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**Antipredační chování, pohlavní výběr a reprodukční úspěch
u vrabce domácího *Passer domesticus***

Disertační práce

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Alena Klvaňová

Poděkování

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Obsah

Úvod

Zásadní úlohou živých organismů je z pohledu současné evoluční biologie rozmnožování za účelem získání maximální zdatnosti, neboli fitness (Krebs & Davies 1993). Vše, co jedinec dělá, by tedy mělo směřovat k produkci co největšího množství co nejkvalitnějších potomků. Aby se však potomstvo dožilo reprodukčního věku, je u obratlovců zpravidla zapotřebí investovat do souboru různých typů chování označovaných jako rodičovská péče. Existuje celé kontinuum úrovní od téměř nulové péče po nejsložitější a v živočišné říši nejvzácnější biparentální péči. U ptáků, cichlid a primátů je však převažujícím typem rodičovské péče (Lack 1968; Clutton-Brock 1991; Bennett & Owens 2002; Reynolds et al. 2002). Původní model biparentální péče předpokládal, že mezi samcem a samicí se ustanovil určitý podíl jednotlivých pohlaví na péči, tzv. „zpečetěná nabídka" (sealed bid), který je výsledkem konfliktu rodičů o péči v evolučním čase a stal se evolučně stabilní strategií (Houston & Davies 1985). Tento konflikt však stále trvá a ukazuje se, že alespoň u některých druhů je podíl konkrétních jedinců na péči spíše výsledkem procesu „vyjednávání" (negotiation) mezi oběma rodiči (McNamara et al. 1999, 2003; Johnstone & Hinde 2006), kdy vzájemně reagují na úroveň péče poskytovanou partnerem v reálném čase (Harrison et al. 2009). Ta zahrnuje různé druhy chování. U ptáků jde o inkubaci vajec, zahřívání a krmení mláďat, obranu před predátory, péči o hygienu v hnízdě a v různé míře i učení potomků (Clutton-Brock 1991). Pomineme-li faktor počasí, je pro úspěšné zvládnutí všech úrovní rodičovské péče a dosažení co nejvyššího fitness klíčové, s jakým partnerem jedinec vytvoří pár. U pěvců je v procesu výběru partnera samice zpravidla tou, která si vybírá. Pro usnadnění této volby vznikl signalizační systém, který díky znakům sloužícím jako poctivé signály kvality, mohou samice používat při výběru kvalitních partnerů (Zahavi 1975; Andersson 1984). S těmi by pak měly dosáhnout co nejlepších potomků a tedy co nejvyšší fitness, ať už díky dobrým genům („good genes model"), které potomci zdědí (Zahavi 1975), nebo díky kvalitní rodičovské péči („good parent model"), poskytované samcem (Hoelzer 1989).

Vrabec domácí *Passer domesticus*, L. je vhodným modelovým druhem pro studium mnoha evolučních teorií týkajících se rodičovské péče a pohlavního výběru. Je celosvětově rozšířený a i přes pokles evropských populací v posledních desetiletích (PECBMS 2010) stále hojný. Žije pospolitě, místy ještě v původních stromových hnízdech, ale i ve volnějších koloniích na lidských stavbách v centrech měst nebo na hospodářských budovách na venkově (Hudec et al. 1983). Pro výzkumníky je výhodou, že hnízdí v nabízených budkách několikrát do roka a o potomstvo se starají oba rodiče, na první pohled dobře odlišitelní díky dimorfnímu zbarvení. Samci navíc mají na hrudi melaninovou skvrnu, tvořenou černými pery s postupně se obrušujícími bílými okraji (Møller 1987; Veiga 1993). Velikost této skvrny slouží jako znak postavení v sociální hierarchii a samci s větší skvrnou jsou dominantní nad samci

s menší skvrnou (Møller 1987; McGraw et al. 2002). Díky nápadnému ornamentu je vrabec také objektem studia signalizačních systémů.

Svůj výzkum jsem začínala experimentálním studiem antipredačního chování u městských populací vrabců domácích. Protože mé výsledky naznačovaly, že intenzita obrany hnízda souvisí s velikostí melaninového ornamentu samců, rozhodla jsem se tomuto druhu věnovat i nadále a zaměřit se na další aspekty rodičovské péče, ve kterých by ornament mohl mít signalizační funkci. Další výzkum potom probíhal na hospodářském statku ve venkovském prostředí jižních Čech, kde jsme společně s kolegy založili a po dobu pěti let sledovali budkovou populaci vrabců domácích. V prezentované disertační práci jsem se věnovala třem okruhům souvisejícím s rodičovským chováním – obraně hnízda, krmení mláďat a signalizaci kvality v pohlavním výběru. Některé výsledky společného výzkumu jsou teprve připravovány k publikaci, ale protože se domnívám, že bez nich není přehled našich poznatků o rodičovské péči u studované populace celistvý, stručně je v úvodu uvádím a cituji z diplomových prací studentek (Martínková 2006; Lusková 2010).

Studované aspekty rodičovské péče

1. Antipredační strategie při obraně hnízda

Hnízdní predace je u ptáků nejčastější příčinou hnízdního neúspěchu (Ricklefs 1969). Obrana hnízda je proto důležitou složkou rodičovské péče, neboť může významně snížit ztráty mláďat způsobené predátory (Andersson et al. 1980; Knight & Temple 1986; Hogstad 2005). Toto chování je však nákladné na čas a energii (Biermann & Robertson 1983) a je spojeno s rizikem zranění nebo dokonce smrti bránícího jedince (Poiani & Yorke 1989). Pro rodiče je proto zásadní vyvážit náklady spojené s obranou hnízda a výhody z ní plynoucí tak, aby dosáhli co nejvyššího reprodukčního úspěchu (Montgomerie & Weatherhead 1988). Podle „hypotézy o hodnotě mláďat" (value of offspring hypothesis) by měli rodiče přizpůsobit svoji investici do hnízdní obrany kvalitě aktuální snůšky, kterou charakterizuje stáří a kondice mláďat, protože starší mláďata a ta v lepší kondici mají vyšší pravděpodobnost přežití, a jsou tak pro rodiče hodnotnější (Andersson et al. 1980; Clutton-Brock 1991). Intenzita obrany by měla vzrůstat také s počtem mláďat, neboť s ním roste i zisk plynoucí z odehnání predátora (Wiklund 1990). Význam pro odhad hodnoty mláďat může mít i fáze hnízdní sezóny, protože snůšky nakladené dříve jsou zpravidla úspěšnější než pozdější hnízdní pokusy (Andersson et al. 1980; Clutton-Brock 1991). Výši rodičovské investice mohou dále ovlivnit také vlastnosti samotných rodičů, protože ptáci v lepší kondici mohou do obrany investovat více energie (Hogstad 2005) a starší jedinci jsou zase zkušenější (Montgomerie & Weatherhead 1988). Svou roli

