experiment (1–2 m away; hereafter ‘paired control photos’). The remaining 135 photos represent random sites of mallard breeding habitat within our study localities (hereafter termed ‘unpaired control photos’). Human volunteers (8 males, 12 females, aged 18–62 years) were asked to search for nests located randomly in the 195 photographs (150 control photos + 45 photos containing nests) that were presented in a random sequence for 10 s on a computer monitor. The pilot experiment showed that a successful search rarely exceeded 10 s (Kreisinger, unpublished data). Volunteers were asked to use a mouse to click on the spot where they believed there was a nest. The search was considered successful when volunteers clicked on the target area where a nest was present, with the ‘target area’ occupying *c.* 2% of the photo (a circle with 4·5 cm diameter on 15″ monitor for all photos containing a nest). The vegetation concealment of each nest was measured following the procedure used in the previous experiment. All photographs were taken 4 m away from the nest, from the direction that provided the highest visibility of the clutch, using a Practica MTL5B with a Helios 50 mm lens and Kodak 200 ASA print film. The focal length of the 50 mm lens corresponds to humans visual system and the 4 m distance provide, based on our experience, an appropriate level of uncertainty about the nest location on photographs (a random nest detected with *c.* 50% probability). The height of the camera was 1·6 m above-ground level.

Humans are frequently used in similar experiments to mimic behaviour of wild visually oriented predators since their prey search is primarily based on visual perception (e.g. Cuadrado *et al.* 2001). However, several potential biases may arise when using humans as a model predator in experiments similar to ours. For instance wild predators usually search for an entire spectrum of potential prey, not only nests; however, our field experiments were performed on a small artificial islands where alternative prey is rather limited and we expect that these sites are visited by predators primary searching for duck nests.

In addition, avian predators, unlike humans, also perceive light in the UV spectrum (300–400 nm). To address this problem, we examined the reflectance of structures whose cryptic efficiency was studied in experiment 1 and 2 (down feathers from the nest material, brown chicken eggshells, mallard eggshells and feathers from the female dorsal surface) and samples of fresh and dry vegetation surrounding nesting microhabitats in our locality (Sedge grass, Common Reed). We recorded the reflectance of five independently collected samples of these materials using an Avaspec 2048® (Avantes, Netherlands) spectrometer equipped with micron fiber-optic probe at a 45° angle to the measured surface. Reflectance data were generated relative to a white standard. The reflectance profile was very similar for dry Sedge grass and dry Common Reed and for fresh green samples of these species. UV reflectance for both dorsal surface of a female mallard and down feathers were negligible. Brown chicken eggs exhibited lower reflectance in the UV spectrum (i.e. more similar to vegetation samples), compared to green mallard eggs, except the small reflectance peak around 320 nm. Since perception in UV spectrum by avian predators (raptors and corvids) is based on violet sensitive cones with maximal sensitivity around 405–420 nm (i.e. Hastad, Victorsson & Odeen 2005), this peak is unlikely do be detected by the most common predators of our experimental nests. Reflectance curves for particular structures are presented in Supplementary Appendix S1.

In conclusion, the use of humans is probably adequate for the estimation of crypsis in our experiment. If UV reflectance of eggshells attracts nest predators, the use of chicken eggs will only cause the estimate of the effect of crypsis and clutch covering in our study to be conservative due to their lower UV reflectance compared to mallard eggs.

STATISTICS

Experiment 1

Nest survival was evaluated using the Mayfield method (Mayfield 1975); that is, the proportion of days survived was calculated for each nest and modelled as a response variable with a binomial error distribution (Aebischer 1999). Due to the short intervals between nest checks, the time of nest predation and hence the number of days of nest exposure were estimated as one-half of the interval between the last positive and first negative check of the nest (Mayfield 1975). Days of nest exposure differed among (but not within) nest triplets, because we did not check nests during unfavourable weather conditions in order to prevent clutch abandonment. Weighting for different lengths of nest observation (days of nest exposure) was included in the analysis (Aebischer 1999; Crawley 2002).

Because nests in the first experiment were spatially grouped in triplets, their outcome cannot be treated as independent in the statistical analysis (i.e. the probability of predation of a single nest may depend on the probability of predation of any of the other nests in the triplet). To control for this issue and to avoid pseudoreplication, the data were analyzed within the framework of the GLMM, (GLMM binomial error distribution, R 2·6·0 software) with the nest triplet identity included as a random effect (e.g. Faraway 2006).

The most complex model contained triplet identity as the random effect and a set of categorical explanatory variables (nest type: incubated, covered artificial or uncovered artificial nests, plus year), continuous variables (vegetation concealment, date of particular experiment initiation) and all two-way interactions between variables as fixed effects. We first assessed the importance of random effect by comparing explained variance of the model including random effect with the model where the random effect was not considered using Akaike information criterion (AIC, Faraway 2006). Backward elimination of non-significant terms was further used to select the best Minimal Adequate Models (MAM), that is, the most parsimonious ones with all fixed effects significant (Crawley 2002). The significance of particular terms on the explanatory power of a model was tested using the deletion test. Data were checked for normality and, in the case of vegetation concealment, data were root square arcsine transformed before calculation.

We also compared the survival of incubated mallard nests in experimental localities but that were not included into the experiment ($n = 252$) with the survival of experimental nests using Aebischer's (1999) method. Since experimental nests were grouped in triplets, we performed three separate models (i.e. non-experimental incubated nests vs. each one of three experimental nest types).

Experiment 2

Statistical procedures are based either on GLM or GLMM (triplet of photos of the same nest included as a random factor) with a binomial response (proportions of cases when different observers correctly identified a particular nest, or proportions of cases when the position of the nest was misidentified respectively [e.g. Cuadrado *et al.* 2001]). Vegetation concealment, clutch cover type and interaction were incorporated as explanatory variables. The procedure for the MAM model selection was identical to that in experiment 1.

Results

THE ROLE OF CLUTCH COVERING AND PARENTAL PRESENCE

The backward reduction of the complex survival model revealed a significant effect of nest type and vegetation concealment on nest survival, whereas the effect of other variables (between year differences, date of experiment initiation and two-order interactions) were statistically negligible, including the focal interaction between nest type and vegetation concealment (Table 1). The relationship between nest survival (i.e. proportion of days survived) and vegetation concealment was positive, with comparable regression slopes for all experimental nest types; incubated nests (slope = 1·852 ± 0·934 SE), artificial covered clutches (slope = 1·717 ± 0·788 SE) and artificial uncovered clutches (slope = 2·033 ± 0·670 SE). When the random effect (nest triplet identity) was deleted from the model, the explained variability decreased significantly (Δ AIC = 3·99), suggesting covariance of

Table 1. Survival model based on GLMM with binomial error structure (Aebischer 1999). Backward eliminations of non-significant terms to select the best minimum adequate model (MAM) with all their effects significant were used. Models were compared using the deletion test. Significant factors included in the MAM are in boldface

Factor	d.f.	χ^2	*P*
Nest type (active + covered + uncovered)	**2**	**31·11**	**< 0·001**
Vegetation	**1**	**12·36**	**< 0·001**
Date	1	2·53	0·112
Year	1	0·67	0·415
Year × Date	1	2·60	0·107
Date × Vegetation	1	0·34	0·562
Year × Vegetation	1	2·22	0·136
Nest type × Year	2	0·98	0·614
Nest type × Vegetation	2	1·54	0·462
Nest type × Date	2	1·16	0·560

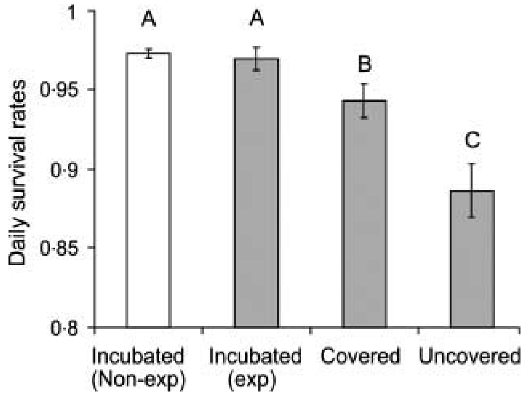

Fig. 1. Daily survival rates (± SE, Mayfield 1975) of active mallard nests that were not included in the experiment (Incubated Non-exp) and of reminding nest groups that were included in the experimental setup: experimental incubated mallard nests (Incubated exp), artificial clutches covered with nest material (Covered) and artificial clutches that were not covered with nest material (Uncovered). Different letters above columns represent significant differences between nest types ($P < 0·05$, based on the Generalized Liner Mixed Models).

nest survival within a particular triplet. The *a posteriori* reduction of nest type categories further revealed that uncovered artificial clutches had significantly lower survival rates than covered artificial clutches (incubated + [covered vs. uncovered], Δ d.f. = 1, $\chi^2 = 11·41$, $P < 0·001$, Fig. 1). The survival rates of incubated clutches was significantly higher than survival of covered artificial clutches ([incubated vs. covered] + uncovered, Δ d.f. = 1, $\chi^2 = 5·06$, $P = 0·024$, Fig. 1). The survival of incubated nests included in the experiment did not differ from the survival of incubated mallard nests found in the same localities not included in the experiment; Mayfield's daily survival rates (DSR) for incubated experimental nests ($n = 60$, DSR = 0·969 ± 0·0072 SE) and incubated nests not included in the experiment ($n = 252$, DSR = 0·972 ± 0·0027 SE) did not differ (GLM, ΔD.f. = 1, $\chi^2 = 0·66$, $P < 0·4$, Fig. 1). On the other hand, and consistent with previous results, incubated nests that were not included in the experiment had a higher survival than artificial covered clutches (GLM, Δ d.f. = 1, $\chi^2 = 10·80$, $P = 0·001$) and artificial uncovered clutches (GLM, Δ d.f. = 1, $\chi^2 = 51·79$, $P < 0·001$, Fig. 1).

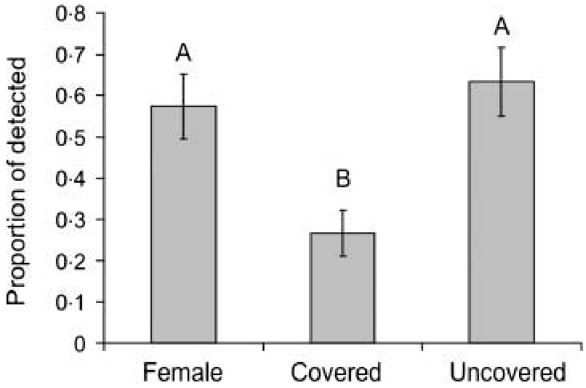

Fig. 2. Bars indicate proportions of nests (mean ± SE) with uncovered clutches (Uncovered), clutches covered by nest material (Covered) and clutches camouflaged by stuffed mallard female (Female) detected on photographs by human volunteers. Different letters above columns represent significant differences between nest types ($P < 0·05$, based on Generalized Liner Mixed Models).

CRYPTIC QUALITY OF EGGSHELLS, NEST MATERIAL AND THE FEMALE BODY

On average, in 6·2 ± 1·2 (SE) % of cases, volunteers identified an incorrect object as a mallard nest on control photos. The frequency of these mistakes did not differ between paired control photos and unpaired control photos (GLM, Δ d.f. = 1, $\chi^2 = 0·63$, $P = 0·427$). Similarly, the proportion of cases in which no nest was found and any object was incorrectly identified as a nests did not differ between pictures containing a nest and control pictures (GLM, Δ d.f. = 1, $\chi^2 = 0·56$, $P = 0·453$), indicating that human observers were no more likely to record false positives on control photographs than on photographs with nests.

If the analysis to pictures is restricted to those containing a nest, the probability of clutch detection by humans decreased with increasing vegetation concealment (GLMM, Δ d.f. = 1, $\chi^2 = 13·66$, $P < 0·001$) and was affected by the type of clutch cover (Δ d.f. = 2, $\chi^2 = 114·94$, $P < 0·001$), but the interaction between these variables was not significant (Δ d.f. = 2, $\chi^2 = 3·00$, $P = 0·223$). A negative relationship between the probability of nest detection and vegetation concealment was detected for all nest groups (regression slope for uncovered clutches: –0·031 ± 0·006 SE, for clutches covered by the nest material: –0·025 ± 0·006 SE and for clutches covered of the female body: –0·029 ± 0·005 SE). Uncovered clutches tended to be detected more often than clutches covered by a stuffed mallard female (Fig. 2); nevertheless when merging these two nest types in the model (i.e. [uncovered clutches vs. clutches covered by female] + clutches covered nest material], this difference was not significant (Δ d.f. = 1, $\chi^2 = 2·81$, $P = 0·093$).

On the other hand, clutches covered by nest material were significantly less likely to be detected than clutches covered by a stuffed mallard female (uncovered clutches + [clutches covered by female vs. clutches covered nest material]; Δ d.f. = 1, $\chi^2 = 70{\cdot}83$, $P < 0{\cdot}001$).

Discussion

The use of feathers as a non-structural nest bowl lining in various bird taxa is assumed to primarily improve the thermal environment of the clutch and consequently the hatchability of young (Hilton *et al.* 2004; McGowan, Sharo & Hatchwell 2004), although this effect on fitness has rarely been demonstrated experimentally (but see Lombardo *et al.* 1995). Our data clearly show that clutch covering by nest material consisting of down feathers and dead grass may also fulfil a cryptic function. Consistent with previous studies performed on artificial nests (Götmark & Ahlund 1984; Salonen & Penttinen 1988; Opermanis 2004), in our study, covered nests suffered a lower predation risk than uncovered artificial nests (Fig. 1). A cryptic function of the clutch covering was simultaneously supported by the experiment with human volunteers, where covered clutches were less likely than uncovered clutches to be detected (Fig. 2). Our experiment does not allow the accurate measurement of anti-predation benefits arising from clutch covering, since clutch covering may fulfil its function only when the female is off the nest, which in the case of the mallard involves 10–15% of the incubation period and a large proportion of the pre-incubation stage (Caldwell & Corwell 1975; Afton & Paulus 1992). However, our data demonstrate that, apart from other mechanisms, predation can be an important factor favouring the evolution of clutch hiding behaviour, especially in species with poorly developed eggshell crypsis. This could be particularly true in ground-nesting species because it is primarily the clutch itself, rather than the nest bowl, that attracts the attention of nest predators (e.g. Weidinger 2002).

The anti-predation function of cryptic colouration is often assumed to increase with decreasing concealment by vegetation (Cott 1940; Stuart-Fox & Ord 2004), but previous studies have generally focused on species that nest in open habitats covered by sparse vegetation (Götmark & Ahlund 1984; Opermanis 2004, but see Salonen & Penttinen 1988), limiting the possibility of testing whether clutch covering actually compensates for poor vegetation concealment (e.g. Cott 1940). The results from our survival model (Table 1) and our human predator experiment, in fact fail to support any interaction between nest covering and vegetation concealment, contrary to previous studies that suggest that clutch covering can compensate for poor nest site concealment.

Although we clearly demonstrate that covering the nest with nest material may strongly improve nest survival in mallards, the fitness consequences of this behaviour may simultaneously involve both better thermoregulation and enhanced development of embryos. Future manipulative experiments should be focused on assessing the relative importance of potential pathways through which clutch covering enhances female fitness.

