

**Jihočeská univerzita v Českých Budějovicích
Přírodovědecká fakulta
2010**



Diplomová práce

Distribuce šelem uvnitř a na okraji lesních habitatů

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Červinka J. 2010. Distribuce šelem uvnitř a na okraji lesních habitatů. [Distribution of carnivores inside and at the edge of forest habitats. Mgr. thesis – in English] – 36 pp., Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic.

Annotation

This thesis is made up of manuscript focused on habitat preferences of carnivores in fragmented landscape. By using the scent-station method, fine-scale utilization of forest-farm edges by mammalian predators in dependence of patch size was examined. The study also provides conservation and management implications and proposals.

Tato práce sestává z rukopisu zaměřujícího se na habitatové preference šelem ve fragmentovaném prostředí. Za použití metody pachových stanic bylo zkoumáno využívání lesních okrajů savčími predátory v závislosti na velikosti fragmentu. Studie také poskytuje přehled důsledků a návrhů pro ochranu a management. Rukopis bude zaslán do časopisu Biological Conservation.

Prohlašuji, že svoji diplomovou práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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V Českých Budějovicích dne 4. ledna 2010

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Jaroslav Červinka

Poděkování

Poděkovat bych chtěl zejména svému školiteli Martinu Šálkovi, za jehož podpory tato práce vznikla. Za jeho přátelský přístup, trpělivost, shovívavost, ohleduplnost, upřímnost, cenné rady a cílevědomost, se kterou mě vedl v terénu i při sepisování této práce.

Obrovský dík patří rovněž mé rodině za jejich bezmeznou podporu, pomoc a porozumění, jež jsem si u nich v průběhu studia notnými dávkami vybíral.

Na tomto místě bych rovněž rád poděkoval za finanční podporu poskytnutou grantem SGA2009016 z Přírodovědecké fakulty Jihočeské univerzity.

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Úvod

Současné intenzivní využívání krajiny způsobuje ve stále větší míře její degradaci. Zemědělské aktivity a urbanizace enormně mění nejen krajinný ráz, ale i biotické a abiotické faktory působící v tomto prostředí (Andrén 1995). Výsledkem toho je, vedle vysoké úrovně znečištění, také degradace půdy a fragmentace prostředí, která má za následek roztržení krajinných struktur do malých ostrůvků (Andrén 1994). Tyto fragmenty jsou od sebe navíc často izolovány málo prostupnými bariérami, což má značně negativní vliv na přirozenou obnovu společenstev na těchto stanovištích. Za bariéry lze, kromě silnic, dálnic a železničních koridorů, považovat i rozsáhlá, zemědělsky využívaná pole, která brání některým, migračně méně schopným, druhům přesouvat se mezi potravními či rozmnožovacími stanovišti (Miko a Hošek 2009).

Středoevropská zemědělská krajina se během uplynulých šedesáti let podstatně změnila. Od poloviny 20. století docházelo v důsledku zemědělství a těžby dřeva ke změnám ve struktuře krajiny doprovázených scelováním pozemků, odvodněním využívané půdy či vymizením tradiční smíšené krajiny (Lipský 2000). V posledních dvaceti letech dochází k exploataci a fragmentaci těchto celků. V důsledku toho se neustále zmenšují nezemědělsky využívané plochy jako louky, lesy apod. V České republice je 34 % z celkové rozlohy tvořeno lesy. Velká část z nich je však hospodářsky využívána a pouze 30 % lze označit jako lesy přírodě blízké (cca 10 % území ČR) (Miko a Hošek 2009). Tato homogenizace prostředí vede ke ztrátě druhové bohatosti a přežívání pouze určitého spektra druhů, většinou generalistů, s rozsáhlým areálem rozšíření (Shmida a Wilson 1985, Miko a Hošek 2009). Miko a Hošek (2009) uvádějí, že zavádění stejnověkých porostů negativně ovlivňuje druhy vázané na lesní prostředí. To dokazují i zahraniční studie popisující nízkou početnost a druhovou diverzitu živočichů ve stejnověkých monokulturách (Kerr a Packer 1997, Lust a kol. 2004). Takto pozměněná krajina pak ztrácí nejen hodnotu, ale i pro člověka důležité vlastnosti. Kromě estetické a rekreační funkce je to mimo jiné schopnost zadržovat vodu. Tuto schopnost ovlivňuje například propojenosť lesních fragmentů (Miko a Hošek 2009). Silně fragmentovaná krajina postrádající tyto prvky je následně dále distrubována v důsledku nepravidelného vodního režimu – záplavy, vysychání.

Další pokračování fragmentace vede k poklesu průměrné velikosti fragmentů, jejich izolaci, změnám tvaru a typu vegetačního pokryvu, v důsledku čehož dochází k dalšímu úbytku biodiverzity, poklesu populačních početností zasažených druhů či dokonce k jejich vymizení (Wilcove 1985, Paton 1994). Vnímavost druhu vůči fragmentaci je závislá

na mnoha faktorech, jako je míra fragmentace, evoluční historie druhu, jeho ekologická valence, mobilita, velikost domovských okrsků, ale také početnost (Hansson a kol. 1995).

Porozumění důsledkům fragmentace na ekologii společenstev je klíčovým bodem ve snaze zajistit ekologickou stabilitu, a proto v současné době i hlavním zájmem ochranářských a managementových aktivit. To je patrné i ze vzrůstajícího počtu studií zabývajících se různými aspekty tohoto fenoménu (například Wilcove a kol. 1986, Andrén a Angelstam 1988, Murcia 1995, Vergara a Hahn 2009). Například jen v databázi „Web of Science“ je přes 1700 studií zabývajících se fenoménem fragmentace a jejím vlivem na biodiverzitu.

Fragmentovaná prostředí mají zpravidla vyšší podíl okrajových struktur, a proto jim je v dané souvislosti věnována velká pozornost (André 1994, Storch a kol. 2005, Vergara a Hahn 2009), jelikož změny indukované na těchto místech vyvolávají změny v biotických a abiotických podmínkách celé lokality (druhové složení a početnost, doba a množství osvitu, atd.) (Saunders a kol. 1991, André 1994, Mortelliti a Boitani 2007). Paradoxně právě zejména na okrajích dochází k největším změnám v důsledku hospodářských aktivit či urbanizace (Hansson 1994, Paton 1994, Lidicker 1999, Dijak a Thompson 2000). Na okraje jsou však vázané druhy nejen z okolí a interiéru lokality, ale i druhy na okraje specializované, které jsou těmito aktivitami následně ovlivněny. Jedinečnost ekotonů byla studována již od počátku 20. století, ale větší druhová diverzita těchto ekosystémů byla popsána až v roce 1933 americkým ekologem Leopoldem jako „okrajový efekt“ (shrnutí v Fonseca a Joner 2007). Podle teorie optimálního potravního chování se predátoři soustředí právě do míst s nejvyšší potravní nabídkou, kterými ektony jsou (MacArthur a Pianka 1966). Početnost mnoha druhů se tak vlivem predátorů dále snižuje, a to nejen přímo, prostřednictvím predace, ale i nepřímo, kdy pod vlivem vysokého predáčního tlaku snižuje kořist svou aktivitu, čímž může být následně ovlivněna i její reprodukce (Norrdahl a Korpimäki 2000).