hraje i pohlaví bránících jedinců, neboť jejich rozhodnutí mohou ovlivňovat jiná východiska – odlišná velikost, možnost náhradního hnízdění, jistota paternity apod. (Montgomerie & Weatherhead 1988). Ačkoliv byla rodičovská péče u vrabce domácího v poslední době intenzivně studována (souhrny např. Anderson 2006; Nakagawa 2007a), antipredační chování bylo spíše opomíjeno. Dosud publikované studie vztahovaly intenzitu hnízdní obrany ke kvalitě snůšky (Reyer et al. 1998; Kopisch et al. 2005), avšak nenašly průkazný vztah. Cílem našeho výzkumu proto bylo vysvětlit variabilitu v intenzitě obrany pomocí parametrů rodičů (pohlaví, kondice, velikost ornamentu samce, intenzita obrany partnera) či mláďat (datum snesení prvního vejce, velikost snůšky, stáří a kondice), které ovlivňují reprodukční úspěšnost a mohly by tak rozhodovat o investicích do obrany hnízda (**Příspěvek I**). Pro vyvolání antipredačního chování jsme použili vycpaninu straky obecné *Pica pica*, kterou jsme umístili přímo na budku každého sledovaného páru. Na tohoto predátora vajec a mláďat zareagovali všichni sledovaní ptáci, vždy ale pouze pár hnízdící v „ohrožené" budce. Intenzitu obrany jsme hodnotili pomocí tzv. risk indexu (podle Windt & Curio 1986; viz také Brunton 1990), který roste s délkou trvání reakce a s její vzrůstající riskantností (od přiblížení bez vokalizace, přes přiblížení s vokalizací až k náletům), zatímco klesá se vzdáleností od predátora. Pro vysvětlení intenzity reakce samic jsme však mezi sledovanými proměnnými nenalezli žádnou, která by měla průkazný vliv. Samci měli tendenci bránit více snůšky, jejichž kladení bylo načasováno dříve v hnízdní sezóně. „Hypotézu hodnoty mláďat" jsme tak mohli podpořit pouze částečně. Výsledky dále souhlasí s hypotézou, že dřívější snůšky mají vyšší pravděpodobnost přežití, a mají tak pro rodiče větší hodnotu než snůšky nakladené později v hnízdní sezóně (Curio et al. 1984). Naopak tento výsledek odporuje „hypotéze potenciálního znovuzahnízdění" (renesting potential hypothesis), podle které by měli rodiče intenzitu péče o mláďata stupňovat v průběhu hnízdní sezóny, protože jejich šance na další zahnízdění klesají (Montgomerie & Weatherhead 1988). Protože ani žádná z předchozích dvou studií hnízdní obrany vrabce domácího (Reyer et al. 1998; Kopisch et al. 2005) nepotvrdila její vztah k hodnotě snůšky, můžeme spekulovat, že rodiče hodnotu snůšky stanovují podle jiných, dosud nezohledněných, aspektů.

Zajímalo nás také, zda rodiče vzájemně přizpůsobují intenzitu obrany hnízda antipredačnímu chování nebo vlastnostem partnera (kondici, velikosti ornamentu samců). Takovéto chování však nebylo potvrzeno a tedy ani „hypotéza odlišných investic" (differential allocation hypothesis, DAH), která předpokládá, že samice spárovaná s kvalitním samcem bude investovat do reprodukčního pokusu více (Burley 1986). Tuto hypotézu u vrabce domácího nepotvrdili ani Mazuc et al. (2003), kteří ji testovali v kontextu frekvencí krmení. Intenzita obrany samců však stoupala s rostoucí velikostí jejich ornamentu – více v podkapitole 3. Signalizace kvality rodiče na str. 8.

Významným činitelem, který ovlivňuje antipredační chování, je také druh predátora (např. Kruuk 1964; Andersson et al*.* 1980). Zaměřili jsme se proto dále na otázku, zda je strategie obrany hnízda

3

u vrabce domácího stabilní, nebo zda se proměňuje s mírou ohrožení, které různí predátoři pro hnízdící ptáky představují (**Příspěvek II**). Atrapy jsme však tentokrát umisťovali 5 m od hnízdiště, nikoliv přímo k hnízdu. V těchto experimentech reagovalo na predátora celé hejno společně zvláštním typem antipredačního chování zvaným „mobing", které bylo u tohoto druhu již dříve popsáno (Wilson 1978; Cramp & Perrins 1994). Při něm se ptáci jednoho i různých druhů shlukují kolem predátora a svou specifickou mezidruhově srozumitelnou vokalizací, nálety a útoky jej obtěžují (Curio 1978). V minulosti bylo vysloveno několik hypotéz o adaptivní hodnotě mobingu (shrnutí např. Curio 1978; Ostreiher 2003), které jej vysvětlují buď jako altruistické chování (např. Curio 1978; Pavey & Smyth 1998), součást rodičovské péče (např. Curio 1978) nebo jako sobecké chování (např. Slagsvold 1984). První skupina hypotéz jako „varování ostatních" (Curio 1978; Frankenberg 1981), „zmatení predátora" (Curio 1978; Ficken 1989) nebo „odehnání predátora" (Curio 1978; Pettifor 1990; Flasskamp 1994; Pavey & Smyth 1998) předpokládá, že hlavním příjemcem výhod z mobingu jsou ostatní členové kolonie nebo mobující skupiny. Hypotézy o mobingu jako součásti rodičovské péče, přepokládají, že z mobingu mají prospěch především mláďata, a zahrnují hypotézy „utišení mladých" (Curio 1975), učení mláďat rozpoznat predátora a chovat se k němu (kulturní přenos; Curio 1978; Curio et al. 1985) a „odlákání predátora" od hnízda (Curio 1978; Tamura 1989). Třetí skupina hypotéz uvažuje o mobingu jako o sobeckém chování, ze kterého těží především sám mobující jedinec, a patří k nim hypotéza signalizace kvality nebo postavení v hierarchii (Slagsvold 1984; Francis et al. 1989; Zahavi 1995) či hypotéza „komunikace s predátorem", podle níž mobující jedinec svým chováním přesvědčuje predátora, že již byl kořistí zpozorován a nemůže tedy využít momentu překvapení (Zahavi & Zahavi 1997). Výše uvedené hypotézy se vzájemně nevylučují a je pravděpodobné, že mobing má více účelů (Ostreiher 2003).