In this study, covered artificial clutches exhibited lower survival than incubated nests guarded by a mallard female (Fig. 1). This pattern is unlikely to be explained by a better cryptic quality of the female body, as nests covered by nest material did not differ in UV reflectance from nests covered by females and were detected less frequently by human observers. Similarly data reported by Opermanis (2004) indicate clutches covered by nest material to be more cryptic to non-human predators than clutches covered by a duck female. Since an incubating female does not necessarily cover its clutch with nest material during every break in incubation (Caldwell & Cornwell 1975), our data provide conservative estimates of nest protection due to parental incubation behaviour, because uncovered nests suffer higher predation risk. Consequently, low predation rates of incubated nests indicate that parental incubation behaviour via direct parental presence improves nest success in mallards. On the other hand, the effect of nest disclosure due to female activity (e.g. Skutch 1949; Martin, Scott & Menge 2000) is unlikely to markedly reduce nest success in our model system.

It is also worth noting that incubated nests included in our study are in fact a sub-sample of nests that survived until the onset of incubation (see also Cresswell, 1997; Weidinger 2002 for similar drawbacks in the methodology). Hence, our experiment might slightly overemphasize the effect of parental behaviour on nest survival by estimating the parental behaviour effect for survivors but not unbiased estimates for the studied population, particularly in the case of high inter-individual variability of the protective component of parental behaviour. Nevertheless, we believe this potential bias is relatively low, since incubated nests were not monitored for only a relatively small proportion of the incubation period (3–5 days, *c.* 15–20% of the incubation period) and losses of unincubated nests and nests during the early incubation stage (0–5 days) due to predation were relatively low (*c.* 5–10%) compared with losses due to clutch abandonment (*c.* 20%).

In line with observed anti-predation effect of nest guarding, experiments based solely on non-incubated artificial nests performed by Opermanis (2004) indicate that the mere passive presence of an inactive dummy female duck on an artificial ground clutch may deter some avian predators. The contribution of parental behaviour to nest success has been experimentally revealed in several open-cup nesting passerines (Cresswell 1997; Komdeur & Kats 1999; Remeš 2005). In waterfowl, nest guarding is known to decrease predation risk in species with large body size such as geese, swans or eiders (Andersson & Waldeck 2006; Samelius & Aulisauskas 2006). We show, however, that parental presence on the nest during incubation may provide protection of the clutch against predators even in ground-nesting ducks with a mallard-like body size.

Under the parental compensation hypothesis, the protective effect of parental incubation behaviour often, but not always (e.g. Weidinger 2002), contributes more to nest success in unsafe (i.e. poorly covered by vegetation) nest sites (Cresswell 1997; Remeš 2005). Several mechanisms have been suggested to explain parental compensation; for example, a lower intensity of nest guarding and higher parental activity for individuals breeding in nest sites exposed to low predation risk (i.e. dense vegetation, McLean, Smith & Stewart 1986; Montgomerie & Weatherhead 1988; Martin *et al.* 2000) can be expected if nest guarding is associated with energetic costs (Montgomerie & Weatherhead 1988; Komdeur & Kats 1999). On the other hand, breeding in dense vegetation may limit the prompt detection of a predator, and preclude the parent from modulating its activity to avoid nest disclosure (Götmark *et al.* 1995).

In mallards in this study, parental incubation behaviour improved nest success regardless of vegetation concealment, despite vegetation concealment itself predicting nest fate (Table 1), providing no support for the parental compensation hypothesis. Consequently our results indicate that none of the suggested mechanisms of parental compensation play a significant role in the mallard. Nevertheless, a detailed analysis of female behaviour, and predation rates nests with experimentally manipulated vegetation concealment, should be performed (i.e. Remeš 2005).

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Mean reflectance for mallard eggs, brown chicken eggs, dorsal surface of incubating duck, down feathers from the nest material, and for fresh green and dry vegetation samples.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2435.2008.01445.x
(This link will take you to the article abstract).

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Corridor versus hayfield matrix use by mammalian predators in an agricultural landscape

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Abstract

Corridors are assumed to be an efficient conservation tool for reducing changes in local biodiversity induced by fragmentation and loss of natural habitats. The importance of corridors for the management of local biota has been previously demonstrated for a few single species; however, there has been little research on this topic for groups of animals, such as mammalian carnivores. In this paper, we test the hypothesis that linear strips (2-12 m wide) of shrubby vegetation and dense high grass are more likely to be exploited by diverse carnivore species than surrounding hayfields. For this purpose a scent station survey was employed. Scent stations placed in linear landscape structures were visited much more frequently than scent stations placed in the surrounding hayfield matrix. The probability of detection was higher in corridors than in the landscape matrix for all carnivore species detected. In addition, we tested if the use of a corridor by carnivores was influenced by the amount of shrub and tree cover and corridor width, but none of these variables affected the probability of carnivore detection. Our study suggests that the maintenance of corridors could be an efficient management practice for the preservation of carnivore populations in agricultural landscapes.

Keywords: Habitat corridors, agricultural landscape, habitat fragmentation, Czech Republic, Doudlebia, carnivores

Introduction

The fragmentation of natural habitats and subsequent loss of connectivity can alter the structure of vertebrate populations, which often results in reduced viability and decreased diversity (Brown and Kodric-Brown 1977; Didham et al. 1998; Crooks and Soulé 1999; Fahrig 2003). Corridors, i.e. narrow linear structures connecting preferred but isolated habitat patches that are spatially segregated by an unsuitable habitat matrix (Forman and Gordon 1986), are often assumed to diminish the negative consequences of habitat fragmentation (Laurance and Laurance 1999; Hilty and Merenlender 2004; but see Simberloff and Cox 1987). These landscape structures are believed to facilitate the exchange of individuals between isolated subpopulations (reviewed in Hilty et al. 2006), and this in turn reduces the negative effects of demographic stochasticity (Brown and Kodric-Brown 1977; Gilpin and Hanski 1991), and/or inbreeding depression due to low gene flow (Aars and Ims 1999). Alternatively, corridors may enable effective dispersal between disconnected but preferred habitat patches within an individual home range (e.g. Dunning *et al.* 1992; Rosenberg *et al.* 1998), or provide extra habitat suitable for some species (e.g. MacDonald *et al*. 2004).

The intensification of agricultural practices in Europe during the past decades has resulted in an increase of intensively cultivated areas and, consequently, a drastic decline of semi-natural refuges suitable for native fauna, such as extensively used grasslands, small woodlots, and hedgerows (Arnold 1983; Smith and Johnson 1993). A web of linear uncultivated margins separating particular field parcels has previously been shown to increase the abundance and diversity of various animal taxa (Arnold 1983; Boatman and Wilson 1988; Hassall *et al.* 1992) and could potentially maintain their dispersal (Aars & Ims 1999; Haddad *et al.* 2003). Nevertheless, despite considerable research and conservation interest in this topic, empirical data are still, in many respects, insufficient and available only for a few model groups (Beier and Noss 1998).

The population structure of carnivore species can be strongly affected by human induced landscape changes (Crooks and Soulé 1999) and other human activities. Area-sensitive specialist predators often exhibit strong population declines in fragmented landscapes. Large carnivorous species such as the brown bear and wolf became extinct during the past centuries in the Czech Republic. There are attempts to restore a population of lynx; however, based on habitat suitability models (Schadt et al. 2002) most Middle European regions are unlikely to maintain a viable population due to a high degree of landscape fragmentation. On the other hand, generalist mesopredator species may benefit from agriculturally induced landscape changes due to their ability to exploit various food items in diverse habitats including ecotones (Crooks and Soulé 1999, Crooks 2002).

The maintenance of linear field margins in a landscape fragmented by intensive agriculture can have considerable conservation value for mammalian carnivores; however, despite some studies in North America documenting the importance of corridors for these predators (Gehring and Swihart 2003; Hilty and Merenlender 2004), surprisingly, preferences for these landscape structures have not yet been explicitly tested in Europe.

The basic aim of this paper is to test the hypothesis that narrow (2-12 m wide) strips of shrubby vegetation and dense long-stemmed grass leading through mowed hayfields are more likely to be used by mammalian predators than the surrounding hayfield matrix in Central European landscapes fragmented by intensive agriculture. To study this, a scent station survey based on a non-reward method with two temporal replications was used. The qualities of particular corridors, such as width or the character of vegetation cover, have previously been shown to affect the densities and diversity of species using them (Laurance and Laurance 1999; Hilty and Merenlender 2004). Therefore as an additional step, we analyzed the effect of corridor character on the probability of its use by various carnivore species.

Materials and Methods

Study Area: The study site encompassed an agricultural landscape located in the České Budějovice basin (48.57 N, 14.28 E), Doudlebia, Czech Republic. The region has a gently rolling topography (with altitudes ranging from 350 to 550 m) and consists of a mosaic of agricultural fields, hayfields, fish ponds, small secondary coniferous or mixed forest patches, all connected by a web of corridors crossing through the hayfields. These hayfields are entirely drained and reseeded with species such as *Lolium sp*, *Phleum sp*, *Festuca sp*, *Dactylis sp* and mowed twice a year, resulting in short vegetation cover (range 15-40 cm) during our experimental treatment.

Corridors in our study area are linear and relatively narrow (2-12 m wide) strips of vegetation situated along ditches that drain the surrounding hayfields. The vegetation within corridors consists primarily of dense long-stemmed grasses (*Calamagrostis sp., Festuca sp., Arrhenatherum sp.*, > 60 cm high), that exceed the maximum height of hayfield vegetation. Also, they are usually covered by shrub or tree canopy dominated by species such as *Prunus spinosa* or *Salix* sp., although the proportion of corridors covered by woody vegetation varies considerably (range: 0-100 % of corridor length covered by woody vegetation).

Scent station survey: We constructed scent stations by clearing 1×1 m areas of debris and grass and covering them with a 2 cm thick layer of fine-grained masonry sand. A 1.5 ml micro centrifuge tube containing an attractant was attached to a wooden stick and placed in the centre of each scent station about 15 cm above the sand. Since our intention was to analyze predator responses to relatively fine landscape structures on a small spatial scale, domestic rabbit urine, a mild attractant (Linhart and Knowlton 1975), was used to avoid luring animals from greater distances.

Mammalian predators were identified based on footprint dimensions and shape characteristics (Anděra and Horáček 2005). We were unable to distinguish between the ermine (*Mustela erminea*) and least weasel (*M. nivalis*) in three cases. Due to similarities in habitat preferences and other aspects of their ecology (Johnson *et al.* 2000; Mitchell-Jones *et al.* 1999) these species were treated as 'small mustelids' in subsequent analyses. Domestic dog footprints (*Canis lupus familiaris*, four cases), footprints that did not allow us to distinguish between red fox (*Vulpes vulpes*) and domestic dog (two cases), and tracks which we were not able to specify to genus level (two cases) were excluded from the dataset; these deletions did not qualitatively affect the results (see Appendix 1 for further details).

Corridor vs. hayfield matrix preferences: To test the hypothesis that carnivores perceive and preferentially use corridors in comparison with the surrounding hayfield matrix, 20 pairs of scent stations were created (Fig 1). For each pair of scent stations, one was placed within a corridor and the second in the adjacent hayfield, 50 – 150 m away from the corridor scent station. To minimize the visitation of multiple scent stations by a single individual the minimal distance between each pair of scent stations was 250 m (mean = 570 m, see Gehring and Swihart 2003); consequently, the study area encompassed 35 km^2. We avoided placing scent stations in the immediate proximity of artificial water bodies that occur in the study area (fish ponds with size 0.5-20 ha, depth usually < 2 m, used for carp (*Cyprinus carpio*) production), as these could represent a movement barrier to carnivores. All experimental corridors were surrounded by hayfield patches on both sides, and thus carnivores were able to use both habitats for movement. Scent stations were exposed during 5 successive rainless nights in October 2005 and June 2006. The presence of tracks was checked every morning, resulting in a total of 400 station-nights.

Corridor characteristics: The original set of 20 corridor scent stations used in the first experiment was increased by 17 in spring 2006 which were placed in an extended area (total study area covered 95 km^2). We used these extra scent stations to increase the sample size in analyses of the effect of corridor characteristics on predator occurrence. Therefore, this subset of data consisted of only one temporal replication (spring 2006) and were not grouped with control hayfield scent stations.

For each corridor segment (200 m) with a scent station, we estimated the proportion covered by shrubs (height < 5 m) and trees (height > 5 m). Only a slight positive correlation between these variables was detected ($r = 0.34$). The width of the corridor was measured at the position of the scent station, although widths were fairly consistent along the entire corridor length, ranging from 2 to 12 m in our study. Although this range is relatively narrow, in general it is a good representative of linear strips of vegetation intersecting hayfields, not only in the studied locality but in the Czech Republic as a whole. Corridors exceeding this range occur relatively rarely.

Statistics

Corridor vs. hayfield matrix preferences: Multiple detections of the same carnivore species during the 5 exposure days at a particular scent station may be caused by the same individual, providing no additional information. Therefore, we treated occurrence of a particular carnivore species as a binary response variable (present or absent during the 5 days). Small mustelid species typically occupy relatively small home ranges (Johnson *et al.*

2000). Corridors could therefore represent a large proportion of small mustelid territory, rather than an opportunistically exploited landscape structure (e.g. MacDonald *et al.* 2004). Consequently, we treated this group as a separate level in the analysis since the majority of scent station visits were ascribed to them (see below), which could bias the general conclusions of our experiment. We considered the domestic cat as a separate level in the analysis since it represents a non-native predator which is usually more closely associated with human habitation and may therefore exploit natural resources only opportunistically. The remaining carnivore species could not be considered separately in the analysis since their detection rates were low. A detailed list of species corresponding to individual species groups is available in Appendix 1.

To avoid spatial pseudoreplications (scent stations placed in a corridor and hayfield were paired and checked twice, during the spring and autumn), we used a Generalized Linear Mixed Model (GLMM) with a logit link function, assuming binomial distribution to fit our data (Bernoulli trial, i.e. predator absence vs. presence), as implemented in R 2.6.0. software. The model contained a random effect specified as scent station identity nested in a scent station pair. Habitat type (hayfield vs. corridor), species identity (coded as a three-level factor; 1. small mustelids, 2. domestic cat, 3. remaining carnivore species), temporal replication (spring vs. autumn) and the interactions between these variables were included as fixed effects in the analysis.

We evaluated the consistence of habitat preferences across species levels as the interaction between habitat type (hayfield vs. corridor location of the scent station) and species identity. Nevertheless the statistical non-significance in this case can be due to limited sample size (i.e. low statistical power); therefore, we performed three separate analyses for individual species levels in the next step; i.e. absence/presence of 1. small mustelids 2. domestic cat or 3. remaining carnivores included as the response variable in these analyses.

The GLMM approach provides approximate results especially in cases when sample size is low (see Faraway 2006). Therefore, to confirm the robustness of GLMM analyses, the McNemar Test was used to test for disproportional use of corridor and hayfield scent stations. Particularly, we used the McNemar Test to test if the number of corridor scent stations that were visited by at least one carnivore individual or that were unvisited during the whole experiment (10 day exposure) differs from the number of visited vs. unvisited hayfield scent stations. The same analyses were also performed separately for individual species levels (i.e. number of visited vs. unvisited scent stations by small mustelids, domestic cat and remaining carnivores).