Mnoho ptačích populací vázaných na okraje lesních prostředí se během posledních desetiletí zmenšilo či dokonce vyhynulo následkem rozsáhlé fragmentace a s ní spojených změn v ekologické stabilitě – ztráta míst vhodných k reprodukci a hnízdění a následná kompetice o ně. (Dijak a Thompson 2000, Larivière 2003, Báldi a Batáry 2005, Hanson a kol. 2007). V případě řady druhů převců je nízká reprodukční úspěšnost způsobena zejména hnízdní predací (Dijak a Thompson 2000). Ta následně nabývá na intenzitě se snižující se velikostí fragmentu a zvyšujícím se podílem okrajových struktur (Keyser 2002).

Hlavní predátory ve fragmentované krajině představují ptačí predátoři a to především krkavcovití ptáci (Corvidae) a savčí predátoři z řádu šelem (Albrecht a kol. 2006). Šelmy (Carnivora) však byly v tomto ohledu jen málo studovány. Důvodem může být vysoká obtížnost sledování šelem, které žijí skrytým a nočním životem, vyhýbají se střetům s člověkem a mají velmi nízké populační početnosti (Sargeant a kol. 2003). V důsledku toho byla ekologie mnoha druhů šelem, ale i reakce na ekologické disturbance, jako je fragmentace prostředí, velmi málo prozkoumána (Crooks 2002). Funkční odpověď šelem se může lišit nejen díky jejich specifickému chování, ale i morfologii. Šelmy mají velkou migrační schopnost a pohybují se na rozsáhlých územích (Nowak 1999). Jejich velké domovské okrsky jsou často mozaikovité, složené i z nevyhovujících částí fragmentovaného území, které jsou nuceny překonávat. Mohlo by se tedy zdát, že jsou vůči fragmentaci imunní. Ovšem každá disturbance ovlivňuje s životním prostředím druhu i druh samotný. To dává prostor druhům invazním, ale i druhům domácím s širší ekologickou valencí, které mohou být v narušeném, nově přetvořeném, prostředí úspěšnější a schopné původní druhy vytlačit. Typickým příkladem invazních druhů šelem u nás jsou mýval severní (*Procyon lotor*), původem ze Severní Ameriky, a psík mývalovitý (*Nyctereutes procyonoides*) z Dálného východu (Plesník 2009). Přesto, že jsou často negativní vlivy těchto šelem na naši faunu nadhodnocovány, přímé důkazy ovlivnění autochtonních druhů chybí. Ovšem pouhým narušením složitého systému trofické kaskády může být spuštěn dominový efekt, který může nepřímo vést k potlačení, v krajním případě vymizení, původních druhů, nehledě na invazní druhy jako přenašeče patogenních organismů (Plesník 2009). Podobně, v případě pokračující fragmentace a prohlubování jejich následků, může dojít ke vzájemné kompetici původních druhů. Lasice kolčava (*Mustela nivalis*), jako potravní specialista, je často vytlačena z potravně bohatých okrajových struktur v důsledku mezidruhové kompetice i predace (Korpimäki a Norrdahl 1989). Synantropní druhy predátorů-generalistů, jako liška obecná (*Vulpes vulpes*) či kuna skalní (*Martes foina*), ovšem nepůsobí jen jako schopnější kompetitoři, ale svou predací ovlivňují i mnohem širší spektrum kořisti (Korpimäki a Norrdahl 1989). Narozený od uvedené lasice kolčavy či hranostaje, jejichž potravu tvoří především drobní savci, jsou predátoři-generalisté jedním z nejvážnějších důvodů snížení hnízdní úspěšnosti řady ptačích druhů, na které svou predací negativně působí (Donovan a kol. 1997, Nour a kol. 1993, Paton 1994, Šálek 2009).

K pochopení habitatových preferencí šelem a tím i jejich vlivu na celá společenstva je ovšem zapotřebí zjistit, za jakým účelem jsou okrajové struktury využívány. Podle hloubky navštíveného okraje lze usuzovat, zda je okraj využíván jako „migrační linie“ (travel line)

poskytující hojnost kořisti, nebo zda se jedná o cíleně navštěvované „místo lovů“ (foraging zone) či zda jsou ekotony unikátní „místa s vysokou hustotou/diverzitou predátorů“ (place with higher predator abundance/diversity) (Larivière 2003). V případě první hypotézy je navštěvována pouze malá část lesní periferie a predátor neprozkoumává okraje hlouběji. Jinak je tomu v případě, kdy je tato oblast místem lovů a predátor tudíž zachází mnohem hlouběji a nejintenzivněji je pak okraj využíván, je-li místem aggregace velkého počtu predátorů (Larivière 2003). Na základě celé řady studií (Andrén a Angelstam 1988, Paton 1994, Söderström a kol. 1998, Batáry a Báldi 2004), je největší počet predátorů zaznamenán především do hloubky padesáti metrů od okraje lesa. Aby však bylo možné pro jednotlivé druhy predátorů podpořit jednu z hypotéz, je nutné jejich habitatové preference srovnat s druhovou charakteristikou (morfologie, mobilita, míra specializace, socialita apod.).

Jako efektivní krok podniknutý ke zmírnění následků fragmentace a okrajového efektu se zdá být zakládání či ponechání úzkého pruhu vegetace na rozhraní dvou prostředí – tzv. biokoridory (Hilty a Merenlender 2004, Šálek 2009). Nejen šelmy tyto koridory využívají k přesunům mezi zbylými fragmenty a tato propojenosť tak zabraňuje úplné exploataci izolovaných ostrůvků (Hilty a kol. 2006, Šálek 2009). Okrajový efekt se mění v závislosti na produktivitě ekosystému, charakteru krajiny a na jeho působení mají vliv i podmínky a charakter dané lokality, jako je například zastoupení a výška keřového a stromového pásma a hustota a pokryv vegetace (Donovan a kol. 1997, Paton 1994). Pro ochranářské a managementové aktivity se proto neukázalo být odstraňování samotných predátorů tak efektivní jako přímé zásahy do charakteru a uspořádání porostu (Gittleman a kol. 2001, Delattre a kol. 1999). Manipulace s početními stavami predátorů navíc naráží na ochranný statut některých druhů. Fragmentovaná, hospodářsky využívaná, krajina s typicky ostrými přechody mezi přilehlými prostředími by se proto měla změnit tak, aby co nejvíce odpovídala přirozenému stavu a snižovala tak predační tlak v ekotonu. Vyšší heterogenita a hustota vegetace v okrajových strukturách znesnadňuje a značně prodlužuje predátorům fázi hledání kořisti (Bowman a Harris 1980, Martin 1993). Postupné přechody na rozhraních mezi lesními fragmenty a zemědělskou krajinou tvořené zmlazujícími porosty lesních dřevin, křovinami a bylinnou vegetací vedou rovněž ke snížení predace a rozvolnění predačního tlaku do širšího území okrajové struktury (Suarez a kol. 1997).