Společná reakce několika jedinců z hnízdní kolonie (**Příspěvek II**) se výrazně odlišuje od chování vrabců v dřívějších experimentech, kdy byla atrapa umístěna přímo u hnízda a kdy reagoval pouze rodičovský pár (Reyer et al. 1998; **Příspěvek I**). Tento rozdíl jasně potvrzuje význam vzdálenosti predátora od hnízda – ten byl již sice dříve popsán, ale její vliv byl zpravidla opačný (Zimmermann and Curio 1988; Kleindorfer et al. 2003). Ptáci zvyšovali intenzitu obrany se snižující se vzdáleností predátora od hnízda. Je-li predátor daleko, pravděpodobně ještě nezjistil přesnou polohu hnízda, a je tedy potřeba jej neprozradit. Pokud je ale predátor tak blízko, že o hnízdě ví, má naopak smysl se pokusit jej od hnízda odehnat. V případě našich experimentů prezentuje umístění vycpaniny predátora přímo na budku zřejmě situaci, kdy už si predátor vybral svou kořist a motivaci jej odehnat mají tedy především rodiče z dané budky (**Příspěvek I**). Je-li však predátor vzdálen 5 m od všech hnízd v kolonii, mají všechna stejnou pravděpodobnost, že budou predována, a všichni hnízdící ptáci jsou tedy stejně motivováni k obraně (**Příspěvek II**). Domníváme se proto, že v tomto experimentu se jednalo spíše o reakci hejna sobeckých párů, bránících své vlastní potomky, než o hejno altruistů

4

riskujících predaci pro dobro celé kolonie. K podobnému závěru došel již Horn (1968) u koloniálních vlhovců pospolitých *Euphagus cyanocephalus*, který uváděl jako důvod skupinového mobingu fakt, že každý pár brání určitý okruh kolem vlastního hnízda a tyto okruhy kolem jednotlivých hnízd v kolonii se překrývají.

Testovali jsme dvě, vzájemně se nevylučující, hypotézy o mobingu koloniálně hnízdících vrabců domácích. Pokud je mobing především součástí rodičovské péče, předpokládali jsme, že jeho hlavním účelem je odehnat predátora z blízkosti hnízda (Curio 1978). Pak by vrabci měli intenzivněji reagovat na hnízdního predátora než na predátora dospělých. Je-li však mobing spíše sobeckým chováním, používají jej vrabci k předvádění svého postavení v sociální hierarchii hejna (Slagsvold 1984; Moholt & Trost 1989; Dugatkin & Godin 1992). Platí-li "hypotéza signalizace postavení", předpokládali jsme, že by samci měli predátora odhánět intenzivněji než samice, bez ohledu na fázi hnízdní sezóny či druh predátora (více na str. 8 v podkapitole 3. Signalizace kvality rodiče).

Vrabci rozlišovali jednotlivé predátory. Jejich počet i intenzita mobingu (měřená opět „risk indexem") se snižovala se stoupajícím rizikem zranění predátorem. Nejvyšší riziko rozpoznávali vrabci v krahujci obecném *Accipiter nisus*, který je významným predátorem dospělců (Gotmark & Post 1996), i když jsme jej pozorovali i při vytahování mladých z hnízdní dutiny (Klvaňová & Hořáková, nepubl.). Střední intenzitu mobingu vyvíjeli vrabci v reakci na sýčka obecného *Athene noctua*, který preduje mláďata i dospělé (Angelici et al. 1997), avšak díky své převážně noční aktivitě se ve dne hůře orientuje a je mobingem stresován (Flasskamp 1994), takže je méně pravděpodobné, že mobujícího jedince napadne. Nejintenzivnější reakce jsme zaznamenali v experimentech se strakou obecnou, predátorem vajec a mláďat (Tatner 1983). Naše výsledky potvrzují hypotézu, že ptáci přizpůsobují svoji strategii obrany potenciální míře ohrožení, kterou různí predátoři představují (Pettifor 1990; Shedd 1982). Méně riskantní reakce na hnízdního predátora než na predátora dospělých byla pozorována také v koloniích racků *Larus* spp. a rybáků *Sterna* spp. (Clode et al. 2000) nebo vlhovců červenokřídlých *Agelaius phoeniceus* (Knight & Temple 1988) a odpovídá hypotéze, že mobing je součást rodičovské péče, protože příjemcem výhod z něj plynoucích jsou především mláďata. Schopnost vrabců rozlišovat mezi dvěma predátory dospělých byla pozorována i u jiných druhů, např. sýkor koňader *Parus major* (Curio et al. 1983). Důvodem odlišně vnímané úrovně nebezpečí, plynoucího ze střetu s oběma predátory, je pravděpodobně jejich rozdílná lovecká strategie (Bildstein 1982; Pettifor 1990). Sýček obecný býval jedním z hlavních vrabčích predátorů (Cordero 1991), a i když v posledních letech z Prahy téměř vymizel (Fuchs et al. 2002), je nadále vrabci vnímán jako nebezpečný. I přes pravděpodobnou dezorientaci a stres (Flasskamp 1994) je zřejmě schopen na vrabce během mobingu zaútočit, stejně jako jiné druhy sov (Motta-Junior 2007). Krahujec tak coby obratný lovec s denní aktivitou může bránícího vrabce ohrozit nejvíce.

Reakce samců byla intenzivnější než v případě samic (**Příspěvek I, II**). Vysvětlení zvýšené obrany samcem můžeme nalézt v rozdělení péče mezi partnery, kdy jednotlivá pohlaví přispívají nerovnoměrně k různým složkám péče. Výsledkem je pak stejný podíl obou rodičů na celkové péči, jak předpokládá teorie u druhů s biparentální péčí (Winkler 1985). U vrabců tráví samice více času inkubací (Hoi et al. 2003; Bartlett 2005; Martínková 2006) a častěji krmí (Voltura et al. 2002; Hoi et al. 2003; Martínková 2006; Lusková 2010), zatímco samci více brání hnízdo. Dále může být mobing příležitostí pro samce k signalizaci vlastní kvality jako rodiče (více v podkapitole 3. Signalizace kvality rodiče na str. 8). Na základě našich výsledků jsme proto dospěli k závěru, že mobing je především složkou rodičovské péče, avšak je pravděpodobně i příležitostí k signalizaci kvality.