Backward elimination of the non-significant terms in the GLMM was used to select the best minimal adequate models (MAM), i.e. the most parsimonious ones with all the effects being significant (Crawley 2007), eliminating at first non-significant interactions and then subsequently non-significant main effects. The significance of a particular explanatory variable was based on the change in deviance between the model containing this term and the reduced model. There was no hint of overdispersion in fitted models; thus we assumed a χ^2 distribution of difference in deviances, with degrees of freedom equal to the difference in the degrees of freedom between the models with and without the term in question (Crawley 2007).

Various carnivore species may be attracted to the same locality due to higher food recourses (Šálek et al. in prep). On the other hand, aggressive interspecific interactions often occur among carnivores. Both these mechanisms may result in correlated (positively or negatively) cross-species visits of scent stations. To address this point, we tested the non-independence of visits at a corridor scent station by individual carnivore groups using the GLMM model with Poisson error distribution. A vector of observed counts corresponding to all possible combinations of absence or presence of individual carnivore groups was included as a response variable (8 possible combinations). For each element of the response, absence or presence of an individual species group was coded as three separate factorial explanatory variables (i.e. small mustellids, domestic cat and remaining species). Identical scent stations were sampled two times, thus scent station identity was included as a random effect. The non-independence of visits was tested by evaluating the significance of interaction between explanatory variables (i.e. Crawley 2007).

We further tested for spatial randomness of the corridor scent stations visits. At first, distances between the two nearest corridor scent stations that were visited by the particular species groups (1. all carnivores regardless of species identity, 2. small mustelids, 3. domestic cat, 4. remaining carnivores) were estimated according to geographical coordinates. In the next step, the number of scent stations that corresponded to the total number of scent stations visited by the particular species group was randomly selected out of all 20 corridor scent stations. This randomization was repeated 100 times and nearest-neighbor distances between randomly selected scent stations were calculated in each step. Finally, real and simulated distances were compared using T tests. There were was no hint of spatial non-randomness in the scent station visits (i.e. distances between visited and simulated scent stations pairs were comparable in all four cases, $P > 0.1$).

Corridor characteristics: The effect of corridor characteristics on the probability of its visitation by carnivores was tested using GLMM. Carnivore presence or absence was included as a binary response variable in the model. As outlined in the previous section, species identity was included as a three-level factor (1. small mustelids, 2. domestic cat and 3. remanding carnivore species) in the analysis. The proportion of the corridor covered by shrubs and trees, corridor width, and two-way interactions between variables were included as explanatory variables in the model. Corridor identity and season were included as random effects. Three separate models for individual species levels were also performed in the next step. We used log transformation in the case of corridor width and arcsine transformation in the case of proportional data to achieve normality of the response variables. Data transformation, however, did not affect the results of the analysis. The procedure of minimal adequate model selection was identical to that in the first experiment.

Results

Corridor vs. hayfield matrix preferences: During the 400 station-nights (20 corridor and 20 hayfield stations checked for 5 nights during autumn 2005 and summer 2006), 36 carnivore scent stations visits were detected. Species detected during the scent station survey included domestic cat (*Felis catus*), red fox (*Vulpes vulpes*), polecat (*Putorius* spp.), ermine (*Mustela erminea*), least weasel (*M. nivalis*), and marten (*Martes* spp.). The detailed list of the number of visits recorded for individual species is given in Appendix 1. Carnivore visits predominated in corridors (35 visits), compared to hayfields (1 visit; see Fig 2).

A higher proportion of visited corridors compared to visited hayfield scent stations was confirmed by the GLMM model (Table 1) and the McNemar Test ($\chi^2 = 12.07, p < 0.001$). The non-significant interaction between species identity and habitat further suggests a consistent preference for corridors regardless of species identity (Table 1). On the other hand, the significant interaction between species and temporal replication indicates non-consistent fluctuations of individual species groups in temporal replications.

When performing separate models for particular species groups, corridor scent stations showed significantly higher probabilities of having a visit compared to hayfields in all cases (Table 1). The significance of these differences was confirmed using the McNemar

Test to compare the proportion of visited vs. unvisited scent stations for corridors and for hayfields ($\chi^2 = 6.75$, $p = 0.009$ for small mustelids, $\chi^2 = 4.17$, $p = 0.041$ for domestic cat and $\chi^2 = 3.2$, $p = 0.074$ for remaining carnivores). The number of visited scent stations remained constant in spring 2006 compared to autumn 2005 in the case of small mustelids; however it was significantly lower for domestic cat (0 vs. 6 scent stations visited, Table 1). A similar although insignificant decrease was observed for remaining carnivore species (4 vs. 1 scent stations visited).

There was no inter-dependence of carnivore presence or absence at a particular scent station during two subsequent temporal replications. This was valid when analyzing both all carnivore visits ($D.f. = 1$, $\chi^2 = 1.53$, $p > 0.2$) or just small mustelids ($D.f. = 1$, $\chi^2 = 0.32$, $p > 0.5$).

The non-significant interaction terms in the contingency GLMM between small mustelids and domestic cat (Δ $D.f. = 1$, $\chi^2 = 0.85$, $p = 0.355$), between domestic cat and remaining carnivores (Δ $D.f. = 1$, $\chi^2 = 1.21$, $p = 0.270$), between small mustelids and remaining carnivores (Δ $D.f. = 1$, $\chi^2 = 3.24$, $p = 0.072$) and between all three species levels (Δ $D.f. = 1$, $\chi^2 < 0.01$, $p = 1.000$) do not indicate an independence of visits. Our data thus do not reveal correlations among visits of individual scent stations by various carnivore groups.

Corridor characteristics: Using data from the 37 scent stations, our study did not detect any significant association between the measured corridor features (shrub and tree cover, corridor width) and its exploitation by carnivores. None of these variables, either alone or in interaction with each other, explained predator occurrence (Δ $D.f. = 1$, $\chi^2 < 1.65$, $p > 0.2$ for all explanatory variables and their interactions). Qualitatively, the same results were obtained when performing separate analyses for individual species levels (all Δ $D.f. = 1$, $\chi^2 < 2.60$, $p > 0.1$).

Discussion

Our data show that all carnivores in fragmented agricultural landscapes tend to perceive and use corridors with higher probability compared to hayfield matrix. Most visits of scent stations were ascribed to small mustelids. This fact might bias our general conclusions about corridor use by mammalian carnivores, since small mustelids often exhibit strong preferences for liner structures in agricultural landscapes (e.g. MacDonald *et al.* 2004). Nevertheless, significant preferences for corridors were revealed even when small mustelids were excluded from the dataset, for both domestic cat and remaining carnivores. In addition, or data do not indicate an interspecific dependence of scent station visits. Such dependence might be expected, for example, if interspecific agonistic interactions constrain the spatial distribution of carnivores (negatively correlated visits, e.g. Palomeras & Caro 2005), or, on the other hand, if different carnivore species tend to exploit the same patches due to enhanced prey densities (positively correlated visits, e.g. Kurki et al. 1998).

Although our results are consistent with recent studies that have reported a much higher probability of carnivore occurrence in corridors compared to a surrounding vineyard (11 times higher) or crop field matrixes (4 times higher) in a North American landscape (Gehring and Swihart 2003; Hilty and Merenlender 2004), the almost complete lack of mammalian carnivores in hayfields in our study area is striking. Most grasslands areas in the Czech Republic (as well as in many other European countries) are subject to intensive landscape management practices which are financially supported by European Council Regulation (EC) No 1698/2005. In most cases, farmers in the Czech Republic are asked to mow grasslands at least twice a year in order to receive financial support. For carnivores, this management practice results in poor vegetation concealment and low abundance of potential prey (rodents; Šálek *et al. unpubl data*) in almost all grasslands areas in the Czech Republic for a large part of the year. Although hayfield mowing might have some positive effects on the native biota, such as temporarily improved foraging opportunities for some species (Atkinson *et al.* 2004, Wuczynski 2005), the low frequency of hayfield visits compared to undisturbed corridors indicate that frequent grass mowing may actually transform grasslands into unfavorable habitats for animal taxa such as mammalian carnivores. However, since our data do not directly test the hypothesis that regularly mowed grasslands are avoided by mammalian carnivores, further research is required.

Contrary to several previous studies (Arnold 1983; Laurance and Laurance 1999; Hilty and Merenlender 2004), we failed to detect any indication that differences in the structure of vegetation cover or corridor width alter the probability of corridor visits by carnivores. The only study that has previously addressed this topic for mammalian carnivores reported stronger preferences for wider (360-1450 m wide) than for narrow corridors (1-28 m wide), and for corridors covered by trees (Hilty and Merenlender 2004). However, the width of corridors in our study was probably below the threshold necessary to for the effect of width to be reflected in the occurrence of mammals. In addition, the structure of vegetation cover of corridors in our locality is comparable to forest/arable landscape edges (i.e. a higher density and diversity of both shrubs and herbaceous cover). Carnivore species detected during our study tend to exhibit habitat preferences for habitat edges compared to forest and hayfield interiors (Šálek et al. unpubl. data, Svobodova et al. unpubl. data). Consequently, if predators perceive corridors as an edge structure, they may use corridors preferentially regardless of their width.

Carnivores exploit linear structures primarily due to the elevated abundance of potential prey, especially birds (Arnold 1983; Vickery et al. 2002), small rodents (Tattersall *et al.* 2002; Šálek *et al.* unpubl. data), or invertebrates (Frank 1997), compared to the surrounding agricultural matrix. However, prey densities generally vary according to corridor width and vegetation cover (Arnold 1983; Green *et al.* 1994; Kotzageorgis and

Mason 1997). Therefore, the lack of an association between the corridor character and its use by carnivores observed in our study could indicate that linear structures may also serve primarily as movement corridors, providing more effective and less costly dispersal between disconnected patches of preferred habitats (e.g. Dunning, et al. 1992; Rosenberg *et al.* 1998).

Although our data indicate that corridors are important for mammalian carnivore populations, this point should be the subject of closer scrutiny. One potentially fruitful approach might be to evaluate the use of corridors and other landscape elements on large spatial scales in varying landscape contexts (i.e. different proportions of unfavorable landscape matrix). Previous theoretical contributions have demonstrated that the area of patches of natural habitats should not decrease below a particular minimal size to maintain a viable population, implying the strong importance of geometrical arrangement of habitats patches in landscapes suffering intense natural habitat loss (e.g. Fahing 1998, Flather and Bevers 2002). Consequently, given that corridors moderate the effect of habitat loss via interconnection of spatially separated habitat patches, one can expect that their importance should increase with increasing proportion of unfavourable matrix in landscapes.

The impact of carnivores on populations of their prey and on ecosystem stability has been widely recognized. Particularly in agriculture landscapes, carnivore populations are involved in the regulation of the intensity and frequency of vole (*Microtus* sp.) outbreaks (Delattre et al. 1992, 1999). For example, Delattre et al. (1992) showed that crop damage correlates negatively with the proportion of land covered by forest patches that serve as refuges for mustelids, suggesting that landscape composition management should be involved in pest control. In line with these findings, our data indicate an enhanced exploitation of broader zones of agriculture matrixes by carnivores due to the presence of corridors, suggesting that maintenance of linear strips of vegetation in arable landscapes may indirectly help to partly mitigate the negative effect of small rodents on crop production. However, a more detailed evaluation is necessary.

On the other hand, conservation of agricultural landscapes is often focused on enhancing linear habitats along field margins to increase biodiversity (Boatman et al. 1999); yet, the question of whether this is really an efficient strategy compared to alternative practices (e.g. set-asides) has been poorly evaluated. Despite the increased diversity of several animal taxa in linear patches compared to agricultural matrixes (Arnold 1983; Frank 1997; Gehring and Swihart 2003; this study), a recent study found only negligible differences in the abundance and diversity of a small mammal community between linear and non-linear patches in an agricultural landscape (Tattersall *et al.* 2002). Linearity could even have some adverse effects on animal communities such as song birds. The elevated probability of predator presence in linear structures, as demonstrated in our study, may lead to increased predation pressure on bird nests (Haensley *et al.* 1987; Major et al. 1999, Willson *et al.* 2001; but see Zuria *et al.* 2007), due to more predictably distributed prey, and consequently a more effective mammalian predator searching strategy in linear versus non-linear patches (e.g. Seymour *et al.* 2004).

In conclusion, our study shows that the maintenance of corridors may be an efficient management practice to preserve carnivore populations in intensively-used agricultural landscapes. However, high densities of predators in linear habitats may have adverse effects on native prey communities due to elevated predation, a subject which requires further research.

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Table 1: GLMM fitting results for the probability of the detection of particular carnivore groups at scent stations. Significance values correspond to deletion tests. Factors included in the minimal adequate model for each carnivore group are in bold print.

		all species		small mustellids		domestic cat		remaning species	
fixed effect [a]	df	χ^2	p	χ^2	p	χ^2	p	χ^2	p
species	2	4.14	0.126	-	-	-	-	-	-
temp. rep.	1	2.53	0.116	0.45	0.503	**9.38**	**0.002**	2.18	0.139
habitat	1	**25.77**	**< 0.001**	**11.19**	**0.001**	**9.38**	**0.002**	**7.4**	**0.007**
species × temp. rep.	2	**9.2**	**0.01**	-	-	-	-	-	-
species × habitat	2	0.23	0.893	-	-	-	-	-	-
temp. × rep. habitat	1	2.16	0.142	1.09	0.297	< 0.01	0.999	< 0.01	0.999

[a] Fixed effects: Habitat - corridor vs. hayfield location of a scent station, Species - small mustelids vs. domestic cat vs. remaining carnivores (not included when analyzing data for individual species), Temp. rep.- temporal replication, autumn 2005 vs. spring 2006.

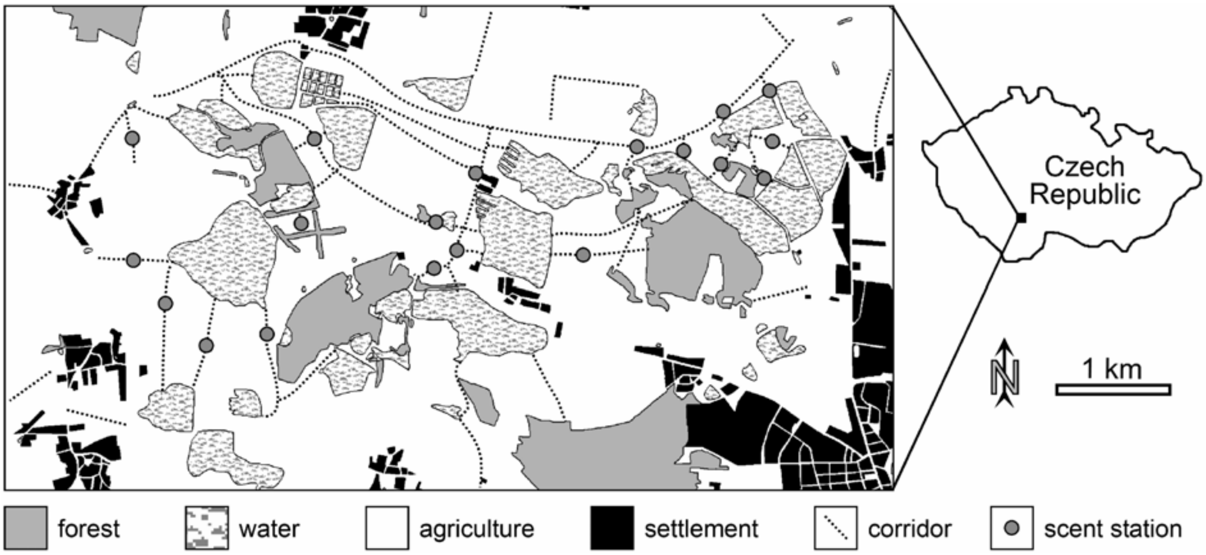

Figure 1. Distribution of corridors and spacing of scent station pairs (corridor and hayfield) in the study area Doudlebia, the Czech Republic during the first experiment.