Aby však mohly být podniknuty další a razantnější kroky vedoucí k obnovení a udržení ekologické stability, musí být ekologie fragmentací postižených druhů (monitoring výskytu, početnosti, habitatové preference aj.), a zejména šelem, důkladněji studována.

K tomu účelu slouží celá řada metod, a to jak přímých, tak nepřímých. Mezi přímé metody se řadí přímé pozorování, radiotelemetrie, specifické značení umělými značkami, využití unikátních vzorů na kůži či srst, ale i odstřel. Avšak přímé metody jsou často neefektivní díky vysoké logistické a časové náročnosti a jejich využití je nevhodné pro sledování více druhů na rozsáhlém území (Šálek 2009). Vzhledem k výše zmíněné náročnosti pozorování šelem nejsou, s výjimkou radiotelemetrie, tyto metody ve velké míře využívány.

Pro studium savčích predátorů se proto častěji využívá nepřímých metod, jakými jsou kamerové pasti, zimní stopování, sběr trusu, umělá hnízda, kryté nášlapné talíře a pachové stanice. Většina těchto metod má však jistá omezení (kamerové pasti – vysoká finanční nákladnost, zimní stopování – omezené na přítomnost sněhu a roční období při nedostatku kořisti, což zkresluje představu habitatové preference atd.) (Šálek 2009).

Díky nízkým nákladům a vysoké efektivitě je proto nejčastěji využívána metoda pachových stanic (Gehring a Swihart 2003, Barea-Azcón a kol. 2006). Tato metoda, vhodná ke stanovení populačních trendů, habitatových preferencí či relativní početnosti druhu, původně široce užívaná v Severní Americe, našla své uplatnění i v evropské krajině (Virgós a kol. 2002, Mortelliti a Boitani 2007, Šálek 2009). Princip pachových stanic spočívá v zachycení stop na ploše, na kterou jsou predátoři nalákáni pachovým atraktantem umístěným uprostřed stanice. Rozmístění, počet stanic, doba expozice, typ substrátu či atraktantu se může lišit v závislosti na druhu sledovaných predátorů, typu krajiny či předmětu výzkumu, ovšem i při zvolení nevhodnějšího postupu má tato metoda své nevýhody. Mezi ně patří snadné ovlivnění návštěvnosti pachových stanic počasím (Nottingham a kol. 1989), sezónou (Wilson a Delahay 2001), lidskou aktivitou v blízkosti stanice (Andelt a kol. 1985), či rozdílnou pozorností jednotlivých druhů vůči vybranému atraktantu nebo celé stanici (Baldwin a kol. 2006, Mortelliti a Boitani 2007). To všechno však vysoce převyšuje výhody a efektivnost využití pachových stanic, které někteří badatelé (Stanley a Royle 2005, Gompper a kol. 2006) doporučují kombinovat s dalšími nepřímými metodami, které slouží k vyrovnaní zmíněných nedostatků. Navíc v podmírkách evropské kulturní krajiny nejsou nevýhody, jako je ovlivnění lidskou aktivitou v blízkosti stanice, tak významné, jelikož jsou predátoři na lidskou činnost víceméně habituováni.

Tato magisterská práce si, právě za použití metody pachových stanic, klade za cíl zjistit habitatové preference savčích predátorů ve fragmentované krajině. Očekávaným výsledkem je preference okrajových struktur. Ovšem ta, jak již bylo zmíněno, se mění i v závislosti na velikosti fragmentu. Ve fragmentech malé velikosti, které jsou často

mnohonásobně menší než domovské okrsky monitorovaných šelem, je možné předpokládat, že se šelmy nebudou striktně držet okrajových struktur a malé fragmenty budou využívat v celém jejich rozsahu. Wilcove (1985) prokázal vyšší predáční tlak ve fragmentech malé velikosti, což by mohlo napovídat, že se savčí predátoři mnohem častěji vyskytují právě zde. Velké fragmenty by však logicky měly poskytovat, vzhledem ke své rozloze, větší potravní a prostorové možnosti. Vzhledem k nedostatku studií zabývajících se hloubkou působení okrajového efektu v závislosti na velikosti fragmentu, bude jedním z cílů této práce na danou otázku odpovědět.

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Fine-scale utilization of forest edges by mammalian predators related to patch size and its conservation aspect

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Abstract

We focused on edge effect in different fragment size patches using scent-station method. We tested whether habitat fragmentation and fragment size relate to mammalian predators' abundance and distribution and whether is contribution of this factors additive or interactive. In May and June 2008 – 2009 we deployed scent stations in total 154 forest fragments of variable area (0,012 – 50,996 km²). This sample size allowed us to perform detailed analyses separately for all detected species. Our findings acknowledge that mammalian predators prefer habitat edges and small forest fragments. The probability of occurrence of carnivores tends to decrease with increasing distance from edge in all 7 detected species. Carnivores' activity was also negatively correlated with area of forest fragments. All detected species tend to prefer small fragments with the exception of badger (reverse nonsignificant pattern) and red fox (no effect of fragment size). Nonsignificant interaction between fragment size and distance to edge suggest independent contribution of both these factors to mesopredator mediated effects on native biota in fragmented landscape. Hence, we suggest that mammalian predators prefer small forest fragments as well as that edge related activity is not affected by patch size.

Keywords: edge effect, fragment size, mammalian predators, fragmentation, scent station, Doudlebia, Czech Republic

Introduction

Edge related nest predation has been described as a major factor of declining of many edge specialist bird populations across many different types of ecosystems (Nour et al. 1993, Paton 1994, Donovan et al. 1997). Higher nest predation near forest edge should be closely connected with level of habitat fragmentation, which leads to decrease of patch size and increase of edge structures in relation to forest interiors (Andrén 1992, Vergara and Hahn 2009). It is known that edge related nest predation depends on variety of biotic and abiotic factors such as type of forest edges (Andrén 1995), structure of surrounding landscape matrix as well as composition of avian and mammalian predator community (Gates and Gysel 1978, Marchand and Litvaitis 2004). Similarly, many researchers have found higher nest losses in smaller forest fragments as well as in shorter distance to forest edges in contrast to unfragmented large forest patches (Wilcove 1985, Hoover et al. 1995, but see Storch et al. 2005). In temperate zone most of predation events were recorded within 50 meters from forest edges (Andrén and Angelstam 1988, Paton 1994, Söderström et al. 1998, Batáry and Báldi 2004), however some studies did not find any relation between nest predation and edge structures (see Storch 1991, Lahti 2001). Hence, higher prevalence of nest predators in forest-farm edges and small forest islands may lead to that the edges may make "ecological trap" (Gates and Gysel 1978).

Bursting human impact in agricultural landscape, high degree of urbanization and increasing of food resources, which are connected with human activities and suburban development, lead to increasing population of many mesopredator communities. In Central Europe, a marked increase of generalist carnivores has been documented, such as red foxes (*Vulpes vulpes*) and martens (*Martes* sp.) which are particularly important nest predators of edge nesting bird species (Seymour et al. 2004, Storch et al. 2005). A multitude of generalist predators penetrated from farmland to forest matrix and vice versa should increase predator diversity and abundance around forest edges. Predator concentration to forest edges should be associated with higher prey densities (Ratti and Reese 1988, Šálek et al. unpubl. manuscript), or alternatively mammalian predators should utilize habitat edges as a travel lines (Bollinger and Peak 1995, Larivière 2003).