2. Krmení a potrava mláďat a jejich vliv na reprodukční úspěšnost

Kvalita potomků, a tak i reprodukční úspěch jejich rodičů, mohou být ovlivněny potravou, kterou jsou mláďata krmena během vývoje na hnízdě (např. Metcalfe & Monaghan 2001). K vyjádření investice rodičů do krmení, coby složky rodičovské péče, bývají vzhledem k časové a energetické náročnosti používány frekvence krmení (Whittingham & Robertson 1993; Sandel et al. 1996). Spolu s nimi je často hodnocena i doba strávená zahříváním mláďat mezi krmeními. V námi studované populaci krmila samice mláďata častěji a věnovala také více času jejich zahřívání než samec (Martínková 2006; Lusková 2010). U ptáků s biparentální péčí se však očekává, že míra investice bude přibližně stejná (Winkler 1985). Rozdíl mezi pohlavími můžeme vysvětlit rozdílným vkladem do různých složek péče, jak bylo uvedeno výše. Do problematiky však vstupují i další faktory. Svou roli může hrát fakt, že samice investuje více energie do produkce vajec než samec do produkce spermií, a tudíž i její investice do rodičovského chování je vyšší (Trivers 1972). Samec také může určitý čas věnovat zvyšování svého reprodukčního úspěchu vyhledáváním mimopárových kopulací s jinými samicemi. V naší populaci jsme zaznamenali několik samců hnízdících se dvěma samicemi zároveň.

Na průměrnou hmotnost mláďat na hnízdě měla vliv pouze frekvence krmení samcem, přestože krmil méně často (Martínková 2006). Tento výsledek potvrzuje důležitost příspěvku samce k rodičovské péči a potažmo i volby partnera pro budoucí reprodukční úspěch samice. Zároveň tento výsledek naznačuje, že kvalitu ani kvantitu rodiči donášené potravy nelze hodnotit pouze frekvencemi krmení. U vrabců domácích bylo experimentálně prokázáno, že pro růst mláďat není podstatná pravidelnost krmení, pokud dostanou určitou přiměřenou dávku potravy denně (Grodzinski et al. 2009). Protože vrabec domácí patří ke druhům, které přinášejí více kusů kořisti najednou, tzv. „multiple prey-loaders" (Orians & Pearson 1979), mohou se jedinci lišit množstvím, velikostí i druhem kořisti, kterou při jedné návštěvě hnízda dopraví mláďatům. Pro kvalitu mláďat může mít význam nejen množství potravy, ale i zastoupení různých složek (Wright et al. 1998), či přítomnost určitých živin

v potravě (Donald 2001; Arnold et al. 2007; Rossmanith et al. 2007). Studie populací vrabců ve Velké Británii (Vincent 2005; Peach et al. 2008) nebo Německu (Mitschke et al. 1999) ukázaly, že kondici mláďat může snižovat nedostatečné množství živočišné potravy, které rodiče kompenzují zvýšenými dávkami rostlinné potravy. V důsledku tohoto zjištění byla snížená reprodukční úspěšnost způsobená hladověním mláďat navržena jako jeden z možných faktorů způsobujících populační poklesy vrabců domácích (Vincent 2005; Peach et al. 2008), ke kterým dochází v posledních desetiletích na území Evropy (PECBMS 2010).

Je však známo, že složení potravy se liší geograficky (Anderson 1984). V České republice navíc nebyly dosud publikovány údaje o potravě mláďat vrabců domácích, na rozdíl od rozboru potravy dospělých (Ašmera 1962), který byl proveden několik desetiletí před nástupem populačního poklesu. Rozhodli jsme se proto dále provést analýzu výkalů (Moreby & Stoate 2000) za účelem zhodnocení potravy a jejího vlivu na kvalitu mláďat v současných venkovských podmínkách střední Evropy. Na základě této analýzy jsme zjistili, že mláďata jsou krmena převážně brouky a dvoukřídlým hmyzem (**Přípěvek III**). To je v souladu s výsledky z jiných oblastí, avšak v potravě naší populace dominovaly druhy typické pro prostředí hospodářského statku, jako jsou koprofágní vrubounovití brouci nebo mouchy a tiplice, zatímco jiní autoři uvádějí většinou jako nejčastější zástupce brouků čeledi Curculionidae a Carabidae (Vincent 2005; Anderson 2006). Mezi nejčastějšími druhy kořisti dále bývají mšice, pavouci a mravenci (Encke 1965; Mitschke et al. 1999; Vincent 2005). V naší analýze jsme z těchto skupin našli pouze pavouky, a to ve čtvrtině vzorků. K tomuto výsledku pravděpodobně přispěla i jejich dobrá stravitelnost. Špatná zachytitelnost bezobratlých s měkkým tělem, a tudíž podhodnocení výskytu této kořisti v potravě, je pravděpodobně největší slabinou zvolené metody (Moreby & Stoate 2000). Avšak vzhledem k tomu, že i studie, ve kterých autoři tyto „měkké" členovce v potravě nalezli (např. Vincent et al. 2005), používaly stejnou metodu analýzy výkalů jako my, a že se tito členovci na naší lokalitě vyskytovali, je pravděpodobné, že zde vrabci tuto kořist zřejmě nepreferují.

Odběr vzorků výkalů jsme prováděli u dvou věkových kategorií – mladších mláďat ve stáří 4-6 dní a u starších mláďat ve stáří 9-11 dní. Starší mláďata byla krmena větším množstvím potravy, což bylo způsobeno nárůstem rostlinné složky, zatímco velikost živočišné složky byla v obou věkových kategoriích srovnatelná. Zvyšující se potravní nároky mláďat tedy rodiče kompenzovali dobře dostupnou rostlinnou potravou, především semeny kulturních plodin a plevelů. Nabízejí se dvě vysvětlení – je možné, že existuje horní limit množství bezobratlých, které jsou rodiče schopni ulovit. Alternativně je pozorovaný fakt výsledkem měnících se preferencí mláďat ve prospěch rostlinné potravy. Potravní preference mladých vrabců se mění v průběhu jejich vývoje a po vylétnutí z hnízda upřednostňují rostlinnou potravu (Mueller 1986).