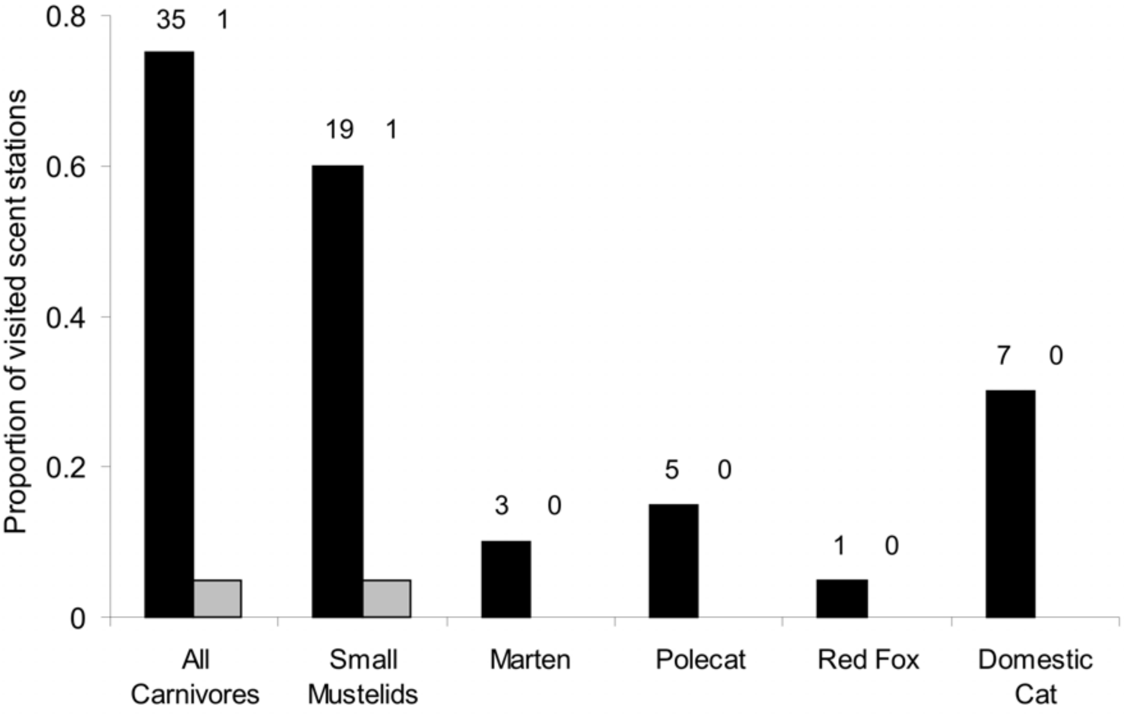

Figure 2. The proportion of corridor (black bars) and hayfield (grey bars) scent stations that were visited at least once by a particular carnivore group during the entire experiment (autumn 2005 + spring 2006 temporal replication, 10 days of exposure; multiple visits of the same scent station were not taken into account).

Svobodová J., Kreisinger J., Šálek M., Koubová M., Albrecht T.:

Testing a mechanistic explanation for mammalian predator responses to habitat edges. (*submitted*)

Testing a mechanistic explanation for mammalian predator responses to habitat edges

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Abstract

Several mechanistic explanations have been suggested to explain increased predation along habitat edges. Most studies have examined increased predator activity along edges as an explanation for these edge effects, but have not, however, been able to explicitly test the hypothesized mechanisms. In this study, we simultaneously measured the distribution of mammalian predators, the predators' main prey (small mammals) and predation rates on simulated nests in four types of landscape elements corresponding to an edge gradient between two habitat types; grassland and forest. We found a contrasting pattern in carnivore habitat preferences between years. Whereas carnivores did not exhibit a significant habitat preference along the forest-grassland edge in the first year of monitoring, they were more likely to be detected along habitat edges in the subsequent year. Our results do not suggest that the increased activity of carnivores at habitat edges arises as a consequence of predator overflow from higher quality habitat through the edge into lower quality habitat, but showed that most predator species focus their activity specifically to the edge structure. We further discuss the possibility that the year-to-year variation in carnivore habitat preferences might be caused by a variation in small mammals abundance.

We did not find a clear relationship between carnivore activity and artificial nest predation, because other nest predators like corvids and wild boar which were not detected by scent stations contributed to nest losses.

Key words: ecotone, edge effect, nest predation, habitat fragmentation, mesopredators

Introduction

Anthropogenic habitat fragmentation primarily includes reductions in patch size, increases in patch isolation and increases in the proportion of habitat edges to interior. These landscape changes often alter ecological processes, which result in the altered distribution of many species. High rates of fragmentation can lead to declines in population density and even to species extinction (Donovan et al. 1995). Small isolated populations are particularly less resistant to disturbances (Brown and Kodric-Brown 1977; Gilpin and Hanski 1991). Moreover, they may not be able to sufficiently withstand environmental changes due to the deleterious effects of inbreeding (Frankham 2005).

In addition, the negative impacts of fragmentation are also associated with changes to the structure and density of predator communities (Chalfoun et al. 2002b). Fragmented landscapes generally maintain a higher numbers of predators, particularly mammalian mesopredators (e.g., Crooks and Soulé 1999) and corvids (*Corvidae*), compared to non-fragmented habitats. This often results in increased nest predation, mainly along edges (edge effect e.g., Andrén 1992) or within small fragments (e.g., Crooks 2002, Winter et al. 2006). Consequently, enhanced predation often lowers the reproductive success of locally breeding birds (Crooks and Soulé 1999) and may lead to population declines of birds throughout entire geographic regions (Schmidt 2003, Wilcove 1985).

Despite the considerable conservation and predictive value of many previous studies, relatively little attention has been paid to the mechanisms underlying increased predation along habitat edges. Several mechanistic explanations have been suggested for this phenomenon, assuming a generally causal link between differences in habitat specific resources and predator occurrence (Ries et al. 2004, Ries and Sisk 2004): (i) A neutral (no) predator response to an ecotone gradient is predicted if there is no variation in resources (resources are supplementary) between both habitats. This represents the null model. (ii) If predator abundances vary between two habitats due to qualitatively different resource availability (say e.g., H+ and H-), penetration of predators from the habitat interior with more abundant predator fauna (H+) into the second habitat (H-) may cause a gradual gradient of predation through the transect between adjacent habitats (the matrix effect senzu Lidicker 1999, see also Andrén 1995, Wilcove 1985). (iiiA) However, if a habitat of lower quality contains complementary (qualitatively different) resources, the predator specialists typical for one habitat may mix with predators typical for the second habitat because both types of resources are more available near the edges. This results in increased abundance and species richness of predators along edges, which may cause potential prey (e.g., bird nests) to be exposed to higher predation pressure. (iiiB) A similar scenario will occur if adjacent habitats are of equal quality but contain complementary resources. (iv) Increased predation pressure does not necessary have to arise through the mixing of interior specialists along habitat edge as was suggested above. At least some predator species can be edge specialists that may prefer edge structures per se due to concentrated and/or complementary resources and/or due to effective displacement along habitat edges (i.e. the "travel line hypothesis"; Bider 1968; (iiiA, B, iv) ecotonal effect).

Although many studies have detected increased predation pressure along the edges of various habitat types (e.g., Bayne and Hobson 1997, Dijak and Thompson 2000, Donovan et al. 1997, Malt and Lank 2007) only few of them were able to explicitly test the competing mechanistic explanations of the edge effect as outlined above. This is might be due to drawbacks associated with the experimental design. First, gradient in the predation risk was often not registered along the entire edge gradient (i.e., in the habitat edge and both adjacent habitats; Albrecht 2004, Chalfoun et al.

2002a, Heske 1995), which means that it was not possible to determine if the edge effect arose as a consequence of predator penetration into adjacent habitat or due to the specifically enhanced activity of edge specialist predator species along habitat edge. Second, since most studies did not collect data on prey distribution (e.g., Dijak and Thompson 2000, Donovan et al. 1997, Hilty and Merenlender 2004), habitat qualities could not be sufficiently evaluated. Third, most studies often failed to reliably determine particular predator species (e.g., Huhta et al. 1998, Pasitschniak-Arts and Messier 1995b, Storch et al. 2005). Therefore, they could not detect if the edge effect arose due to the presence of "edge specialist predators" in habitat edges or solely due to exploitation of the habitat edge by specialists from both habitat interiors.

Surprisingly little attention has been paid to an evaluation of mechanisms underlining mammalian carnivore distributions along habitat edges in fragmented landscapes, even though the significance of their contribution to altered predation patterns in human modified landscapes has already been demonstrated (Crooks and Soulé 1999).

The aim of this study is to test mechanisms resulting in the emergence of the edge effect in a landscape fragmented by agriculture in Southern Bohemia, the Czech Republic. To do this, we simultaneously studied the distribution of mammalian predators, the distribution of small mammals (dominated by various rodent species in our locality) as the main prey (Goszczyński 1986, Lanszki and Heltai 2007, Lanszki et al. 2007, Martinoli et al. 2001), and predation rates on simulated nests in four types of landscape elements corresponding to an edge gradient between two habitat types. "Interior habitats" consisted of secondary mixed forest and hay-producing meadows. Following the definition of Lidicker (1999), "edge habitats" comprised the borderline part of forests and the borderline of meadows. Our experimental design enabled us to confront empirical data with predictions underlining the alternative hypothetical mechanisms leading to the edge effect as discussed above: (i) A neutral predator response to an ecotone gradient, as a consequence of no variation in habitat specific resources, is considered to be the null model. (ii) If the edge effect is caused by predators typical for farmland (or alternatively for forest) which penetrate to forest edges (or farmland edges), there would be expected a gradient of decreasing predator abundance and simultaneously decreasing predation rate from the core of the first habitat, across the edge of the first and second habitat, to the core of the second habitat (i.e., the matrix edge effect is a sufficient explanation for the observed predation gradient; Lidicker 1999). In contrast, the following two hypotheses predict that predator abundances will be enhanced in edge habitats (ecotonal effect; Lidicker 1999): (iii) If edge effect arises due to a mixture of matrix interior specialists typical for forest and agricultural habitats within their edge, one would expect higher predator abundance and richness there. (iv) Finally, if the edge effect arises due to prevailing edge specialists in fragmented landscapes, then at least some predator species will be more abundant in edge habitat than in core habitats. A relationship between the distribution of carnivore activity and nest predation can be expected, though nest predation by mammalian predators is mostly incidental (Vickery et al. 1992).

Study area and methods

The study area was situated in Southern Bohemia (the Czech Republic) in the Písecké hory Mts. region (49°11′ – 49°18′ 14°09′ – 14°22′, 350 a.s.l., 60.3 km^2). The area was formed by a complex of coniferous, deciduous and mixed production forests surrounded by farmland consisted mostly of hayfields, extensively used pastures, and cultivated fields that were partitioned by line habitats such as shrub and tree growth along draining channels and roads (see below).

Carnivore sampling design

The spatial distribution of mammalian predators was studied using scent stations during May 2006 and 2007. In total, 80 scent stations were installed both years at the same localities (n = 20), with four habitat types represented: 1) grassland interior, 2) forest interior (interior scent stations were set up 100 m away from the nearest forest/grassland edge), 3) grassland edge and 4) forest edge (edge scent stations were set up in a 5 m wide margin strip of grassland or meadow immediately adjoining the forest/meadow border). Whereas the minimum distance between adjacent scent stations within a locality was 100 m, the minimum distance between neighbouring localities was 300 m in order to achieve independence of the replicate sites (e.g., Gehring and Swihart 2003). In order to ensure predefined habitat and distance criteria for scent station positions, sites were prior selected using digitized aerial ortho-photo-maps of the study area using GIS software (ArcView GIS 3.2a).

All habitats studied were highly modified by agriculture and other human activities, as described below:

1. Grasslands mostly consisted of production hayfields and extensively used pastures. Hayfields were almost entirely drained and reseeded with competitive nitrogen-demanding species such as *Lolium multiflorum*, *Phleum pratense*, *Festuca pratenis* and *Dactylis glomerata*.
2. Forests were composed of intensively managed stands; the tree canopy was typically dominated by conifers (*Picea abies* and *Pinus sylvestris*), with occasional broad-leaved tree species such as oak (*Quercus* spp.), birch (*Betula pendula*) and

beech (*Fagus sylvaticus*). Shrub and herbal undergrowth was very sparsely developed.

3. Forest edges were usually fringed with oak, linden (*Tilia* spp.) and managed-stand trees such as spruce, pine as well as poplar (*Populus* spp.) and birch. The shrub layer was usually dense, consisting mainly of shrubs (*Corylus avellana*, *Prunus spinosa*) and saplings of canopy trees. This habitat type was also characterized by dense and diversified herbaceous vegetation mainly originating from the nearby grassland.

4. Grassland edge vegetation was sparsely developed in comparison to grassland interior hayfields, but the species composition was mostly identical.

For the purpose of this study, scent stations were constructed as a 1×1 m square filled with a 2 cm thick layer of fine-grained masonry sand. To analyze predator distribution on a relatively small spatial scale, and hence to avoid alluring animals from greater distances, domestic rabbit urine was used as a mild attractant (Linhart & Knowlton 1975). Rabbit urine in a 1.5 ml microcentrifuge tube was fixed to a wooden stick and placed in the centre of each scent station, approximately 15 cm above the ground. Scent stations were monitored every morning for five consecutive days.

Mammalian predators were identified according to the size and shape of their footprints (Anděra and Horáček 2005). Since closely related species were difficult to distinguish from each other, the following predators were classified: red fox (*Vulpes vulpes*), marten (*Martes martes* and *M. foina*), small mustelid (*Mustela nivalis*, *M. erminea*), western polecat (*Mustela putorius*), european badger (*Meles meles*), domestic cat, domestic dog, and unidentified carnivore.

Distribution of small mammals

To estimate prey distribution, we examined the abundance of small mammals during the same years using random subsample of the same localities (8 in total) as in the mesopredator survey described above, including all four habitat types. Small mammals were captured using regular snap traps which were baited with wicks dipped in fat and flour. At each of eight localities, traps were placed in 4 lines of 35 traps each, with 5 m between traps (so the total length of each line was about 175 m). Thus, a total of 1120 traps were set each year (8 localities, 4 lines per locality, with 35 traps per line). . Since the trap efficiency can be affected by the capture from the previous day, all traps were set for 24 hours. Trap lines were positioned using similar habitat and distance criteria as for the scent stations (see above).