Although predator activity has been studied especially using nest predation experiments on artificial or natural nests, data about direct fine scale utilization of forest-farm edge gradient of mammalian predators have been sporadically performed (but see for example Šálek et al. unpubl. manuscript, Svobodová et al. unpubl. manuscript). These contributions

are however based on small or medium scale experiments that focus primary on the overall response of mesopredator fauna to landscape elements. This large scale experiment by contrast allowed us to evaluate spatial pattern of distribution at species specific level. In addition, edge effect is not the only mechanism how landscape fragmentation contributes to population declines due to increased predation risk. Increased abundance of mesopredators in small habitat fragments may occur due to negative interactions with more habitat sensitive top predators (Crooks and Soule 1999) or simply due to *per se* preferences for these fragments (Wilcove 1985). This point was however not subject of some detailed research in European conditions. In addition, although both these consequences of habitat fragmentation (i.e. edge effect and preference for small patches) may contribute additively to overall predation risk in fragmented landscape, alternative scenarios were rarely evaluated at least in European context. Complex biotic interactions may be based on theoretical models and empirical data both enhance or reduce the strength of edge effect in habitat fragments of small size. In this contribution, we examined fine-scale utilization of forest-farm edges by mammalian predators in relation to different size of forest patches. We predicted that predators' activity is greater along edge than in the forest interior and that it is negatively associated with fragment size. Similarly, we tested if distribution of mammalian carnivores along forest edge interior continuum differs with respect to fragment size.

Methods

Study area

Our study was conducted in 1502 km² of highly fragmented agricultural landscape in České Budějovice basin (between 48° 48' N, 14° 10' E and 49° 13' N, 14° 30' E), Doudlebia, Czech Republic. This region is characterized with predominantly flat or gently downy topography and is situated in altitudes mostly varying from 380 to 410 m. Terrestrial climate of study area is distinguished by annual mean temperature 7,5 °C and rainfall ranging from 600 to 650 mm. The region is characterized by diverse mosaic of agricultural land with cultivated crop fields, grasslands, exclusively used pastures and extensive variety of fishponds. The secondary coniferous or mixed forests are dominated by common spruce (*Picea abies*), scots pine (*Pinus sylvestris*), with occasional broad-leaved tree species such as oak (*Quercus* spp.), birch (*Betula pendula*) and beech (*Fagus sylvatica*). Ground vegetation is represented by shrubs and saplings of canopy trees (*Acer platanoides* / *pseudoplatanus*, *Corylus avellana*). Forest-farm edges are composed by dense shrub

vegetation, consisting mainly of shrubs (*Corylus avellana*, *Prunus spinosa*) as well as diversified herbaceous vegetation mainly originating from the nearby grasslands.

Design of the experiment

Distribution of mammalian predators on forest-farm edges was studied in 154 transects in forest patches of different size (0,012 – 50,996 km²) from May to June in 2008 and 2009. Selected period corresponds to the nesting season of the most birds in the study area (e.g., Hudec 1983). Study localities were chosen based on digitized aerial orthophotograph maps (1:5000) using geographical information system (GIS, ArcView 3.2a - Environmental Systems Research Institute, Inc. 2000). Minimum distance between neighboring localities was 500 m in order to achieve independence of the replicate sites (e.g., Gehring and Swihart 2003); however, its average distance was 3400 m. In each location we placed transect of four scent stations for monitoring carnivores (see below) in forest matrix at four distances from the forest edges (0, 25, 50, 100 m). For purpose of our work, we defined forest edges as the sharp boundary between forest and grassland habitat. Grassland habitats were entirely composed of production hayfields (for detailed description see Šálek et al. 2009). Minimal distance between two adjoining scent stations in one transect was 50 m. Scent stations are usually arrayed in lines, however linear arrangement generally produces spatially dependent data (Sargeant et al. 2003). Consequently, scent station placement within one set was not linear in our study design. We excluded two-sided forest-farm edge effect from our monitoring because the data from preliminary research showed very low proportion of visited scent stations in hayfields (Červinka unpubl.) and similar utilization of this habitats was recorded from other researches in the same study area (Šálek et al. unpubl. manuscript, Svobodová et al. unpubl. manuscript, Šálek et al. 2009).

Mammalian predators' distribution

To assess distribution and habitat utilization of mammalian predators various types of methods were developed (see Long et al. 2003, Gompper et al. 2006) and these method are always facing specific ecological and behavioral features of carnivores such as wariness of humans, nocturnal activity, secretive habits as well as their low population densities (Sargeant et al. 2003). For our research, we decided to use scent station, which is one of the most used methods for large spatial scale observation of carnivores (e.g. Linhart and Knowlton 1975, Zielinski & Stauffer 1996, Crooks and Soulé 1999, Gehring

and Swilhart 2003, Long et al. 2003, Mortelliti and Boitani 2007). 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, at the same time without attraction of animals from greater distances, domestic rabbit urine was used as a mild attractant (Linhart and 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 for eight consecutive days. Presence of footprints was checked every second morning. In case of rainfall, the observation was interrupted and restored scent stations were checked again after 2 days.

The mammalian predators' identification was based on footprint dimensions and shape characteristics (Bouchner 2003, Anděra and Horáček 2005). In our study area there is a documented occurrence of least weasel (*Mustela nivalis*), ermine stoat (*Mustela erminea*), polecat (*Putorius sp.*), martens (pine marten *Martes martes*, stone marten *Martes foina*), Eurasian badger (*Meles meles*), red fox (*Vulpes vulpes*) and human's residential carnivores (domestic cat *Felis catus* and domestic dog *Canis lupus familiaris*) (Svobodová et al. unpubl. manuscript, Bouchner 2003, Anděra and Horáček 2005, Šálek et al. 2009). We excluded domestic dogs from our analysis because their occurrence is mostly dependent on human activities (see Lenth et al. 2008).

Statistical analysis

Multiple detections of the same carnivore species during the 8 exposure days at a particular scent station may be caused by the same individual. We therefore treated occurrence of a particular carnivore species as a binary response variable (present or absent during the 8 days).

At first, we fitted "complex" model, where outcome of each scent station (presence or absence) for every carnivore species detected during the survey (in total 7 species) was considered. This model enabled to test for the interspecific consistency of all explanatory variables evaluated using the interaction between species identity and particular factor in the question (see Šálek et al. 2009 for further details).

There are two sources of data nonindependence in this dataset. At first, stations at each locality (i.e. scent stations quadruplets, see section *Experimental design*) might be visited non-independently due to close proximity. In addition, outcome of each scent station was considered separately for all species detected during the experiment. However,

the probability of the detection of particular species does not have to be independent with the respect of spatial distribution of remaining carnivores. To avoid these sources of spatial pseudoreplications (Sargeant et al. 2003), 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 2.10.0. software. The model contained a random intercept, specified as the scent station identity nested in a locality.