Hmotnost vzorku, jeho živočišné složky a okrajově také množství brouků v potravě starších mláďat mělo pozitivní vliv na kondici mláďat. Význam bezobratlých v potravě pro kondici mláďat vyzdvihl také Anderson (1977). Jelikož mláďata s vyšší kondicí mají větší pravděpodobnost, že budou vyvedena (Cleasby et al. 2010), ovlivňuje množství živočišné složky v potravě mláďat také reprodukční úspěšnost jejich rodičů. Lepší kondice mláďat, krmených větším podílem brouků, byla zaznamenána i ve Velké Británii, kde byl zároveň prokázán opačný vliv mravenců v potravě (Vincent 2005). Protože na námi studované lokalitě se mravenci také vyskytovali, aniž by byli zaznamenáni v potravě, je možné, že jimi vrabci krmí svá mláďata pouze v místech s chudou potravní nabídkou. U jiné britské populace byla nízká kondice mláďat naopak dávána do souvislosti s omezeným výskytem mšic v okolí hnízdišť (Peach et al. 2008). Fakt, že na naší lokalitě dosahovala mláďata vysoké kondice navzdory absenci mšic v potravě, tak ukazuje, že jsou vrabci schopni tuto kořist nahradit jinou živočišnou potravou.

3. Signalizace kvality rodiče

U mnoha druhů s biparentální péčí se během evoluce vyvinul signalizační systém, v němž určité znaky, korelované s kondicí či kvalitou rodičovské péče, mohou využívat zástupci vybírajícího si pohlaví k usnadnění volby kvalitních partnerů v pohlavním výběru (Andersson 1994). U ptáků jsou těmito signály většinou znaky v opeření, jako jsou intenzita zbarvení či velikost ornamentů a perních ozdob (např. Hill 2002; Jawor & Breitwisch 2003).

Samci vrabce domácího mají na hrudi černou skvrnu variabilní velikosti tvořenou melaninem. Na otázku, zda je potenciálním signálem a co signalizuje, se pokoušelo odpovědět mnoho studií, jejichž výsledky shrnuli v recentní meta-analýze Nakagawa et al. (2007a). Podle této analýzy je velikost ornamentu signálem postavení v sociální hierarchii, stáří a okrajově i kondice, nesignalizuje však zřejmě míru rodičovské péče, paternity nebo reprodukčního úspěchu. Jako rodičovskou péči uvažovali autoři pouze čas strávený inkubací a frekvenci krmení, nezahrnuli však obranu hnízda z důvodu nedostatku studií na toto téma. Vztahem ornamentu a antipredačního chování u vrabce domácího se zabývali pouze Reyer et al. (1998), kteří zjistili, že frekvence, s jakou se samci přibližovali k atrapě predátora, rostla s velikostí jejich ornamentu a naopak u jejich partnerek úměrně klesala. Autoři předpokládali, že vyšší investice do obrany by mohla souviset s vyšší mírou jistoty paternity samců s větším ornamentem. Vztah paternity a velikosti ornamentu však nebyl později u jiných populací vrabců potvrzen (Whitekiller et al. 2000; Veiga & Boto 2000; Stewart et al. 2006). Navíc ani práce studující jiné druhy pěvců, ve kterých byli známi genetičtí rodiče mláďat, neprokázaly vliv paternity na obranu hnízda samcem (Lubjuhn et al. 1993; Griggio et al. 2003; Rytkönen et al. 2007).

V naší studii (**Příspěvek I**) jsme do analýzy obranného chování zahrnuli jako možné faktory jak parametry snůšky, tak také parametry obou rodičů. Intenzita reakce na predátora rostla s velikostí ornamentu samce, avšak samice svou reakci nijak nepřizpůsobovala chování svého partnera. Podobně Quesada & Senar (2007) popsali pozitivní korelaci intenzity obrany hnízda u samců sýkory koňadry *Parus major* a velikosti jejich melaninového ornamentu, černého pruhu na hrudi. Vysvětlení vyšší intenzity reakce vrabců s větším ornamentem může spočívat v jejich lepší fyzické kondici (Veiga & Puerta 1996), která jim umožňuje vydat více energie a lépe předcházet možnému zranění ze strany predátora. Hogstad (2005) popsal agresivnější chování k predátorům u drozdů kvíčal *Turdus pilaris* v lepší kondici. Korelace mezi velikostí ornamentu a kondicí je však u vrabce domácího spíše slabá (Nakagawa et al. 2007a) a u sýkor koňader nekorelují tyto dvě vlastnosti samců vůbec (Senar et al. 2003). U námi studované populace navíc nebyl ani vliv kondice jedince na intenzitu obrany hnízda prokázán. Protože velikost ornamentu se zvětšuje se stářím jedince (Nakagawa et al. 2007a, b), mohl by námi nalezený vztah pouze znamenat, že starší ptáci reagují na predátora silněji díky své předchozí zkušenosti (Smith et al. 1984). Na naší studijní lokalitě je však straka obecná běžně přítomná, a mladí vrabci tak mají příležitost naučit se ji poznávat jako hnízdního predátora během hnízdní sezóny od svých rodičů (Curio et al. 1978). Ačkoliv jsme neznali přesné stáří dospělých jedinců, většina ostatních prací neprokázala u pěvců stoupající trend intenzity obrany s věkem (např. Winkler 1992; Hatch 1997). Samci s většími melaninovými ornamenty mají vyšší hladinu testosteronu v plazmě, která způsobuje vyšší agresivitu, která se uplatňuje v antagonistických interakcích a pozitivně tak ovlivňuje postavení v sociální hierarchii (Jawor & Breitwisch 2003; Senar 2006; Ducrest et al. 2008; Buchanan et al. 2010). Hladina testosteronu je ovlivňována pleiotropním účinkem genů řídících melanogenezi (Ducrest et al. 2008), které dále ovlivňují vyšší sexuální aktivitu, lepší snášenlivost stresu, silnější imunitní odpověď a vyšší rychlost metabolismu (shrnutí Ducrest et al. 2008). Všechny tyto aspekty mohou přispívat k vyšší intenzitě hnízdní obrany. Zatímco ostatní samci využívají ornament jako signál usnadňující rozhodnutí, zda se účastnit antagonistických interakcí, pro samice by mohla být užitečná informace o schopnosti samce chovat se agresivně vůči predátorům. Protože obrana hnízda může významně ovlivnit reprodukční úspěch páru (Knight & Temple 1986), domníváme se, že velikost ornamentu by mohla být využívána samicemi jako hodnotný signál investice do této složky rodičovské péče, zvláště v místech s vysokou mírou predace, kde může být výhodnější spárovat se se samcem, který více brání hnízdo, než s tím, který více krmí mláďata. V našich experimentech samice neinvestovala do obrany hnízda více, byla-li spárována se samcem s větším ornamentem, jak předpokládá hypotéza odlišných investic (Burley 1986), ani méně, jak popsali Reyer et al. (1998). Výhoda těchto samic tedy spočívala v nadprůměrné investici jejich partnerů do obrany hnízda ve smyslu „good parent model" (Hoelzer 1989). Ačkoliv jsme nezaznamenali dostatek predovaných hnízd samců se změřenou velikostí ornamentu, abychom mohli

analyzovat, zda má vliv na míru hnízdní predace, studie jiných pěvců ukázaly, že úspěšně vyvedená mláďata byla v hnízdě bráněna s větší intenzitou než ta, která podlehla predaci (Knight & Temple 1988, Weatherhead 1990).