Nest predation

Nests predation was investigated using experimental nests at the beginning of May in 2007. Artificial ground nests were evenly distributed in the same four habitat types as for scent stations (grassland and forest interiors, grassland and forest edges). In total, 240 nests were concurrently installed in 60 localities representing all four habitat types. All habitat and distance criteria for nest positions were the same as for scent stations (see above). Since nests were exposed during the same time as scent stations, a minimum distance between neighbouring nests and stations of 300 m was used.

The artificial nests were constructed by digging small ground depressions, and then lining them with small amounts of dry plant material resembling the nest linings of ground nesting birds such as pheasant (*Phasianus colchicus*) or grey partridge (*Perdix perdix*, Hudec and Šťastný 2005). Each nest was baited with two domestic hen eggs, one of which was filled with wax for predator identification

(Pasitschniak-Arts and Messier 1995b). Wax eggs were anchored in the nest pits with a string and nail in order to prevent predators from carrying them away.

Each nest was checked after a 14-day exposure period. A nest was considered depredated when at least one of the two installed eggs was damaged, removed from the nest bowl or missing. Nest predators were identified by beak or tooth marks left on the wax eggs, which were compared with marks simulated using the skulls of potential mammalian predators (Nour et al. 1993). The following categories of experimental nest predators were distinguished: red fox, marten, corvid, small mammals, unidentified mammal, and unidentified predator.

Data analysis

The effect of habitat type on the distribution of mammalian predators (and predation risk) was evaluated using a generalized linear model with mixed effects (GLMM), with a predator visit to a scent station as the dependent variable. Since a scent station could have been repeatedly visited by the same predator during the five days of exposure, the predator visit variable was fitted as variable binary response variable (present/absent). In addition, habitat type, effect of year and locality were included in the model. The habitat type and year were considered as fixed effects, To avoid spatio-temporal pseudoreplications the locality was included as a random effect nested to the year of the study.

The distribution of nest predation and small mammals were also analysed using a GLMM. Whereas the fate of experimental nests was tested as a dependent variable with binomial distribution, numbers of captured small mammals in the lines of 35 traps were analysed assuming a Poisson distribution of errors. Similarly for both models, habitat type was fitted as a fixed effect and locality (nested to the year of the study) as a random effect. Since small mammal distributions were investigated during two breeding seasons, the effect of year was also included in the model.

In all analyses, the significance of both explanatory variables and their way interaction, was calculated by a change of deviance between the model containing particular term and the reduced model (deletion tests; Crawley 2002). The best minimal adequate model (MAM - the model with the lowest parsimony and all variables being significant) was achieved by backward elimination of non-significant effects. All analyses were performed in R 2.6.2 software.

The mechanism leading to the emergence of the edge effect was assessed by pooling specific levels of habitat type (posterior tests; Crawley 2002). To test predator preferences for ecotones, interior habitats and edge habitats (i.e., grassland edge + forest edges and grassland interior + forest interiors) were pooled, respectively. Then, by pooling grassland interior with grassland edge and forest interior with forest edge, it was tested if predators penetrate from habitat interiors to the edges.

Results

Mesopredator distribution

We recorded 70 visitations by seven predator species during 800 station-nights (8.8 % +/- 0.07 SE visitation probability per night, Table 2). The species with the highest visitation rates included house cat (*Felis silvestris catus*, 17x), small mustelids (10x), red fox (10x) and domestic dog (*Canis lupus familiaris*, 8x). However, since dogs usually follow the movement of their owners and are assumed to not contribute considerably to nest predation in our locality, they were excluded from subsequent analyses. Nevertheless, this exclusion of domestic dog did not affect the conclusions of further statistical analyses.

We found a significant interaction between year and habitat type (Table 4, Fig 1.), suggesting inconsistent habitat preferences over time. Although predator visits to scent stations were slightly higher in 2007 (30 %) than in 2006 (22.5%), the year main effect was not significant after eliminating the year vs. habitat type interaction from the model (Table 4). On the other hand, deletion of the habitat type main effect from the model resulted in a significant increase of the residual deviance. Due to the significance of this year vs. habitat type interaction in the initial model, we further analyzed differences in the probability of visits to particular localities for each year separately. Whereas in 2006 no difference was found between particular habitat types (χ^2 = 0.31, Δdf = 3, P = 0.957), in 2007 posterior comparisons revealed that predators used forest and grassland interiors and forest and grassland edges (χ^2 = 0.37, Δdf = 1, P = 0.544), respectively, with comparable intensity. However, the significant contrast between forest edge and forest interior (χ^2 = 8.16, Δdf = 1, P = 0.004), and grassland edge and grassland interior (χ^2 = 13.42, Δdf = 1, P < 0.001), indicated that predators had a preference for edges in year 2006. Considering the activities of particular predator species, domestic cat was the most frequent predator at grassland edges (Tab. 2).

Distribution of small mammals

In total, 105 small mammals were captured during 2006 and 2007. However, in 2006 the numbers of small mammals were almost 9 times lower (1.4 ± 0.19 SE numbers per line) than in the consecutive year (11.8 ± 0.35 SE numbers per line).

The GLMM model revealed that numbers of small mammals changed significantly between years and habitat types. However, the interaction between these variables was insignificant (Table 5). The highest numbers of small mammals were recorded at forest edges and the lowest in grassland interiors (Fig. 2). Posterior comparisons indicated similar small mammal abundance between the interiors and edges of particular habitats. However, while grassland edge with grassland interior (χ^2 = 0.48, Δdf = 1, p = 0.490) were pooled without significant change to the residual deviance, the contrast between forest edge and forest interior was marginally significant (χ^2 = 2.994, Δdf = 1, p = 0.083). On the other hand, pooling both edges (χ^2 = 27.99, Δdf = 1, p < 0.001) and both interiors (χ^2 = 18.29, Δdf = 1, p < 0.001), respectively, led to significant changes to the residual deviance.

Distribution of nest predation

The distribution of nest predation, investigated only in 2007, did not show any relationships to mesopredator distribution. Predation on experimental nests did not vary between habitat types (χ^2 = 3.50, Δdf = 3, p = 0.321). Fox and small mustelids were identified as the most frequent nest predators; however, a high proportion of predators were not classified (70.7 %, Table 3).

Discussion

Increased predation risk along habitat edges is a widely observed pattern, at least in the northern temperate zone (e.g., Bayne and Hobson 1997, Dijak and Thompson 2000, Donovan et al. 1997, Malt and Lank 2007). This phenomenon, together with the adverse effects of habitat lost and population fragmentation, has reduced the viability of many bird populations (Batáry and Báldi 2004, Stephens et al. 2003). However, most previous studies have generally used only proxy measures to estimate overall predation risk (e.g., nest survival). Our study focused primary on the distribution of mammalian mesopredators, which are assumed to have serious effects on songbird populations (Crooks and Soulé 1999, Heske et al. 1999). In particular, we focused on the environmental gradient corresponding to the transition between the interior/edge of two habitats - grassland and secondary forest.

Interestingly, our data show large temporal variation in the contribution of carnivores to predation risk along the interior/edge continuum. In the first year of our study, carnivores did not exhibit preferences for any particular habitat type, suggesting that under some circumstances carnivores do not need to substantially respond to forest/grassland edges in agricultural landscapes. This result is partly in support of the null hypothesis (i.e. no response of predators to transitions between the two habitats). However, a contrasting pattern of predator distribution was found in the subsequent year. Our data showed, as have many previous studies (e.g., Dijak and Thompson 2000, Donovan et al. 1997), increased activity of predators specifically along habitat edges, irrespective of the edge type (forest or grassland edge). Moreover, predator activity within grassland and forest interiors was significantly lower and did not differ between both habitat interiors (Fig. 1). Hence, the possibility that the contribution of mammalian predators to the edge effect is a result of overflow from one habitat through the habitat edge into a second habitat (i.e. the spillover model, matrix edge effect senzu Lidicker 1999) was not supported during the second year. Although the spillover model might be the simplest explanation of the edge effect mechanism (i.e., increased predation risk along edge habitats), only few studies have been able to reject this hypothesis, since predation patterns have rarely been measured across the whole ecotone continuum (but see Gates and Gysel 1978, Ratti and Reese 1988).

The higher activity of carnivores along grassland/forest edges clearly supports the ecotonal edge effect model, which suggests the emergent property of predator distribution across the edge continuum (Lidicker 1999). Consistent with this conclusion, the tendency of mammalian predators to avoid habitat interiors and at the same time to prefer edge structures has previously been demonstrated for a forest-to-meadow transition in a Central European landscape (Šálek et al. *unpubl. manuscript*). At least two alternative mechanisms for a specific increase in predation risk and/or predator abundance at habit edges (i.e. the ecotonal edge effect model) have been suggested. Firstly, increased predator abundance along an edge may appear due to the mixture of predator faunas that differ between adjacent habitats (Ries et al. 2004). Alternatively, some species of predators may focus their activity specifically to edge structures (i.e. "edge habitat specialist"; Larivière and Messier 2000). Our data lends support to this second possibility, because all species detected in our study tended to more likely occur at the edge of habitats compared to the interiors. In addition, we found no species that tended to prefer the grassland interior over the other habitat types.

Although the edge effect model has been supported over the matrix effect model (Lidicker 1999) by empirical data in several cases (Heske 1995, Šálek et al. *unpubl. manuscript*, this study), a mechanistic explanation for this pattern still remains elusive. As recently suggested by Ries & Sisk (2004), increased predation along habitat edges may be due to a mixture of resources (exploited by predators) that differ qualitatively or quantitatively between habitats. Alternatively, a high abundance of resources at least partially specific for habitat edges might be involved in the process of habitat selection by predators. Densities of small mammals (rodents) that may form up to 80 % of the diet of mammalian mesopredators (Goszczyński 1986, Lanszki and Heltai 2007, Lanszki et al. 2007, Martinoli et al. 2001), were previously found to affect habitat preferences of mesopredators in fine spatial scales (Šálek et al. *unpubl. manuscript*). However surprisingly, our data do not provide straightforward evidence for an association between the habitat-specific quantity of food resources and predator distribution. The abundance of small mammals was approximately 3-4 times higher in forest compared to grassland habitats in both year of the study (irrespective if measured in edges or interiors, see Fig 1). We did not observe the predicted spatial shift in the distribution of mammalian carnivores, however (i.e. both forest and meadow habitats were visited with similar intensity). It is necessary to stress that our study did not attempt to quantify the habitat-specific distribution of alternative food resources that may complement part of the carnivore diet such as passerine birds, bird clutches, amphibians or insect. Nevertheless, these resources are usually a less important part of the diet of mammalian carnivores compared to small mammals (Goszczyński 1986, Genovesi et al. 1996, Lanszki et al. 2007, Martinoli et al. 2001), and most of these are also likely to be more abundant at forest edges compared to heavily exploited grasslands (Buse and Good 1993, Flashpohler et al. 2001, Lázaro et al. 2005, Šálek et al. *in press*).

On the other hand, small mammals density was slightly higher at forest edges compared to forest interiors. Thus, the higher abundance of carnivores at forest edges might be at least partly explained by the spatial pattern of the distribution of food resources. Interestingly, carnivores did not exhibit a significant preference for the forest-grassland edge in the year with low small mammals abundance, whereas they were more likely to be detected at habitat edges in the year with high small mammal abundance (with an 8-9 fold increase in small mammals abundance, Fig 1). This suggests that carnivores switch their search efforts from habitat edges that are most profitable in years with high small mammals densities to a more diverse spectrum of habitats that may provide supplementary resources in small mammals - poor years. As carnivores seek prey in a wider band (Larivière 2003), increased activity might also be observed at grassland edges. Alternatively, carnivores may seek prey only within forest edges, and use grassland edges just for moving between preferred landscape segments (i.e. the travel line hypothesis; Bider 1968). However, our experimental design did not allow us to distinguish between these two alternatives.

We also attempted to evaluate the contribution of mesopredators to nest predation risk. However, our artificial nest experiment did not find increased predation risk along forest-grassland edges in the year when carnivore activity was higher in this habitat. Hence, we were unable to confirm a clear relationship between carnivore activity and nest predation risk. Although patterns of predation risk may differ between real and artificial nests (e.g., Major and Kendal 1996, Zanette 2000, but see Part and Wretenberg 2001), this apparent discrepancy is rather likely to be caused by the different community of predators identified by the two survey techniques. In particular, house cat, the most frequent predator in scent stations at grassland edges, are not expected to be able to rob eggs (Kays and DeWan 2004). On the other hand, the activities of other nest predators like jay (*Garrulus glandarius*), other species of corvids or wild boar, which are not detected by scent stations, are not directly influenced by the distribution and dynamics of small mammals.

In conclusion, our study has shown temporal variation in carnivore habitat preferences which could have been caused by the variation in small mammals abundance. Our results suggest that the emergence of the edge effect is not necessarily caused by mesopredator penetration from habitats with higher predator density into habitats with lower predator density, but that it is caused by predator concentration along the edge itself. The proximate explanation for higher abundances of mammalian mesopredators at edges compared to interiors remains unknown, but possibly includes higher prey availability and/or effective displacement along habitat edges. Nevertheless, generalizations about predation risk in fragmented landscapes should also take local predator composition into account, because other nest predators like wild boar and corvids can significantly contribute to nest losses.

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Tab. 1 Visits of individual species to particular habitats. Numbers in parenthesis are proportions of visited scent stations. In total, 120 scent stations were randomly distributed within four habitat types (Southern Bohemia in 2006 and 2007).

	Grassland interior	Grassland edge	Forest edge	Forest interior	Total
House cat	2 (0.10)	12 (0.60)	3 (0.15)	0 (0.00)	17 (0.21)
Red fox	0 (0.00)	5 (0.25)	3 (0.15)	2 (0.10)	10 (0.13)
Martens	1 (0.05)	2 (0.10)	1 (0.05)	1 (0.05)	5 (0.06)
Small mustelids	2 (0.10)	2 (0.10)	4 (0.20)	2 (0.10)	10 (0.13)
Western polecat	0 (0.00)	3 (0.15)	4 (0.20)	0 (0.00)	7 (0.09)
European badger	0 (0.00)	1 (0.05)	2 (0.10)	2 (0.10)	5 (0.06)
Domestic dog	0 (0.00)	12 (0.60)	1 (0.05)	1 (0.05)	8 (0.01)
Unidentified	1 (0.05)	4 (0.20)	3 (0.15)	0 (0.00)	8 (0.01)
total	6	35	21	8	70

Tab. 2 Numbers of small mammals captured along edge gradients in Southern Bohemia, 2006 and 2007. In each habitat type, 8 lines of 35 traps were installed.

	Grassland interior	Grassland edge	Forest edge	Forest interior	Total
Yellow-necked mouse	1	7	39	26	73
Wood mouse	3	2	10	5	20
Bank vole	0	0	2	3	5
Common vole	4	2	0	0	6
Common shrew	0	0	0	1	1
Total	8	11	51	35	105

Tab. 3 Numbers of depredated nests by particular predator species for all studied habitats in Southern Bohemia, in 2007. The number of nests exposed in particular habitat types is given in parentheses.