Significance of following main effects and all their two way interaction was evaluated: the year of the study (2008 vs. 2009), the species identity (red fox, domestic cat, marten, polecat, stoat, least weasel, and badger), the log fragment size (range 0,012 – 50,996 km²), and the distance to the habitat edge (1, 25, 50 and 100 m). The last variable was considered as continuous; however, identical results were obtained when including distance to habitat edge as a categorical variable with 4 levels. In addition the complex model contained two three way interactions: *fragment size × distance to edge × year* and *fragment size × distance to edge × species* to test for between year and between species consistency of the focal interaction: *fragment size × distance to edge*.

In addition, we fitted 7 single species models, where factors affecting the probability of detection of particular species were tested. Similarly as in the complex model the response variable was assumed to be binary, corresponding to the presence or absence of particular species at the scent station. We evaluated significance all main effects and two-way interactions that were considered in complex model.

Backward elimination of the non-significant terms in the GLMM was used to select the best minimal adequate model (MAM), i.e. the most parsimonious ones with all the effects being significant (Crawley 2007), eliminating at first non-significant interactions and subsequently non-significant main effects. The significance of a particular explanatory variable is derived from 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).

We also tested for spatial randomness of the scent stations visits using randomization procedure described in Šálek et al. (2009). In brief, observed distances between two nearest localities (scent stations sets) visited by a particular predator species were compared

with distances that were simulated under the assumptions (1) that predators are distributed randomly and (2) probability of their detection is consistent with empirical data. There 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 seven cases, $P > 0.2$).

Results

During the 4928 station-nights, we recorded 268 visitations of 7 mammalian predators' species. The average detection of carnivore on scent station was $0,054 \pm \text{SE}$ detections per station-night. We detected least weasel (*Mustela nivalis*, 32 visits, 5,2 % scent stations visited), ermine stoat (*Mustela erminea*, 59 visits, 7,5 % scent stations visited), polecat (*Putorius sp.*, 31 visits, 5,0 % scent stations visited), martens (*Martes sp.*, 57 visits, 7,9 % scent stations visited), Eurasian badger (*Meles meles*, 16 visits, 1,8 % scent stations visited), red fox (*Vulpes vulpes*, 26 visits, 3,6 % scent stations visited) and domestic cat (*Felis catus*, 39 visits, 5,4 % scent stations visited).

According to the complex model, the probability of carnivore detection varied sustainably between years (56 visits and 22,6 % scent stations visited at least once in year 2008 vs. 127 of individual visits and 34,5 % scent stations visited at least once in year 2009 Table 1). In addition, the marginally significant “*year × species*” interaction suggest that these temporal fluctuations are not consistent for all species detected (Table 1). Single species models show significant decrease of the detection probability for Stoat in year 2008 compared to year 2009 (Table 2). On the other side, between years variation in the probability of detection was not revealed for remaining species (Table 2).

Backward reduction of the complex model further demonstrate highly significant preferences of carnivores for forest/farmland edges, since the probability of their detection decreased with increasing distance to these structures (Table 1, Figure 1). Our data however do not suggest considerable interspecific differences in response to the habitat edges (i.e. nonsignificant interaction: “*species × distance to edge*”, Table 1). All species tend to be more likely detected near habitat edges and interspecific differences in this correlation were rather low (Figure 3). In addition, according to single species model, significant preferences for habitat edges were revealed for all species with the exception of least weasel (Table 2).

Based on the complex model, carnivores were generally more likely to be detected in small fragments (highly significant main effect “*fragment size*”, Table 1, Figure 2);

however, the marginally significant interaction “*species* × *fragment size*” suggests inconsistent interspecific response to fragment area (Table 1, Figure 4). Separate single species models revealed significantly higher probability of detection in smaller fragment size for domestic cat and marten (Table 2). However, after removing these two species from the complex model the “*species* × *fragment size*” interaction as soon as the “*fragment size*” main effect remain still significant ($\Delta D.f. = 4, \chi^2 = 9.94, p = 0.0415$ and $\Delta D.f. = 1, \chi^2 = 5.49, p = 0.0191$ respectively). This indicates that interspecific differences in patch size preferences are driven not only by the contrast between two species with highly significant preferences for small patches (domestic cat and marten) vs. remaining carnivores. The slope of the relationship between fragment size and probability of carnivore detection tend to be negative for all detected species with the exception of red fox (no pattern) and badger (nonsignificantly positive relation, Figure 4). When we finally excluded data on badger from the complex model the “*species* × *fragment size*” interaction was no more significant ($\Delta D.f. = 5, \chi^2 = 6.66, p = 0.2476$).

Finally, there was also in general no evidence for different response to habitat edges in large and small fragments (nonsignificant interaction: “*fragment size* × *distance to edge*”) suggesting additive independent contribution of these to factors. This appears to be consistent across the species level (nonsignificant interaction: “*fragment size* × *distance to edge* × *species*”, Table 1). No effect of the “*fragment size* × *distance to edge*” interaction was confirmed for all detected species according to single species model, with the exception of badger. However, marginal significance of this interaction in this species was driven by just two visits that occurred both in relatively large fragments and relatively apart from forest edge (50 m from forest edge in fragment of 31556 m² and 100 m in fragment of 58410 m²). When excluding these two visits from the dataset its significance was lost suggesting the lack of robust support for the interactive effect of distance to edge and fragment size in badger.

Table 1. GLMM fitting results for the probability of the detection of carnivores at scent stations. Significance values correspond to likelihood ratio tests. Factors included in the minimal adequate model are in bold print.

Fixed effect*	Δ D.f.	X ²	p
Distance to edge	1	35.55	<0.0001
Year	1	16.24	0.0001
Species	6	38.12	<0.0001
fragment size	1	17.54	<0.0001
species × fragment size	6	12.92	0.0444
year × species	6	18.61	0.0049
year × distance to edge	1	3.35	0.0672
species × distance to edge	6	3.70	0.7173
Fragment size × distance to edge	1	0.96	0.3262
year × fragment size	1	0.38	0.5380
Fragment size × distance to edge×year	1	3.16	0.0753
Fragment size × distance to edge × species	6	9.06	0.1702

* Fixed effects: Distance from edge, (0-100 m distance to forest agricultural ecotone); year, temporal replication in year 2008 and 2009; Fragment size (0,012 – 50,996 km²); species, red fox, domestic cat, marten, polecat, stoat, least weasel, badger.

Figure 1. Predicted relation between the probability (\pm SE) of the detection at least one carnivore at the scent station during 8 exposure nights and distance to forest/farmland edge. Prediction based on GLMM assuming distance to edge both as a categorical and continuous variable is presented.