Ani na naší lokalitě nebyla potvrzena korelace velikosti ornamentu samců a jejich frekvence krmení či doby, kterou trávili inkubací, ani jejich reprodukční úspěšnosti (Martínková 2006). Domníváme se, že jednotlivé složky rodičovské péče mohou být ovlivňovány opačným směrem. Tato „trade-off" by mohla být způsobena hladinou testosteronu v plazmě, který pozitivně ovlivňuje míru agresivity, využitelnou vnitrodruhově při kompetici o hnízdní možnosti (Veiga 1993; Gonzalez et al. 2002) nebo mezidruhově při obraně hnízda, avšak potlačuje jiné složky rodičovské péče jako zahřívání a krmení mláďat (Mazuc et al. 2003).

Vztah velikosti ornamentu a intenzity obrany jsme prověřili v dalším příspěvku (**Příspěvek II**), ve kterém jsme chtěli zjistit, zda se strategie obrany hnízda mění v závislosti na druhu predátora. Samčí intenzita obrany hnízda průkazně stoupala s velikostí ornamentu pouze v experimentech se strakou a sýčkem, zatímco na krahujce reagovali všichni vrabci stejně opatrně bez ohledu na velikost jejich ornamentu. Dominantní samci tak bránili hnízdo s vyšší intenzitou jak proti hnízdnímu predátorovi (straka), tak proti predátoru dospělých (sýček). Bylo-li však riziko napadení predátorem pro bránící jedince příliš vysoké (krahujec), rozdíl mezi samci s malým a velkým ornamentem vymizel. Riskantnější reakce na hnízdního predátora než na predátora dospělých popsali i Knight & Temple (1988) u vlhovců červenokřídlých, u nichž měli nejagresivnější samci také nejlepší úspěch v pohlavním výběru. V mé studii však může být důvodem absence vlivu velikosti ornamentu na intenzitu reakce na atrapu krahujce také poměrně malý vzorek reagujících samců, způsobený tím, že na tohoto predátora často reagovali pouze pasivním mobingem ve skrytu, kde nebylo možné zaznamenat velikost jejich ornamentu.

Lotem et al. (1998) navrhli, že i chování, které samo o sobě nemá původně funkci signálu, může obsahovat signalizační složku. Předpokládáme, že mobing je vhodnou příležitostí pro signalizaci vlastní kvality, avšak nemůžeme s jistotou rozlišit, zda samci signalizovali spíše vlastní dominantní postavení v hierarchii ostatním samcům v hejně nebo svou rodičovskou kvalitu coby schopného obránce hnízda současným i potenciálním partnerkám, protože mobingu se účastnili všichni členové hejna a příjemci signálu mohli tedy být jak samci, tak samice. Domněnka, že u koloniálních druhů mohou členové hejna demonstrovat svou kvalitu či postavení prostřednictvím intenzity mobingu byla již dříve publikována (Maklakov 2002). Vysvětlením by mohla být např. snaha dosáhnout mimopárové kopulace (Slagsvold 1984), či zajistit, že současná partnerka se samcem zahnízdí i v dalším hnízdění. Obě možnosti jsou u vrabce domácího možné, neboť hnízdí 2 – 5 krát do roka (Hudec et al. 1983) a cca 10 - 28 % mláďat pochází z mimopárových fertilizací (Wetton & Parkin 1991; Cordero et al. 1999; Václav & Hoi 2002).

Závěr

Naše výsledky ukazují, že na rodičovskou péči je třeba pohlížet jako na složitý komplex různých typů chování, které mohou být protichůdně ovlivňovány týmiž faktory. Takový vliv mají např. hladiny hormonů, jako je tomu v případě testosteronu, který omezuje krmení mláďat a inkubaci a naopak posiluje agresivitu při obraně hnízda. Hladinou testosteronu je ovlivněna i velikost melaninových ornamentů, u samců vrabce domácího se jedná o skvrnu na hrudi. Při hledání signalizační funkce tohoto znaku je proto nutné rozlišovat mezi jednotlivými složkami rodičovské péče.

Dále se projevila důležitost metodického přístupu ke studiu rodičovských investic. V případě antipredačního chování má význam především typ predátora a jeho vzdálenost od hnízda. Častá nejednotnost v metodice totiž omezuje srovnatelnost jednotlivých studií. Výsledky experimentů s různými druhy predátorů nám umožnily rozvinout hypotézu signalizační funkce ornamentu a mobingu o poznatek, že výhodnost tohoto chování pravděpodobně závisí na riziku plynoucím z konkrétní situace a daném specializací predátora.

Přestože jsme přímo nestudovali příčinu poklesu populací vrabců domácích, můžeme na základě našich výsledků tvrdit, že případný úbytek bezobratlých v prostředí může způsobovat nižší reprodukční úspěšnost, a tak přinejmenším oslabit produktivitu populace. K odhalení příčin úbytku by pravděpodobně pomohly i srovnávací regionální studie, neboť trendy početnosti vrabce domácího v Evropě se různí.

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Klvaňová A. & Exnerová A. (*submitted*). Mobbing strategy during the breeding season in colonial house sparrow *Passer domesticus* varies with predator type.

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

Za autorský tým

Doc. Mgr. Alice Exnerová, PhD.

Příspěvek I

Nest defence intensity in House Sparrows *Passer domesticus*

in relation to parental quality and brood value.

1   Nest defence intensity in House Sparrows *Passer domesticus* in relation to parental quality

2   and brood value

3

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7

8   Abstract

9   We investigated whether brood value (laying date, brood size, nestling age and condition) and

10   parental quality (condition, male badge size) affect experimentally provoked nest defence in

11   House Sparrows in the Czech Republic. We included the badge size (a melanin-based throat

12   feather patch) because it serves as a signal of social status, age and condition. We presented a

13   mounted Black-billed Magpie to 19 pairs of sparrows. To assess the defence intensity we used

14   the „risk index" increasing with time spent reacting and riskiness of the reaction (number of

15   approaches and attacks), while declining with increasing distance from the predator. Females

16   did not adjust their nest defence to the brood value and males did so only partially, tending to

17   defend the early broods more intensely, which marginally supports the "value of offspring

18   hypothesis". The birds did not adjust their nest defence to quality or defence intensity of their

19   partners, thus the "differential allocation hypothesis" was not supported. Male nest defence

20   was more intense than in females and increased with male badge size. As male contribution to

21   nest defence may affect the breeding success, we hypothesize the badge size could be used as

22   a signal of nest defence intensity used by females.