	Grassland interior (56)	Grassland edge (61)	Forest edge (58)	Forest interior (58)	Total (233)
Red fox	0	2	2	3	7
Small mustelids	1	2	4	1	8
Wild boar	0	3	1	2	6
Bird	2	2	0	1	5
Mammal	2	0	2	2	6
Unidentified	19	10	18	13	60
Total	24	19	27	22	92

Tab. 4 GLMMs results for probability of the occurrence of a mammalian predator at scent stations in Southern Bohemia, 2006 and 2007. Domestic dog was excluded from the analysis.

Factors	Δdf	AIC	χ^2	P
Habitat	3	182.39	13.82	0.003
Year	1	191.04	1.17	0.279
Habitat × Year	3	180.61	8.62	0.035

AIC = Akaike's Information Criterion

Tab. 5 GLMMs results for small mammal abundance in Southern Bohemia, 2006 and 2007.

Factors	Δdf	AIC	χ^2	P
Habitat	3	119.777	49.73	>0.001
Year	1	157.026	8.48	0.004
Habitat × Year	3	116.703	2.59	0.459

AIC = Akaike's Information Criterion

Fig. 1. Proportion of scent stations visited by mammalian predators in particular habitat types of Southern Bohemia in 2006 and 2007. Domestic dog was excluded from the analysis. Habitat types where the scent stations were visited with the same intensity are marked by the same symbols.

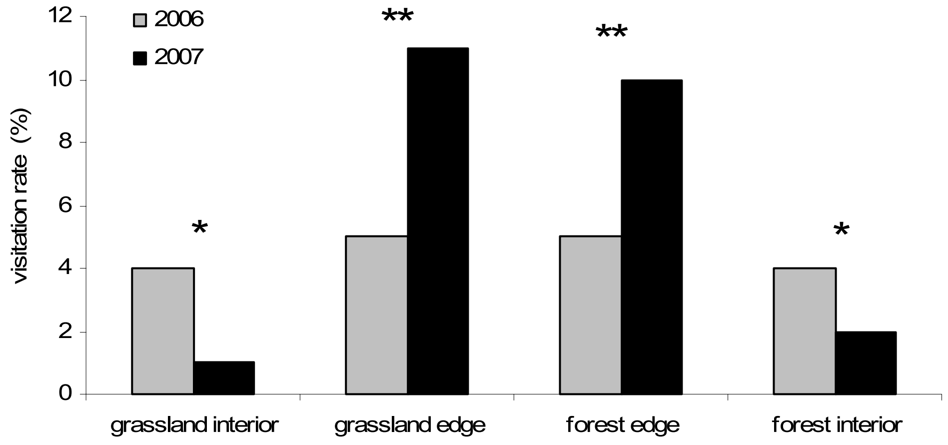
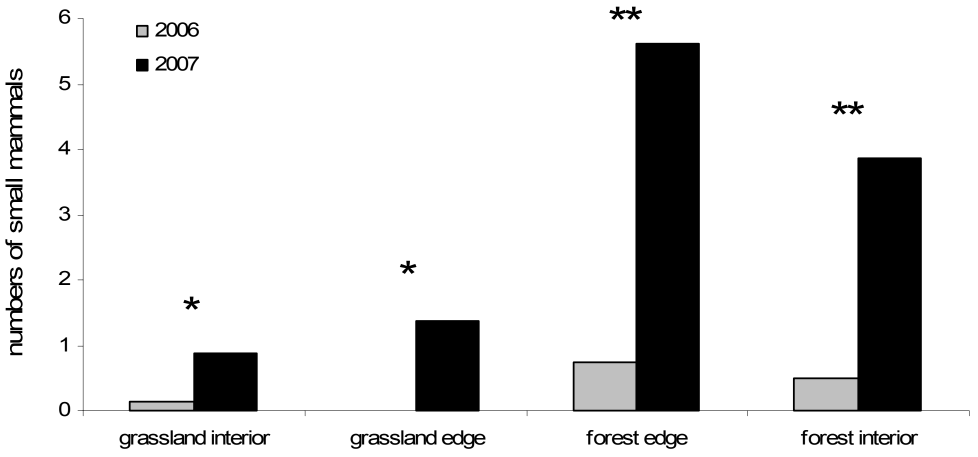


Fig. 2. Mean numbers of small mammals per line (35 traps) in particular habitat types, Southern Bohemia, 2006 and 2007. Habitat types with similar abundances of small mammals are marked by the same symbols. The posterior comparison between forest edge and forest interior was marginally significant.



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Research Article

Factors Determining Pochard Nest Predation Along a Wetland Gradient

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Abstract

*Waterfowl management on breeding grounds focuses on improving nest success, but few studies have compared waterfowl nest success and factors affecting nest survival along a wetland gradient and simultaneously identified nest predators. We monitored nests (n = 195) of common pochards (*Aythya ferina*) in Trebon Basin Biosphere Reserve, Czech Republic, during 1999–2002. Daily nest survival rates (DSRs, logistic-exposure) declined from island (0.985, 95% confidence interval, 0.978–0.991) to overwater (0.962, 0.950–0.971) and terrestrial (0.844, 0.759–0.904) nests. The most parsimonious model for DSRs included habitat class (DSRs: island > overwater > terrestrial) and nest visibility. Nest survival was improved by reduced nest visibility, increased water depth, and increased distance from the nest to habitat edge in littoral habitats. On islands, nest success increased with advancing date and increased distance to open water. A model of constant nest survival best explained the data for terrestrial nests. There were no observer effects on DSRs in any habitat. In 2003, artificial nests (n = 180; 120 contained a wax-filled egg) were deployed on study plots. The model that best explained variation in DSRs for artificial nests included only 1 variable: habitat class (DSRs: island ≥ overwater > terrestrial). Mammalian predation of artificial nests (by foxes [*Vulpes vulpes*] and martens [*Martes *spp.]) was more likely in terrestrial habitats than in littoral habitats or on islands. By contrast, corvids and marsh harriers (*Circus aeruginosus*) prevailed among predators of overwater and island nests. Our data indicate that artificial islands and wide strips of littoral vegetation may represent secure breeding habitats for waterfowl because those habitats allow nests to be placed in areas that are not accessible to, or that are avoided by, mammalian predators. Management actions should be aimed at preserving these habitats. This, along with creation of new artificial islands, could help to enhance breeding productivity of pochards and possibly other waterfowl species inhabiting man-made ponds.* (JOURNAL OF WILDLIFE MANAGEMENT 70(3):784–791; 2006)

Key words

artificial nests, Aythya ferina, *common pochard, Czech Republic, edge effect, nest predators, nest success, observer effect, waterfowl, wetlands.*

Nest predation is a leading cause of reproductive failure in waterfowl and can reduce nest success by as much as 90% (Sargeant and Raveling 1992). Hence, factors modulating variation in nest predation have long attracted the attention of waterfowl biologists and play a major role in improving productivity of ducks (Kadlec and Smith 1992). Despite the important role of nest success in determining annual recruitment and population dynamics (Johnson et al. 1992), research on this topic has been largely neglected in Europe.

As a response to selection pressure from predation, waterfowl have evolved various antipredator tactics, such as nesting in dense cover (Clark and Nudds 1991), nesting in association with aggressive species able to repel nest predators (Väänänen 2000), and spacing the nests over large areas, making each nest more difficult to detect (Owen and Black 1990). Nesting over water and on islands, and other tactics, have traditionally been viewed as adaptive responses to, and effective ways of avoiding, high rates of predation on terrestrial nests (Kaminski and Weller 1992). Natural duck nests situated over water or on islets survived substantially better than upland nests in several North American systems where mammalian predators predominated (Krapu et al. 1979, Giroux 1981, Arnold et al. 1993, Koons and Rotella 2003). In areas dominated by avian predators, however, the effect of island and overwater nest site selection is less clear because of limited research (e.g., Hill 1984). High densities of waterfowl nests reported from islands (Giroux 1981) may attract avian predators and theoretically lead to islands acting as ecological traps (Ratti and Reese 1988), particularly in agriculture-dominated European landscapes where populations of generalist avian nest predators are rapidly increasing (Hagemeijer and Blair 1998).

The idea that overwater and island nest sites are more secure is based on the premise that some predator species avoid these areas when foraging or forage less effectively there. Proximate causes of variation in nest success, however, remain unclear for many upland–overwater–island systems because few studies have evaluated patterns of spatial distribution of nest predators over those habitats (Jobin and Picman 1997). In addition, nest predation rates in wetlands may be affected by the composition of adjacent upland habitats (Jobin and Picman 1997) or by distances to abrupt wetland/arable land edges (Albrecht 2004), but few studies have addressed these issues using natural waterfowl nests (Brua 1999, Zoellick et al. 2004).

We monitored nest survival of common pochards inhabiting artificial wetlands in a mosaic, agriculture-dominated landscape in central Europe. Our objective was to identify factors related to

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nest success in 3 habitats potentially representing a gradient of accessibility to nest predators: terrestrial mainland, overwater habitats, and artificial islands. We evaluated nest success and predation rates on natural nests in these 3 habitat classes. We hypothesized that predation rates would be a function of 1) habitat class, 2) water depth, 3) vegetation characteristics, 4) distance to nearest edge, and 5) island size and distance to upland. We evaluated predator response to the various nest situations by placing artificial nests in the 3 habitat classes and measuring predation by avian and mammalian predators. Results of our study should allow us to better understand proximate mechanisms that may limit productivity of breeding waterfowl, and thus lead to better management of wetlands for duck populations.

Study Area

We located pochard nests in the Trebon Basin Biosphere Reserve, Czech Republic (approx. 49°00′N, 14°46′E). The study site (ca 180 km^2) encompassed more than 300 artificial fishponds (ranging from 0.5 to 400 ha). We randomly selected 26 (0.5–58.5-ha) fishponds from approximately 280 fishponds that were <150 ha in size and not used for commercial duck rearing. We had no a priori knowledge of pochard breeding on selected or unselected fishponds. Islands (0.02–1.5 ha, $n = 30$) were present on 10 of the selected fishponds. The fishponds were excavated about 500 years ago; the islands were built by disposal of spoil material from maintenance dredging activities that took place 20–30 years ago. The ponds are actively managed for the production of carp (*Cyprinus carpio*), with fish standing crops sometimes reaching 1,000 kg/ha (Korinek et al. 1987). In central Europe artificial fishponds with controllable water levels and their associated islands represent the most important source of overwater and island habitats for breeding populations of pochards (Bezzel 1969) and other diving duck species (e.g., tufted duck [*Aythya fuligula*] and red-crested pochard [*Netta rufina*]). The fishponds, typical for the Trebon Basin region, were relatively shallow, with maximum water depths ranging from 90 to 140 cm. Margins of the fishponds were vegetated (in bands 2–50 m in width) with cattail (*Typha* spp.), manna grass (*Glyceria maxima*), and reed (*Phragmites australis*). Reed and manna grass patches regularly extended from water to terrestrial (upland) habitat (pochard nests placed there are referred to as terrestrial nests, see below). Habitat surrounding fishponds comprised a mosaic of crop fields, hay meadows, pastures, and small woodlots. Pochard nesting sites were dominated by reed, cattail, manna grass, raspberry (*Rubus* spp.), or stinging nettle (*Urtica dioica*).

Methods

Nest Searching and Nest Site Characteristics

We searched for nests in all potential nest sites (wetland margins; emergent vegetation; reed, manna grass, and cattail patches; nettle and raspberry patches if <50 m from the shore) from mid-May until the first week in July for 4 years (1999–2002). We found nests by walking slowly to flush incubating females or by systematically searching potential sites. After nests were located, we checked them at 1–20-day intervals (mean = 8 d) to determine their fate. We usually approached nests from the open water and tried to follow a different path each time to minimize disturbance to vegetation. We determined age of eggs using floatation (Westerskov 1950) during the first visit. Nests (observation intervals) were classified as successful (nest active; at least 1 duckling hatched), depredated (at least 1 egg removed or destroyed and no signs of ongoing parental activity at the nest; no duckling hatched), or abandoned. Though we found some nests that were already depredated, only nests that were active when found were included in the analysis of nest survival.

We constructed a detailed habitat map from aerial photography, and we updated the map in June of each year based on field observations. We used ArcView 5.0 (Environmental Research Institute 1996) to delineate and measure each vegetation patch, and we assigned it to 1 of 3 habitat classifications (HABITAT): terrestrial, littoral (water levels >0 cm), or island.

Nest site characteristics were measured at several spatial scales. When each nest was found, we judged the percentage of the nest that was visible by looking directly down on the nest (NVISIB). We recorded the maximum height of vegetation (to the nearest 5 cm; HEIGHT) within a 1-m radius surrounding the nest and the dominant vegetation types (cattail + reed, raspberry, nettle, or manna grass; VEGTYPE). Water levels were measured at each nest to the nearest 5 cm (WDEPTH). We measured distances in the field from the nest to open water (DISTW), to the nearest habitat edge (DISTEDGE), and to the nearest terrestrial land (DISTTER). If a distance exceeded 20 m, we measured from the digitized habitat map of the study site (scale of 1:2,000). We measured each island's total area (AREAISL), the distance from the island to the nearest terrestrial land (TERISL), and the distance to the nearest habitat edge (EDGEISL). Habitat edges were defined as distinct interfaces between the wetland (water surface + littoral patches and/or adjoining terrestrial patches of reeds and manna grass) and agricultural land.

Artificial Nest Experiment

We deployed 90 artificial nests during each of 2 experimental periods in 2003 (180 nests total). The nests were constructed of dead leaves shaped into a cup closely resembling a natural pochard nest. Each nest contained either 3 brown chicken eggs (30 nests per period) or 2 chicken eggs and 1 chicken eggshell filled with wax (60 nests per period). The use of wax-filled eggs allowed for the identification of nest predator guilds via beak and tooth imprints (Pasitschniak-Arts and Messier 1995). Pochard feathers were added to the nests to mimic the scent of natural nests (Guyn and Clark 1997).

Artificial nests were deployed on dry shore (representative of terrestrial nest sites, $n = 30$), in patches of littoral vegetation (representative of overwater nest sites, $n = 30$), and on islands ($n = 30$). Each habitat had 20 nests with 1 wax egg and 2 chicken eggs and 10 nests with 3 chicken eggs and no wax egg. We usually placed unmarked artificial nests in vegetation patches known to have been pochard breeding sites during previous years. To standardize nest locations, we placed all overwater nests 5–15 m from the nearest terrestrial land and at water depths of 20–40 cm, which is similar to the average placement of pochard nests within our study plots (distance: $x = 8.1$ m, SD = 5.7; water depth: $x = 36.4$ cm, SD = 14.8). We placed all nests >50 m from the nearest agricultural edge. We kept the minimum distance between neighboring nests at 100 m (range = 100–520 m) for shore and overwater nests. Of the 30 island nests, most were separated by 100 m, but some were closer (20–90 m). Nests were exposed to predators for 14 days, and then we recorded their fate. We ran the experiment twice, first on 25 May 2003, and again on 18 June 2003 with new nest locations.