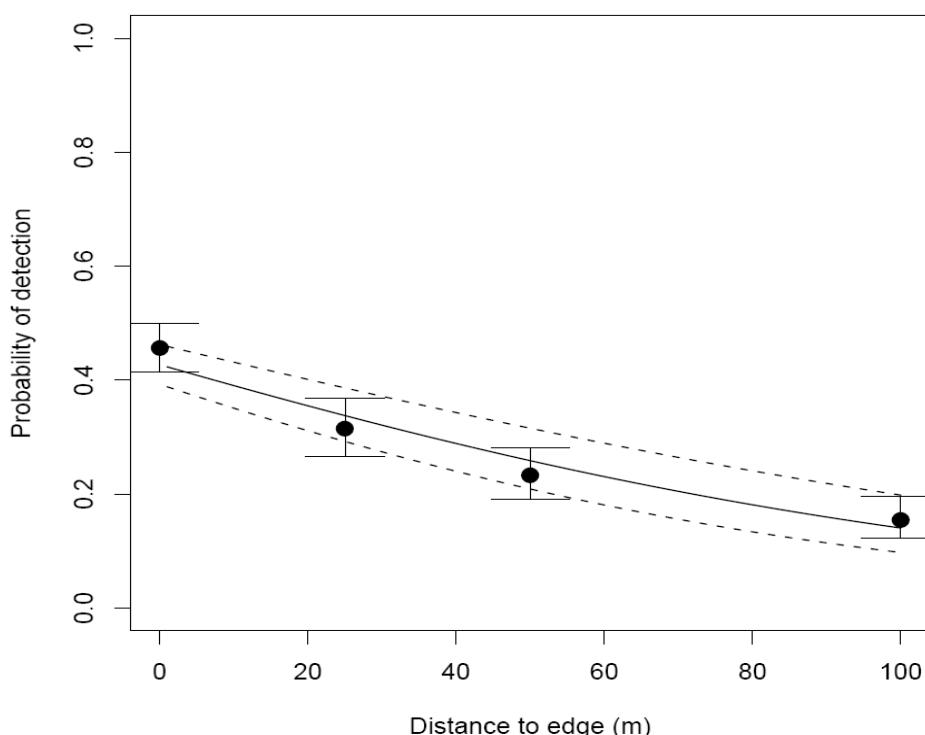


Table 2. GLMM fitting results for the probability of the detection of particular carnivore species (single species models) at scent stations. Significance values correspond to likelihood ratio tests. Factors included in the minimal adequate model for each carnivore group are in bold print.

Species	Fixed effect*	Δ D.f..	χ^2	p
Domestic Cat	distance to edge	1	13.71	0.0002
	fragment size	1	5.80	0.0160
	Year	1	1.13	0.2887
	distance to edge × fragment size	1	1.32	0.2511
	distance to edge × year	1	1.13	0.2879
	year × fragment size	1	0.00	0.9639
Red fox	distance to edge	1	5.21	0.0225
	Year	1	0.66	0.7177
	fragment size	1	0.04	0.8430
	distance to edge × fragment size	1	0.09	0.7652
	distance to edge × year	1	0.00	1.0000
	year × fragment size	1	1.73	0.1881
Badger	distance to edge	1	9.48	0.0021
	fragment size	1	0.12	0.7281
	distance to edge × fragment size	1	4.01	0.0453
	Year	1	0.31	0.5796
	distance to edge × year	1	0.00	1.0000
	year × fragment size	1	2.89	0.0892
Marten	distance to edge	1	10.42	0.0012
	fragment size	1	7.64	0.0057
	distance to edge × fragment size	1	3.29	0.0697
	Year	1	1.82	0.1773
	distance to edge × year	1	0.00	1.0000
	year × fragment size	1	0.64	0.4226
Polecat	distance to edge	1	8.13	0.0044
	Year	1	0.66	0.4176
	fragment size	1	0.67	0.4121
	distance to edge × fragment size	1	0.88	0.3490
	distance to edge × year	1	0.00	1.0000
	year × fragment size	1	2.28	0.1309
Stoat	distance to edge	1	5.26	0.0219
	Year	1	9.34	0.0022
	distance to edge × fragment size	1	3.52	0.0606
	fragment size	1	1.87	0.1715
	distance to edge × year	1	0.00	1.0000
	year × fragment size	1	0.08	0.7767
Least Weasel	distance to edge	1	2.28	0.1311
	Year	1	1.56	0.2110
	fragment size	1	0.82	0.3656
	distance to edge × fragment size	1	0.00	1.0000
	distance to edge × year	1	0.28	0.5960
	year × fragment size	1	0.28	0.5960

* Fixed effects: Distance from edge, (0-100 m distance to forest agricultural ecotone; year, temporal replication in year 2008 and 2009; Fragment size, small vs. large forest fragments.

Figure 2. Predicted relation between the probability (\pm SE) of the detection at least one carnivore at the scent station during 8 exposure nights and log transformed fragment size. Prediction based on GLMM.

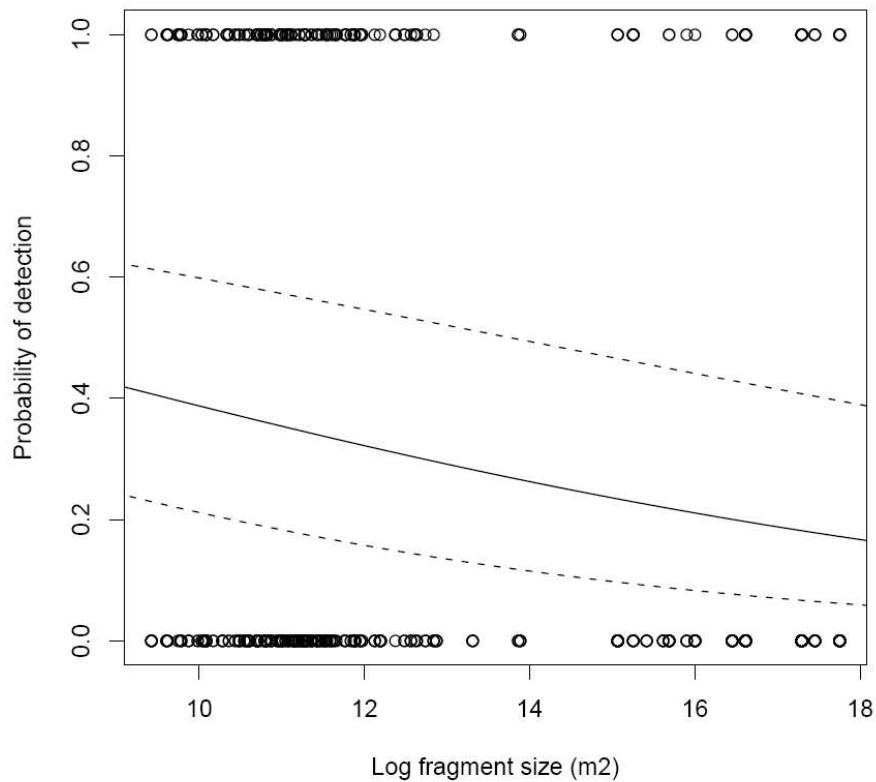


Figure 3. Interspecific differences in forest/farmland edge preferences expressed as the GLMM slope (\pm SE) between probability of detection of individual species and distance to habitat edge (i.e. negative values correspond to higher likelihood of detection near habitat edge).