23

24   Key words: Nest defence, House Sparrow, Badge size, Brood value, Black-billed Magpie

25   Suggested running title: Nest defence in House Sparrow

1 Introduction

2 Parental care is a complex behaviour which enhances the offspring survival, in birds including

3 mainly nest building, incubation of eggs and brooding of nestlings, food provisioning and nest

4 defence (Clutton-Brock 1991). While nest predation is the most common cause of breeding

5 failure in birds (Ricklefs 1969), nest defence is an important component of parental

6 investment, because it can significantly reduce the loss of young taken by predators

7 (Andersson et al. 1980, Knight & Temple 1986, Hogstad 2005). However, this behaviour is

8 associated with several costs for parents including time and energy expenditure (Biermann &

9 Robertson 1983), risk of injury or death (Poiani & Yorke 1989). Therefore it is crucial for the

10 parents to balance costs and benefits in reaction to the predator to maximise their reproductive

11 success (Montgomerie & Weatherhead 1988). According to the "value of offspring

12 hypothesis" (Andersson et al. 1980, Clutton-Brock 1991) parents should adjust their

13 investment in nest defence to current brood quality as age and condition, because older

14 nestlings and those in better condition have higher chances for survival and thus are more

15 valuable for parents. Nest defence intensity should also increase with the brood size as the

16 benefits of deterring the predator will be positively correlated with nestling number (Wiklund

17 1990). Finally, the clutches laid sooner in the breeding season should be defended more than

18 later broods, because the former are usually more successful (Andersson et al. 1980, Clutton-

19 Brock 1991). Parental investment may also be affected by the individual quality of the parent,

20 while birds in better condition may invest more energy in defence (Hogstad 2005) and older

21 individuals may utilize their experience from previous encounters with predators and thus

22 provide more effective defence (Montgomerie & Weatherhead 1988). The intensity of nest

23 defence may also vary according to the sex of the parent resulting from different costs and

24 benefits of males and females due to different size, renesting potential or confidence of

25 genetic parentage (Montgomerie & Weatherhead 1988).

1   In House Sparrow *Passer domesticus*, a sexually dichromatic and socially monogamous

2   species with biparental care, the nest defence behaviour was rarely studied, although in recent

3   decades this species attracted considerable attention as an ideal model for studies of parental

4   investment. Kopisch et al. (2005) investigated individual consistency of parental effort and

5   found no relationships between nestling feeding or brood size and nest defence. In a

6   population studied by Reyer et al. (1998) age and number of nestlings also had no effect on

7   nest defence. Their study took into acount the melanin-based throat patch of feathers (so

8   called badge) displayed by males and found that frequency of risky approaches to the predator

9   increased with badge size in males and decreased proportionally in their females. Thus

10   females benefited from the higher investment of larger-badged males, because they could

11   reduce their own effort. Therefore the authors discussed the possible function of badge as a

12   signal of parental investment. They supposed that more intense reaction of larger-badged

13   males was due to the fact that their certainty of paternity was higher than that of smaller-

14   badged males. However, the relationship between the badge size and the certainty of paternity

15   has not been supported by subsequent studies on different populations (Whitekiller et al.

16   2000, Veiga & Boto 2000, Stewart et al. 2006).

17   In many species with biparental care a signalling system has evolved, where certain male

18   traits correlated with condition or parental care may be used by females to choose high quality

19   partners in sexual selection (Andersson 1994). In birds often the plumage characteristics serve

20   as such traits (e.g. Hill 2002, Jawor & Breitwisch 2003). Many studies have aimed to find

21   correlates of badge size in House Sparrow. The results were reviewed in a meta-analysis by

22   Nakagawa et al. (2007a), who concluded that badge size signals status in social hierarchy, age

23   and possibly reflects body condition, but found little association between the badge size and

24   parental care, certainty of paternity or reproductive success. Therefore Nakagawa et al.

25   (2007a) stated that badge size does not signal parental care. However, they included only

1 studies measuring parental care as time spent incubating and nestling provisioning, while nest

2 defence was not analysed because of the lack of studies on this topic.

3 Possible function of plumage ornaments as signals of nest defence intensity was studied in

4 two other passerine species. In Rock Sparrows *Petronia petronia* males increased their nest

5 defence not according to their own carotenoid-based breast patch size, but according to that of

6 their partners, independently of brood value variables (Griggio et al. 2003). This result does

7 not corroborate the ornament as a signal of male nest defence. However, since patch size in

8 female Rock Sparrows predicts their phenotypic quality (Pilastro et al. 2003), it is in

9 accordance with "differential allocation hypothesis" (Burley 1986). According to this

10 hypothesis individuals can enhance their fitness by increasing their parental investment in

11 offspring sired by a partner of high quality, because such offspring would be more viable

12 (Fisher 1930) or attractive (Møller & Alatalo 1999). Quesada & Senar (2007) investigated the

13 role of melanin- and carotenoid-based coloration in nest defence of Great Tits *Parus major*.

14 Males with larger black breast-stripe defended their nests more vigorously, while the yellow

15 breast coloration had no effect. Taken together, the results of Reyer et al. (1998) and Quesada

16 & Senar (2007) indicate that melanin-based ornaments may signal nest defence intensity. This

17 presumption agrees with the fact that they often correlate with individual´s fighting ability

18 and aggression (Jawor & Breitwisch 2003, Senar 2006, Ducrest et al. 2008). Compared to the

19 widespread function of melanin ornaments in intrasexual communication, their role in female

20 choice is less well supported because it is less clear what benefits females could gain by

21 choosing more melanized males (Griffith & Pryke 2006, Hill 2006). Mating with a healthy

22 partner might be such possible benefit as it was shown, at least in some bird species, that

23 melanin based coloration correlates positively with resistance to stressors, immune response

24 against nonpathogenic antigen (reviewed in Ducrest et al. 2008) and negatively with

25 ectoparasite load (Fitze & Richner 2002).

1   As parental care is a complex behaviour, its components may be influenced in opposite

2   directions. Such a trade-off could be caused by male sex hormones (e.g. testosterone plasma

3   level on which melanocortins have a positive effect) supporting fighting ability (competition

4   for nest sites: Veiga 1993, Gonzalez et al. 2002, nest defence), while supressing other aspects

5   of parental care (nestling brooding and feeding: Mazuc et al. 2003). Given this presumption,

6   the lack of evidence of direct benefits for females choosing males with larger melanin

7   ornaments is not surprising, because the male parental behaviour that was extensively studied

8   (like brooding the nestlings, feeding frequency), is not positively associated with melanin-

9   based coloration on hormonal basis.