A nest was considered preyed upon if any eggshell was damaged or any egg was missing. Because of potential shortcomings associated with the use of artificial nests (Guyn and Clark 1997, Weidinger 2001), we used this experiment only to assess relative (not absolute) predation pressure and local predator-assemblage composition (Major and Kendal 1996).

Data Analyses

We estimated the daily survival rate (DSR) of nests and evaluated the effects of explanatory variables (hereafter referred to as predictors) potentially related to nest survival by using the logistic-exposure nest survival model, which is a generalized linear model with a binomial error distribution and a logistic-exposure link function (Shaffer 2004). This method models nest fate during each observation interval as a Bernoulli response (0 = failure, 1 = success), incorporating the length of the interval in the link function. Each nest-visit interval was treated as a separate observation. Intervals of uncertain status or those during which nests failed for reasons other than predation (e.g., inclement weather, disturbance by human activities) were excluded from the analysis ($n = 5$; <1.5% of intervals). All analyses were conducted with Proc GENMOD (SAS Institute 2001).

To evaluate the effects of individual predictors on nest survival, we used an exploratory analysis restricted to a set of exploratory models selected a priori to avoid excessive data dredging (Burnham and Anderson 1998). We contrasted a set of candidate models, which included habitat type, main effects of habitat features (singly only to reduce the candidate model set), and the interaction of habitat type and the continuous predictor added. Predictors irrelevant for some habitat classes (e.g., DISTTER, WDEPTH) were not considered at this stage. Because our main objective was to compare nest success among 3 classes of nesting habitat, we included models with the effect of habitat entered as a categorical predictor with 3 levels or 2 levels (data from 2 habitats lumped, resulting in 3 alternative scenarios: terrestrial + littoral vs. island, terrestrial + island vs. littoral, terrestrial vs. littoral + island). As a result, we obtained a set of 20 candidate models for the combined data from all 3 habitats.

Because the models lend support for interactions between habitat class and some of the continuous predictors, and because some predictors were habitat specific, we ran additional models to analyze nest survival separately within each habitat. The habitat-specific sets of candidate models were defined as all possible combinations of relevant predictors with the restriction that each model could contain only 1 predictor from each of 4 predictor groups (distances: DISTW, DISTTER, DISTEDGE; water depth: WDEPTH; vegetation characteristics: NVISIB, HEIGHT, VEGTYPE; date: Julian date centered within each year where the median laying date = 0, DATE), under the assumption that predictors are somewhat redundant within these groups. We assumed no interaction between date and vegetation characteristics because vegetation covering the nest was already fully developed at the beginning of the pochard nesting season. Resulting sets comprised 24 (terrestrial habitat), 64 (littoral), and 32 (island) candidate models.

We evaluated potential observer effect on nest survival using a generalized linear model with a binomial error distribution and a log-link function (Rotella et al. 2000). Addition of covariates to the observer effect model (Koons and Rotella 2003) had little influence on the value of estimated observer effect. Hence, we present model-fitting results only for the 1-parameter survival model and the 2-parameter observer effect model.

Because most natural nests were observed over more than 1 interval (mean = 2.0, range 1–5), and because nests themselves were spatiotemporally clustered, we used a mixed model approach implemented in Proc NLMIXED (SAS Institute 2001) as suggested by Shaffer (2004). Although the data have a hierarchical structure (intervals within nests, nests within localities), currently available procedures enable entering of only 1 random effect at a time. Models that had the locality–year combination as the random effect fit marginally better (based on Akaike's Information Criterion [AIC]; see description of this statistic below) than those with a random effect of nest individuality. However, addition of random effects to the candidate models did not change conclusions on their relative adequacy in any analysis. Because of this, and because random effects could not be included in the analysis of terrestrial (small sample size: mean = 1.7 nest-visit intervals per locality–year combination) and artificial (see below) nests, we present only the results based on fixed effects models.

Fate (0 = failure, 1 = success) of artificial nests was analyzed using binary logistic regression (Proc GENMOD; SAS Institute 2001) because all nests were exposed over a constant period. The unit of analysis was a nest. Because the experiment was designed to avoid temporal (only 2003 season) or spatial (with exception of islands, see discussion of spacing above) factors in the clustering of nests, we did not consider random effects. We modeled only the effect of habitat class and the potential incremental effects of TRIAL (May vs. Jun), type of artificial eggs (chicken vs. chicken + wax-filled; EGGTYPE), and their interactions with HABITAT. We did not model environmental factors because the nests were positioned to control for environmental covariates.

We assessed the adequacy of the candidate models according to the AIC with finite sample correction ($\mathrm{AIC_c}$), following guidelines by Burnham and Anderson (1998). All models that differed in $\mathrm{AIC_c}$ from the best-supported model (the model with lowest $\mathrm{AIC_c}$) by a factor less than 2 were considered to be similarly supported. In addition to the parameter estimates resulting from the best-supported model, we calculated parameter estimates averaged across the set of candidate models using model weights (w). The latter reflect both the uncertainty associated with the given model and the uncertainty in selecting that model (Burnham and Anderson 1998). For each predictor we also present its cumulative weight (cw), which is a sum of model weights over all models containing that predictor.

Results

Natural Nests

The data used to analyze nest survival comprised 400 nest-visit intervals, representing 195 nests clustered in 54 locality–year samples. We searched 139.25 ha of pochard habitat during the

1999–2002 period. We found higher than expected numbers of nests on islands (total number of pochard nests found/expected [including already depredated nests] = 28/64, 113/112, and 99/64 in terrestrial, littoral, and island habitats, respectively; expected numbers of nests are based on proportional area searched for nests in each habitat class, assuming equal nest densities). Neither nest visibility nor vegetation height estimates differed among the 3 habitat classes considered (analysis of variance [ANOVA], $P > 0.10$ in both cases).

The constant survival model estimated the daily survival as 0.969 (95% confidence interval [CI]: 0.962–0.975), yielding a nest success estimate of 0.36 (95% CI: 0.29–0.44) over a 32-day period. The most important determinant of nest survival in pooled data was HABITAT (Tables 1 and 2). The model with separate survival estimates for the 3 habitats ($\Delta AIC_c = 6.7$; Fig. 1) clearly stood out as better than the constant survival model ($\Delta AIC_c = 50.1$) and fitted the data well (Hosmer and Lemeshow goodness-of-fit test: $\chi^2 HL = 10.23$, df = 8, $P = 0.25$; Hosmer and Lemeshow 1989). Categorization to 3 habitat classes was better supported than categorization to only 2 habitats, with the distinction between terrestrial and the other habitat as the most informative ($\Delta AIC_c = 19.3$). Of the continuous predictors considered in addition to HABITAT (Tables 1 and 2), the best-supported model contained NVISIB and its interaction with HABITAT; there was also some support for an effect of DISTEDGE and its interaction with HABITAT.

A separate analysis of terrestrial nests supported the constant survival model, although sample size was small and some effects may have remained undetected (Tables 3 and 4). For littoral nests, the best approximating model (Tables 3 and 4) contained effects of NVISIB (−0.022; 95% CI: −0.034 to −0.010), WDEPTH (0.042; 95% CI: 0.015 to 0.072), and DISTEDGE (0.032; 95% CI: 0.003 to 0.065), of which DISTEDGE was generally less informative (cw = 0.69) than WDEPTH (cw = 0.98) and NVISIB (cw = 0.99). For island nests, the best approximating model (Tables 3 and 4) contained effects of DISTW (0.414; 95% CI: 0.078 to 0.905) and DATE (0.052; 95% CI: 0.008 to 0.098), both of which were about equally informative (cw = 0.78 and 0.81, respectively). Some support was found also for an effect of HEIGHT.

We explored the utility of additional descriptors of island habitat (not included in the set of models shown in Table 3) as potential predictors of nest survival. The models containing effects of TERISL and EDGEISL received similar support (all differences in $AIC_c < 1.5$) as the corresponding models with nest-specific distances (Table 3). We found only weak support for the effects of AREAISL, entered either separately ($\Delta AIC_c = 4.9$) or in combination with other predictors. We found little support for an observer effect in any habitat. All observer effect estimates were <1 (suggesting negative effect on survival), but their 95% CI overlapped 1 (terrestrial: 0.413, 0.076 to 2.236; littoral: 0.957, 0.835 to 1.096; island: 0.993, 0.922 to 1.070; combined: 0.969, 0.879 to 1.028).

Artificial Nests

Two artificial overwater nests were used by pochard females as the base for their own nests, 1 in May and 1 in June, and 1 additional nest was flooded; 82 of the remaining 177 artificial nests were preyed upon. The resulting nest survival (DSRs extrapolated over 32 days) for artificial nests was lower (0.24; 95% CI: 0.17–0.32) than that for natural nests (see above). The global model containing all main effects and interactions (Table 4) fitted the data well ($\chi^2 HL = 1.64$, df = 8, $P = 0.99$). Of the candidate models evaluated, the model with separate survival rates for the terrestrial versus other habitats was the best supported from the data and was marginally better than the models with separate survival for all 3 habitats (Fig. 1) or islands versus other habitats. We found little support for models including the effects of egg type or trial, which were controlled for the effect of habitat (Tables 5 and 6).

Avian predators caused most nest losses, with predation by corvids (59% of all predation by an identified species, $n = 46$) and marsh harriers (*Circus aeruginosus*; 13%) prevailing. The proportion of nests depredated by mammals tended to decrease along a wetland gradient from islands to terrestrial land, whereas the opposite was found for avian predators (mammalian/avian predation: island 0/12; overwater nests 1/12; terrestrial nests 10/11; exact G test for 3 × 2 contingency table, $P = 0.002$). Martens (*Martes* spp.) and red foxes (*Vulpes vulpes*) were identified as mammalian predators of upland nests. One overwater nest was destroyed by wild boars (*Sus scrofa*).

Discussion

Our data support the idea of general security of overwater and island habitats for breeding waterfowl. Predation rates were low on artificial islands, whereas upland nests and those placed over water were exposed to exceptionally high and intermediate rates of predation, respectively. Nest survival differed by as much as 60%

Table 1. Model-fitting results for the nest survival of common pochard, Trebon Basin Biosphere Reserve, Czech Republic, 1999–2002. Models are compared according to number of parameters (K), model deviance (D), Akaike's Information Criterion corrected for sample size (AIC_c), the difference in AIC_c from the best supported model (ΔAIC_c), and model weight (w). The remaining candidate models had $\Delta AIC_c > 7.0$ and $w < 0.01$.

Model[a]	K	D	AIC_c	ΔAIC_c	w
HABITAT + NVISIB + INTERACTION	6	344.2	356.2	0	0.37
HABITAT + DISTEDGE + INTERACTION	6	344.7	356.7	0.5	0.29
HABITAT + NVISIB	4	350.0	358.0	1.8	0.15
HABITAT + DATE	4	350.7	358.7	2.5	0.11
HABITAT + DATE + INTERACTION	6	349.9	361.9	5.7	0.02
HABITAT + DISTEDGE	4	354.8	362.8	6.6	0.01
HABITAT	3	356.9	362.9	6.7	0.01

[a] Model terms: habitat class (HABITAT), distances from a nest to the nearest agricultural land (DISTEDGE), nest visibility (NVISIB), Julian date centered within each year (DATE).

Table 2. Model-averaged parameter estimates and cumulative weights (cw) of predictors from models of nest survival of common pochard, Trebon Basin Biosphere Reserve, Czech Republic, 1999–2002.

Effect[a]	Estimate	SE	cw
CONSTANT	4.207	0.423	
HABITAT (terr)	−2.427	0.631	>0.99
HABITAT (litt)	−0.844	0.612	
DATE	0.004	0.007	0.13
DISTEDGE	0.001	0.001	0.31
DISTW	0.003	0.007	0.01
NVISIB	−0.003	0.006	0.53
HEIGHT	<0.001	0.003	0.01

[a] Model terms: habitat class (terrestrial, littoral, island = reference category; HABITAT), distances from a nest to an open water surface (DISTW) or the nearest agricultural land (DISTEDGE), nest visibility (NVISIB), maximum height of vegetation surrounding the nest (HEIGHT), Julian date centered within each year (DATE).

among these sites. We know of no studies that have used Mayfield estimates to calculate nest success rates over the upland–littoral–island gradient, and only a few studies have looked at upland versus littoral or upland versus island habitats. Mayfield success for overwater mallard (*Anas platyrhynchos*) nests reached up to 44% in Manitoba, which is substantially higher than the 12% found for upland nests (Arnold et al. 1993). The same pattern was reported for 2 diving duck species (lesser scaup [*Aythya affinis*] and ring-necked duck [*Aythya collaris*]) by Koons and Rotella (2003). Similarly, island nests experienced lower rates of predation than mainland nests in studies of king eiders (*Somateria spectabilis*; Kellett et al. 2003), mallards, and tufted ducks (Hill 1984). Our finding of higher than expected numbers of nests on islands was consistent with reported breeding preferences of pochards for this habitat (Bezzel 1969). Though our data are derived from a restricted sample of fishponds, those included in our study represent a typical type for the Trebon Basin and perhaps for central Europe as well (also Korinek et al. 1987).

Our results correspond well with the findings of Jobin and Picman (1997) that terrestrial ground nests are accessible to a diverse predator community. For example, mammalian predation was almost exclusively restricted to terrestrial habitats in our artificial nest study. We therefore conclude either that water poses an effective physical barrier to at least some mammals, or that local mammalian predators (mostly martens and foxes) avoid overwater stands as foraging habitats. Indeed, natural pochard nests placed over deep water survived much better than those in shallows, suggesting that water itself deterred some nest predators. Spatial distribution of mammalian predators over wetlands could thus be an important factor contributing to differences in predation rates, at least between upland and overwater habitats. Aversion by corvids to landing over water and their reduced mobility in overwater habitat should also be considered as a possible factor (Sullivan and Dinsmore 1990). Note that raccoons (*Procyon lotor*) and minks (*Mustela vison*), North American species that may forage in littoral zones (Brua 1999), have recently expanded their range into Europe, including the Czech Republic (Mitchell-Jones et al. 1999), but were absent in our study plots during the 1999–2003 study period. There is a relatively large body of knowledge concerning factors affecting predation rates on upland waterfowl nests, but few studies address overwater nests; those have conflicting results as to the effect of nest concealment (Featherstone 1975, Maxson and Riggs 1996, Brua 1999). We found that concealment improved survival of overwater nests, which is consistent with the prevailing under-

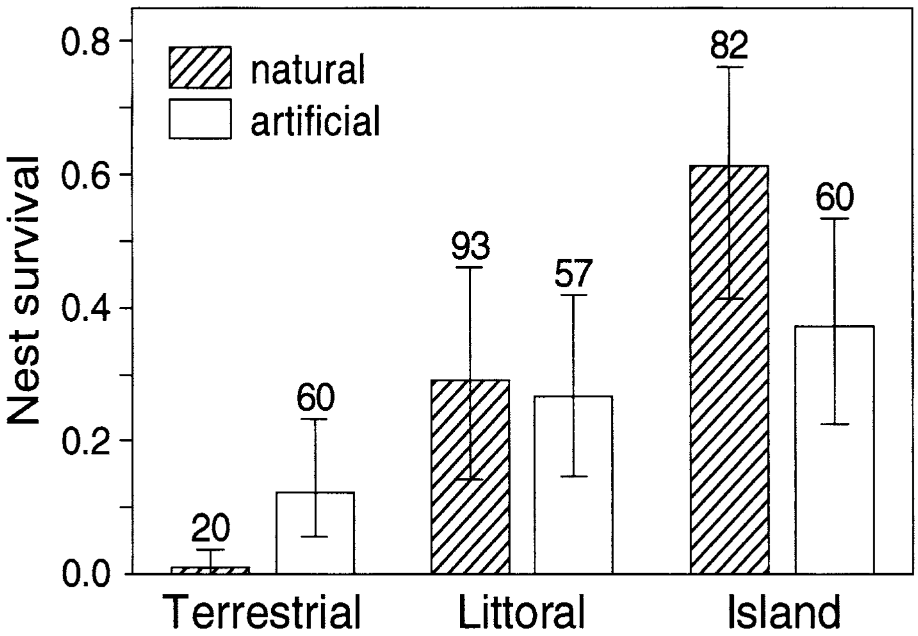

Figure 1. Survival of natural and artificial common pochard nests in 3 classes of nesting habitat in the Czech Republic, 1999–2002. Nest survival was calculated by extrapolating the daily survival rate over 32 days (8 days laying plus 24 days incubation). The daily survival rate (natural nests, Table 1) and the survival rate over experimental trial (artificial nests, Table 5) were estimated by the models including only the effect of habitat class: logit (daily survival, natural) = 4.22 (SE 0.23) – 2.52 (0.36) * terrestrial – 0.98 (0.27) * littoral; logit (14-day survival, artificial) = 0.62 (0.27) – 1.02 (0.38) * terrestrial – 0.37 (0.38) * littoral. The approximate 95% CI and the number of nests are shown.