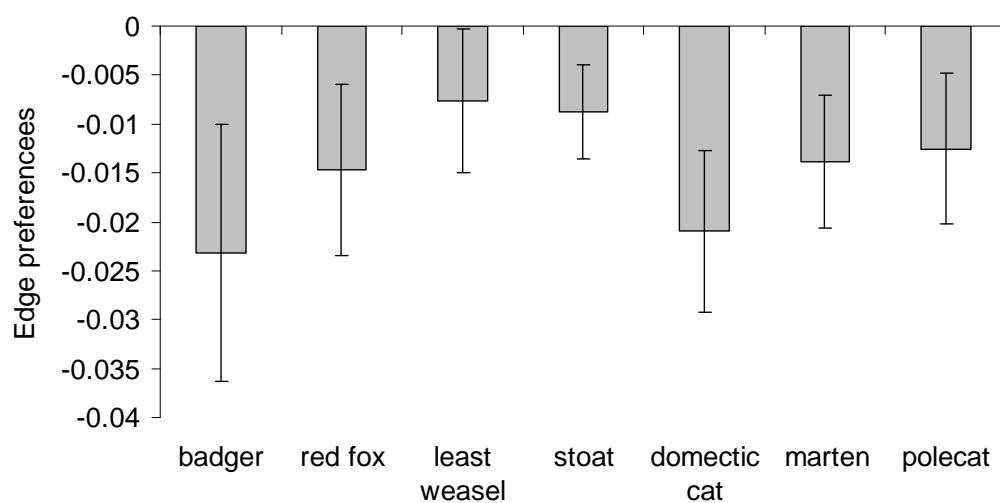
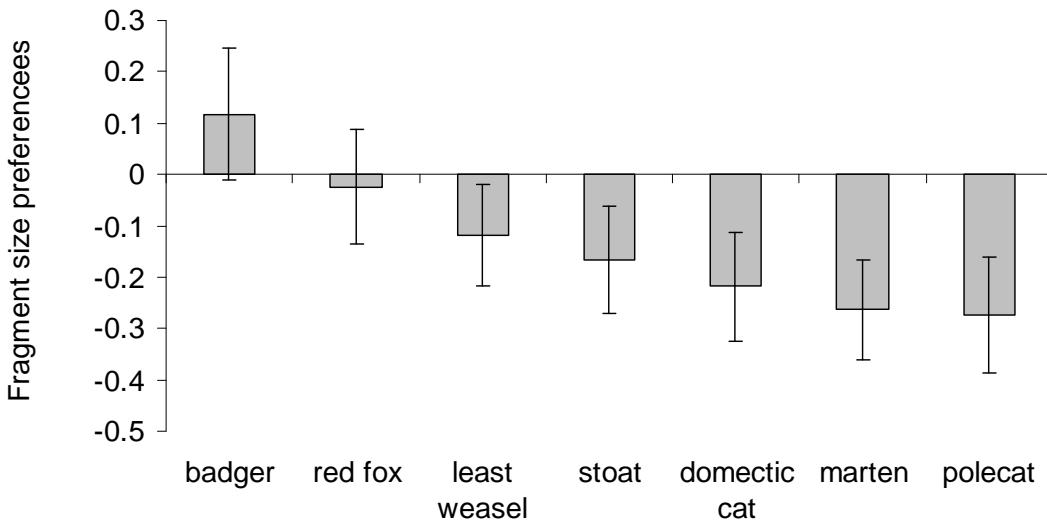


Figure 4. Interspecific differences in fragment size preferences expressed as the GLMM slope (\pm SE) between probability of detection of individual species and fragment size (i.e. negative values correspond to preferences for small fragments and positive values indicate preferences for large fragments).



Discussion

Marked negative impact of habitat fragmentation and edge effect on many populations of bird species belong to recently major concern of conservation biology (e.g. Fahring 2003). Our study brought data that predicate of forest-farmland edge related activity of mammalian predators, as an important factor of predation risk, in diverse mosaic of fragmented agricultural landscape. In compliance with our previous results (Šálek et al. unpubl. manuscript, Svobodová et al. unpubl. manuscript) and studies by Andrén and Angelstam (1988), Paton (1994) etc., we were documented that mammalian predators' distribution in fragmented landscape is primarily restricted to narrow strip of forest edge. The priority for edge structures was not record only in larger forest fragments but also in the small woodlots patches. Similarly, to studies by Wilcove (1985) and Vergara and Hahn (2009) we also found preferences for small fragments, where carnivores tend to be more likely detected.

The distance, which predators penetrate from habitat edge, is often debated in variety of geographical locations and it may vary in dependence on different biotic and abiotic factors. Although enhanced nest predation have been found mostly within 50 m from an edge (Wilcove et al. 1986, Burger et al. 1994, Paton 1994, Batáry and Báldi 2004) some authors take this determination for subjective and arbitrary (Andrén and Angelstam 1988, Flashpohler

et al. 2001, Larivière 2003, Storch et al. 2005). Our findings show the significant decreasing of carnivores' occurrence with increasing distance from forest edge. Almost 90 percent of records have been found within 50 meters from the forest edge. Similarly, Bider (1968) reported high prevalence of mammalian activity along forest-field edges in the first 50 m from forest edge than further in interior. We assume that this could be closely connected to landscape type and level of habitat fragmentation and type of habitat edge. Elevated edge related predators' activity in forest fragments has been documented in highly and moderately fragmented landscapes (Donovan et al. 1997, Lahti 2001) as well as in the areas with high agricultural utilization or residential development (Bayne and Hobson 1997, Dijak and Thompson 2000, Keyser 2002). Similarly previous studies have suggested that nest predation in forest edges occurred between two habitats with steep gradient productivity (forest/farmland edges, see Angelstam 1986, Wilcove et al. 1986, Paton 1994, Andrén 1995) however its prevalence is less obvious in lower gradient habitats such as forest interiors (clercuts/contigous forest, Saracco and Collazo 1999, Malt and Lank 2009). Our edges represent however hard ecotone boundary between forest and farmland landscape (see methods for further details).

Landscape composition and type of edge structures should have marked influences not only on predators' distribution and abundance but also on its prey. Predators should focus their foraging activity to areas where the food sources are abundant (Macdonald 1983, O'Donoghue et al. 1998, Jepsen et al. 2002, Fuller et al. 2007, Sidorovich et al. 2007, Zub et al. 2008). Similarly higher prevalence of carnivores' activity in forest edges should be caused by higher densities of potential prey, especially small mammals (Ratti and Reese 1988, Pasitschniak-Arts and Messier 1998) and birds (Gates and Gysel 1978, Austen et al. 2001). Our previous research has shown that abundance of mammalian predators and small mammals consistently increased in habitat edges (Šálek et al. unpubl. manuscript), however in the years of low abundances of small mammals carnivores did not exhibit edge preferences (it is much less obvious) (Svobodová et al. unpubl. manuscript).

Unlike previous studies were performed on carnivores' edge preferences in central European conditions (Šálek et al. unpubl. manuscript, Svobodová et al. unpubl. manuscript) our contribution based on large sample size allowed to test edge preferences for all species detected. Increase carnivore activity along habitat edges was supported for all detected species. In case of least weasel, the trend was not as significant as in case of other species (Table 2). We hypothesize that in predator rich edge habitats the least weasel should suffer inter-specific competition and intra-guild predation by larger generalist predators (King 1983,

Korpimäki and Norrdahl 1989). Thus, they should be forced out from forest edges, which results in more homogeneous utilization of whole transect.

The strength of edge effect may vary in dependence on several factors (remnant size, shape, position in landscape, wind, water flux, sunlight etc.). Many previous researches have founded increased nest predation as forest size decreased (Wilcove 1985, Yahner and Scott 1988, Paton 1994, Keyser et al. 1998). Wilcove (1985) determinated that increasing edge related nest predation in small fragments is caused by higher proportion of edges in relation to forest interiors (Wilcove et al. 1986, Andrén and Angelstam 1988, Murcia 1995, Vergara and Hahn 2009). In line of these results, we assumed that the smaller forest patch should force carnivores to explore the whole habitat and not only the edges. Nevertheless, our data did not show any differences in edge activity in the different forest patch size. Edge preferences of mammalian predators were same in the small and large forest patches and these results were consistent across the species level.

Similarly, population densities of medium-sized mammalian predators may be greater in smaller forest patches than in larger forest fragments, because predators should concentrate their foraging activity into remaining forest fragments (Wilcove 1985). However, larger forest fragments should maintain higher number of predator territories and the populations that should be - in contrary with smaller fragments - less endangered of local extinction (Vergara and Hahn 2009).

Although, based on martens prints, we were not able to distinguish between both species (stone marten *Martes foina* and pine marten *M. martes*), which inhabit our study area. We assume that most of the records belong to stone martens which are characteristic inhabitant of fragmented agricultural landscape (Libois and Waechter 1991, Virgos et al. 2000, Rondinini and Boitani 2002, Mortelliti and Boitani 2007). Stone marten also show more generalist habitat preferences and synantropic behavior (Šálek et al. 2005, Herr et al. 2009), however in contrary the distribution of pine marten is strictly focused on large homogeneous forest fragments and seems to be sensitive to human related activity and fragmentation (Červený et al. 2003). Santos and Santos-Reis (2009) determinated large habitat plasticity of utilization of different forest patches, however their work was focused on forest fragments with complex geometric forms with a higher amount of edge habitats. We believe that the utilization of smaller forest fragments in our study is associated with higher availability of feeding resources, especially small mammals, birds, insects and fruits, which are mainly connected with open farmland and urban residence or other human-related resources (Tellería et al. 1991, Austen et al. 2001). This should be also true for domestic cat

Felis catus however its activity is mainly concentrated in vicinity to human settlements where the resting sites are mainly situated (Barratt 1997, Germain et al. 2008). High density of small farms and rural settlements spreading throughout agricultural landscape are characteristic feature of study area and create low permeability barrier for most of species.

Management implications

In accordance with many previous studies (Andrén and Angelstam 1988, Donovan et al. 1997, Chalfoun et al. 2002, Keyser 2002, Larivière 2003, Vergara and Hahn 2009), we found strong edge effect on forest-farm edges in carnivore distribution in highly fragmented landscape. Edge-related activity of mammalian predators has important management implication and especially in connection with conservation of many populations declining farmland bird species (Dijak and Thompson 2000, Gehring and Swihart 2003, McWethy et al. 2009). Edge effect should change in dependence on ecosystem productivity, landscape characteristics, and types in local habitat features surrounding the edges (Paton 1994, Donovan et al. 1997, McWethy et al. 2009). Fragmented landscape dominated of human activities and suburban development leads to increasing population densities of many generalist predators (Gehring and Swihart 2003, Šálek et al. unpubl. manuscript) which are able to search in variety of different habitats, however their activity is predominantly focused on prey rich edge habitats (Winter et al. 2000). Management of generalist predator should have marked impact on breeding success of local breeding birds and biodiversity (Shafer 1999, Gehring and Swihart 2003) however large-scale removal programs are usually noneffective and problematic especially with carnivores positive effect on ecosystem stability and function (such as regulation of small mammals outbreaks) (Gittleman et al. 2001, Delattre et al. 1992, 1999). Moreover some carnivores (e.g. *Putorius putorius*, *P. eversmanni*) inhabiting Central European agriculture landscape (Anděra and Hanzal 1996) belong to endangered species with conservation concern which should result in conflict between carnivore protection and conservation of focal prey populations. Thus, effectiveness conservation steps should be as concentrate of landscape structure and configuration – as a spatial relationship between individual landscape elements - because landscape structure may have major impact in predator-prey interactions (Donovan et al. 1997, Chalfoun et al. 2002, Virgos et al. 2002, Gehring and Swihart 2003, Pita et al. 2009). Larger forest patches should have adequate proportion of core area

to increase of nest success because mammalian predators have a lower chance to move deeply into forest interior (Vergara and Hahn 2009).

Finally, on local scale, vegetative features and nest site characteristic should influence edge related nest predation and has important conservation aspect (Davis 2004). Enhanced vegetation heterogeneity and complexity (e.g. regenerating shrub cover) along forest-farm edges may decrease nest predation by reducing predator search efficiency (Bownan and Harris 1980, Martin 1993). Similarly, linear abrupt forest edges should be utilized as a travel lines (Bollinger and Peak 1995, Larivière 2003) and higher predation rates around edges should be also attribute of incidental nest predation (Vickery et al. 1992, Seymour et al. 2004). Suarez et al. (1997) found twice higher nest predation for those nests located on abrupt compared with gradual edges. We suggest that management practices designed to establish more gradual buffer zones between forest farm edges in fragmented landscape should have important value to conservation of endangered bird species. However, for drawing this conclusion further research is needed.

Acknowledgement

This research was supported by the grants no. 6007665801 of the Ministry of Education of the Czech Republic (MSMT) and SGA2009016 of the Faculty of Science, University of South Bohemia.

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Závěr

Porozumění habitatovým preferencím savčích predátorů je důležitým krokem k zajištění ekologické stability a trvale udržitelného rozvoje krajiny. Tyto poznatky mohou být následně využity pro další ochranářská a managementová opatření.

Předložená práce se zabývala využíváním okrajových struktur savčími predátory v závislosti na velikosti lesního fragmentu. Podařilo se nám prokázat jednoznačné preference pro okrajové struktury. Naše výsledky tak potvrzují výrazné působení savčích predátorů ve fragmentovaném prostředí, čímž negativně ovlivňují početní stavy své kořisti včetně mnohých druhů ptáků. Pravděpodobnost výskytu savčích predátorů se snižovala s rostoucí vzdáleností od okraje, přičemž naprostá většina záznamů byla pořízena v rozmezí padesáti metrů od okraje lesa. To platilo, jak v podmírkách velkých lesních celků, tak i v malých lesních fragmentech, což bylo v rozporu s našimi prvotními předpoklady. Okrajový efekt tedy působí ve všech fragmentech bez ohledu na jejich velikost. Pro vyvození jednoznačných závěrů, za jakým účelem jsou tyto struktury savčími predátory navštěvovány, je však nutné provést ještě další výzkum.