Table 3. Model-fitting results for the nest survival of common pochard in terrestrial, littoral, and island nesting habitats, Trebon Basin Biosphere Reserve, Czech Republic, 1999–2002. Models are compared according to number of parameters (*K*), model deviance (*D*), Akaike's Information Criterion corrected for sample size (AIC_c), the difference in AIC_c from best-fitting model (ΔAIC_c), and model weight (*w*). Only the 5 best-supported models are given. The remaining candidate models had $w < 0.05$.

Model[a]	*K*	*D*	AIC_c	ΔAIC_c	*w*
Terrestrial					
CONSTANT	1	28.8	30.9	0	0.16
DISTEDGE	2	27.9	32.0	1.1	0.09
DATE	2	28.1	32.3	1.4	0.08
VEGTYPE	3	26.3	32.6	1.7	0.07
NVISIB	2	28.7	32.7	1.8	0.07
Littoral					
DISTEDGE + WDEPTH + NVISIB	4	173.4	181.4	0	0.48
DISTEDGE + WDEPTH + NVISIB + DATE	5	173.2	183.3	1.9	0.18
WDEPTH + NVISIB	3	178.2	184.3	2.9	0.11
DISTTER + WDEPTH + NVISIB	4	177.6	185.5	4.1	0.06
DISTW + WDEPTH + NVISIB	4	177.9	185.9	4.5	0.05
Island					
DISTW + DATE	3	112.4	118.4	0	0.31
DISTW + HEIGHT + DATE	4	111.7	119.8	1.4	0.16
DISTW + NVISIB + DATE	4	112.4	120.4	2.0	0.11
DISTW + VEGTYPE + DATE	6	109.2	121.3	2.9	0.07
DISTW	2	117.8	121.8	3.4	0.06

[a] Model terms: Julian date centered within each year (DATE), distances from a nest to an open water surface (DISTW), the nearest terrestrial land (DISTTER) or the nearest agricultural land (DISTEDGE), water depth (WDEPTH), nest visibility (NVISIB), maximum height of vegetation surrounding the nest (HEIGHT), the dominant vegetation type (cattail + reed, manna grass, nettle, raspberry; VEGTYPE).

Table 5. Model-fitting results for the survival of artificial nests, Trebon Basin Biosphere Reserve, Czech Republic, 1999–2002. Models are compared according to number of parameters (*K*), model deviance (*D*), Akaike's Information Criterion corrected for sample size (AIC_c), the difference in AIC_c from best-fitting model (ΔAIC_c), and model weight (*w*). Only 5 best supported models are given. The remaining candidate models had $\Delta AIC_c > 3.0$ and $w < 0.05$.

Model[a]	*K*	*D*	AIC_c	ΔAIC_c	*w*
HABITAT (terrestrial versus other)	2	237.6	241.6	0	0.34
HABITAT	3	236.6	242.6	1.0	0.21
HABITAT (island versus other)	2	239.7	243.7	2.1	0.12
HABITAT + EGGTYPE	4	236.0	244.0	2.4	0.10
HABITAT + TRIAL	4	236.5	244.5	2.9	0.08

[a] Model terms: habitat class (HABITAT), experimental trial (May vs. Jun; TRIAL), type of artificial egg (chicken vs. chicken + wax-filled; EGGTYPE).

standing of the impact of avian predators that mostly rely on visual cues of nests (Sullivan and Dinsmore 1990). The high species richness of local predator assemblages, with predators employing nest-searching tactics based on a combination of cues, may account for the lack of effect of nest visibility and other factors on nest predation in upland habitat. Alternatively, our sample sizes were insufficient to detect such effects.

Predation rates on island nests were apparently low. Because water probably does not pose a barrier to birds, it is unclear why avian predators did not preferentially prey upon clumped island nests closely resembling terrestrial nests in terms of dry-land placement, concealment, and other attributes. Crows (*Corvus corone*) and marsh harriers, the most important avian predators in our study, are habitat generalists, probably foraging opportunistically on the most available prey items (Andrén 1992, Opermanis 2001). Unfortunately, we lack precise data on the alternative prey abundance in the landscape surrounding the fishponds. Meadow-crop field mosaic acted as preferred hunting areas for both avian species. Further, both crow and harrier occurrences are positively associated with the proportion of arable land in the Trebon Basin area (Albrecht and Kurz, unpublished manuscript). It is thus possible that the distant location of islands from human-altered open lands (usually >100 m), combined with their small size (0.02–1.5 ha) and obvious scarcity over the entire landscape, may have led avian predators to not prefer or even to avoid these habitats for hunting, particularly if waterfowl eggs were not their preferred food items (Ackerman 2002). Nest success was higher on small islands and on those situated farther away from uplands in several other studies (Giroux 1981, Kellett et al. 2003, Zoellick et al. 2004). Predators may tend to incidentally prey on pochard nests in areas surrounding their preferred foraging habitats

Table 4. Model-averaged parameter estimates and cumulative weights (cw) of predictors from models of nest survival of common pochard in terrestrial, littoral, and island nesting habitats, Trebon Basin Biosphere Reserve, Czech Republic, 1999–2002.

	Terrestrial			Littoral			Island		
Effect[a]	Estimate	SE	cw	Estimate	SE	cw	Estimate	SE	cw
CONSTANT	1.749	0.492	2.098	0.591		3.722	0.528		
DATE	0.007	0.015	0.32	0.001	0.005	0.28	0.041	0.028	0.81
DISTEDGE	−0.010	0.021	0.28	0.022	0.020	0.69	<0.001	<0.001	0.06
DISTW	−0.007	0.022	0.20	−0.001	0.003	0.07	0.313	0.247	0.78
DISTTER	nd[b]	nd	nd	0.002	0.006	0.08	<0.001	0.001	0.07
WDEPTH	nd	nd	nd	0.043	0.015	0.98	nd	nd	nd
NVISIB	0.001	0.003	0.19	−0.021	0.006	0.99	<0.001	0.002	0.18
HEIGHT	0.017	0.087	0.17	−0.001	0.002	<0.01	0.069	0.159	0.23
VEGTYPE 1	nd	nd		nd	nd		0.028	0.138	
VEGTYPE 2	0.230	0.473		nd	nd		−0.090	0.196	
VEGTYPE 3	−0.024	0.139	0.17	<0.001	0.001	<0.01	−0.102	0.206	0.13

[a] Effects: Julian date centered within each year (DATE), distances from a nest to an open water surface (DISTW), the nearest terrestrial land (DISTTER) or the nearest agricultural land (DISTEDGE), water depth (WDEPTH), nest visibility (NVISIB), maximum height of vegetation surrounding the nest (HEIGHT), the dominant vegetation type (manna grass = reference category, raspberry = VEGTYPE1, nettle = VEGTYPE2, cattail + reed = VEGTYPE3).

[b] nd = Not defined for this habitat.

Table 6. Model-averaged parameter estimates and cumulative weights (cw) of predictors from models of survival of artificial nests, Trebon Basin Biosphere Reserve, Czech Republic, 1999–2002.

Effects[a]	Estimate	SE	cw
CONSTANT	0.204	0.527	
HABITAT (terr)	−0.472	0.560	0.47
HABITAT (litt)	−0.160	0.293	
TRIAL	0.009	0.049	0.12
EGGTYPE	0.083	0.171	0.18

[a] Effects: habitat class (terrestrial, littoral, island = reference category; HABITAT), experimental trial (May vs. June; TRIAL), type of artificial egg (chicken vs. chicken + wax-filled; EGGTYPE).

(Vickery et al. 1992). We found evidence for edge-related nest predation in littoral patches adjacent to agricultural land, and a similar mechanism (i.e., edge effect) cannot be ruled out when explaining the exceptionally low predation rates on islands.

High nest success accompanied by high proportion of nests found on islands adds support to the idea of adaptive habitat selection by breeding pochards in our study area. The fact that mammalian predators only occasionally visited littoral patches and mostly avoided islands is particularly important from the evolutionary and conservational perspectives. Mammalian predation may exert a strong selective force in the evolution of habitat selection rules by the prey. Unlike predation by many avian predators, predation attacks by mammals often result in death or injury of the incubating female duck (Sargeant and Raveling 1992), thereby resulting in the loss of future reproduction. Evidence lends support to the idea that survival of nesting females is higher on islands (Dufour and Clark 2002). The high density of nests on islands may lead to increased inter- or intraspecific brood parasitism rates (Dugger and Blums 2001), but potential fitness costs could be offset by the relative inaccessibility of island habitats to mammalian predators. Based on our data, we conclude that nesting over water or on islands may represent important means of escaping mammalian predation in pochards.

Management Implications

We found that artificial islands may well function as a protective breeding habitat for pochards in our study area. Similarly, overwater nests were exposed to only moderate predation and the predator community preying on artificial nests differed between terrestrial versus overwater and island breeding habitats. Most importantly, our data indicate that mammalian predators present on our study area do not invade littoral stands and islands; the likelihood that they would prey on nests in littorals decreased with increasing water depth around the nest. We therefore recommend that water levels of artificial ponds with controlled water levels should be steadily maintained at high levels during the breeding season to improve the nesting success of pochards. We also conclude that management efforts in the Trebon area, designated as a Special Protection Area according to the European Union Birds Directive (Council Directive 79/409/EC on the conservation of the wild birds), should be, in line with the directive and with Czech Government Decree 680/2004, focused on saving appropriate breeding habitats on artificial islands and also on preserving dense littoral patches surrounding fishponds. The finding that the proximity of human-altered edges may alone, irrespective of other factors, affect nest predation rates in wetland margins highlights the need to maintain wide strips of littorals and extensive undisturbed wetland patches to improve nesting success of waterfowl and, possibly, other littoral nesting birds.

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Stručný souhrn publikací:

Tato práce obsahuje čtyři články které jsou zaměřené na různé aspekty hnízdní predace antipredačních strategií a distribuce predátorů v krajině.

První příspěvek “*Nest protection in mallards (Anas plathyrhynchos): Untangling the role of crypsis and parental behaviour*” (Kreisinger & Albrecht 2008) se zaměřuje na analýzu vlivu antipredačních strategií na reprodukční úspěšnost u kachny divoké. Naše experimentální data ukazují, že hnízdní úspěšnost ovlivňuje současně řada antipredačních strategií jako je výběr umístění hnízda, antipredační vliv rodičovského chování a krypse v důsledku zakrývání hnízda hnízdním materiálem během přestávek v inkubaci. Na rozdíl od některých dřívějších studií naše data ukazují že relativní efekt krypse a rodičovského chování na přežívání hnízd není v interakci s antipredačním efektem zakrytí hnízda vegetací.

V článku “*Corridor versus hayfield matrix use by mammalian predators in an agricultural landscape*“ (Šálek et al. *in press*), byla testována hypothésa že lineární pásy pokryté křovinatou vegetací vzrostlou trávou jsou preferovány savčími mesopredátory před pravidelně kosenými loukami. Experiment potvrdil že pravděpodobnost detekce všech druhů šelem byla vyšší v koridorech než okolní krajinné matrix. Naše práce tudíž naznačuje že udržování těchto krajinných elementů v zemědělské krajině může být účinnou metodou pro ochranu populací drobných šelem.

Fragmentovaná krajinu obecně obývá větší množství predátorů v porovnání s nefragmentovanou krajinou. Častým důsledkem toho je zvýšená míra predace, a to především v habitatových rozhraní (tzv. "edge effect"). V práci “*Testing a mechanistic explanation for mammalian predator responses to habitat edges*“ (Svobodová et al. *submitted*) jsme se zaměřili na test mechanismů které podmiňují distribuci predátorů na habitatovém rozhraní mezi lesem a obhospodařovanými loukami. V této práci jsem současně hodnotily gradient v abundancích savčích mezopredátorů a jejich hlavního typu kořisti, drobných hlodavců na přechodu mezi dvěma sledovanými biotopy. Naše výsledky ukazují značnou temporální proměnlivost v habitatových preferencích šelem. Zatímco šelmy nevykazovaly výrazné habitatové preference v prvním roce studia, v druhém roce byly šelmy výrazně preferovaly okrajové habitaty mezi lesem a loukou, než interiory těchto habitatů. Naše výsledky však nepodporují hypotézu, že by habitatové preference predátoů byli přímo ovlivněny množstvímpotravní nabídky. Naše data nejsou rovněž konzistentní ani s představou že zvýšený výskyt predátorů v habitatových rozhraních vzniká v důsledku difuze predátorů z kvalitnějšího do méně kvalitního biotopu.

V článku *"Factors determining pochard nest predation along a wetland gradient"* (Albrecht et al. 2006) se zaměřujeme na analýzu environmentálních faktorů ovlivňujících hnízdní úspěšnost u poláka velkého (*Aythya ferina*). Riziko hnízdní predace bylo nejnižší u hnízd umístěných na ostrovech v porovnání s litorálními a terestrickými habitaty, kde bylo naopak nejvyšší. Riziko predace bylo vyšší umělých snůšek umístěných v pobřežních habitatech než u snůšek v litorálu nebo na ostrovech. Na druhou stranu u hnízd umístěných v litorálu převládala predace korvidy a motákem pochopem (*Circus aeruginosus*). Naše data ukazují že ostrovy a široké pásy litorální vegetace můžou představovat bezpečné hnízdní habitaty pro vrubozobé v důsledku redukce rizika pradace terestrickými predátory.