10 In the present study we aimed to analyze the variation in the nest defence in House Sparrows,

11 taking into account several features of parents (sex, condition, male badge size, partner´s nest

12 defence behaviour) and offspring (laying date, brood size, nestling age and condition) that

13 may affect the breeding success, and thus influence the intensity of nest defence behaviour.

14

15 Methods

16 Study area and population

17 Our study was conducted in the cow-shed in Veselí nad Lužnicí, Czech Republic (49°11'N,

18 14°41'E), during the breeding seasons 2005 and 2006. In autumn 2004 we erected 50 nest

19 boxes (25 x 15 x 15 cm) and monitored them every other day for signs of nesting activity

20 since April 2005. Once egg laying had begun, we checked the nests to determine the date of

21 hatching. When the nestlings reached the age of 10 days, they were ringed with aluminium

22 rings and marked with unique combination of plastic colour rings. Each nestling was weighed

23 using spring scale to the nearest 0.1 g and morphological measurements were taken (tarsus

24 and wing length). We caught the adults using mist nets and nest-box traps during feeding the

25 nestlings (May-June). The adults were ringed, weighed and measured in the same way as the

1 nestlings. To estimate the condition of the birds we used the scaled mass index (Peig & Green

2 2009) computed separately for the males, females and nestlings (mean condition per brood

3 calculated from averaged nestlings´ measurements). This index is based on mass and tarsus

4 length and recognizes the scaling relationship between different measures of body size. We

5 gathered data on 19 broods of individual pairs. However, we had information on condition

6 only of 16 females and 16 males, because we did not succeed to catch all individuals and

7 some of them escaped during manipulation before taking all the measurements needed.

8 Experimental procedures and behavioural observations

9 Prior to each trial we watched the colony for 15 min to make sure that both parents were

10 present and feeding the nestlings and that no disturbing event had happend. All trials were

11 conducted at an average of 9.21 ± 0.76 (3–14) days of age of the nestlings from the first

12 broods, between 12 and 30 June 2005 (7 nests) and between 12 May and 10 June 2006 (12

13 nests) during morning (6:00–11:00 GMT) or afternoon (15:00–19:00 GMT) when the birds

14 were most active. There was no effect of time of the day on the defence behaviour of the birds

15 (T-test: df = 36, t = 0.158, p = 0.875) measured as „risk index“ (for explanation see below).

16 To induce defence behaviour we used mounted Black-billed Magpie *Pica pica*, a predator of

17 eggs and fledglings, which does not threaten the adult birds. We chose this predator species to

18 test parental investment and eliminate the probability of self-defence. Predator was fixed

19 directly on the roof of each nest box. All trials were recorded for 20 min from the arrival of

20 the first bird (after Reyer et al. 1998) to the vicinity of the nest (< 5 m from the nest box) with

21 a digital video camera JVC from a hiding place that was at least 10 m distant from the nest

22 boxes. To minimize the possible effect of habituation the next trial with neighbouring nest

23 box followed after at least 3 days interval. After exposition of the predator model one or both

24 parents of the nestlings from the nest box arrived and started to perform the reaction. The

25 male was the first one in 5 trials as well as was the female, while in remaining 9 trials both

1 parents arrived together. The reaction was defined as the presence of the bird in the view, less

2 than 5 m from the predator model. The birds moved to and from the model alternately,

3 uttering alarm calls, and sometimes also flew over the model. During a 20 min trial each bird

4 arrived to the vicinity of the model and flew out of the view several times, which means that

5 each bird performed several reactions during one trial. When the parents did not detect the

6 predator together, the second bird arrived on average 93 ± 43 s after the first one. Although

7 there was less than 20 minutes left for the reaction of the second bird, time spent reacting

8 within the trial did not differ between the first and second bird (Wilcoxon matched-pairs test:

9 $N = 10$, $T = 19$, $Z = 0.866$, $p = 0.386$). The most risky reaction of the second birds was

10 performed on average 80 ± 37 after their arrival, which was never later than 10 minutes after

11 the arrival of the first bird. We recorded the following variables of the reaction for each parent

12 observed during the trial:

13 1.   Number of approaches. We distinguished approach to the predator model (< 5 m

14 from the model) with and without alarm calls.

15 2.   Number of attacks. As an attack flight directly over the predator model was

16 considered.

17 3.   Time reacting (s). Time the bird spent in view (< 5 m from the model) performing

18 approach or attack.

19 4.   Distance (m). The mean distance between the bird and the predator model. We

20 estimated the distance from 1 to 5 m (to the nearest 1 m) each 10 s of the bird´s reaction.

21 From these distancies (1-5) we calculated mean distance during performance of each type of

22 behaviour (approach or attack) for each bird.

23 To assess the risk taking of individual mobbing reaction we used the „risk index" (RI)

24 (modified after Windt & Curio 1986; see also Brunton 1990):

25                              $RI = R\,(t_r/d_r),$

1   where R is the rank value of defence behaviour r, t_r is time spent in behaviour r, and d_r is the

2   mean distance from the predator during t_r (calculated from 10 s intervals of t_r). The rank

3   values of defence behaviour were assigned according to its increasing degree of risk: 1.

4   approaches without alarm calls, 2. approaches with alarm calls, and 3. attacks. The risk index

5   assumes that risk increases with time spent reacting (t_r) and rank value of the reaction (R),

6   while it declines with the distance from the predator (d_r). In presented analysis the sum of risk

7   indices of all reactions performed by each idividual during 20 min of a trial was considered.

8   Latency was not analysed for the same reason as in Reyer et al. (1998), because it was

9   influenced rather by the foraging pattern than the nest defence, as the parents noted the

10 predator when returning to the nest with food.

11 Badge measurements

12 Badge size was estimated from detailed digital photographs. Males were photographed in

13 standard conditions laying on their backs when holding the bill perpendicular to the body

14 axis. Badge size increases with time because of the abrasion of white feather tips concealing

15 the badge (Møller 1987). Therefore we measured badge size from May onwards when it

16 should be almost fully developed (Møller & Eritzoe 1992). We measured the area (mm^2) of

17 the "black" and "total" badge in UTHSCSA Image Tool 3.0 program (University of Texas,

18 Houston, TX, USA, http://ddsdx.uthscsa.edu/dig/itdesc.html) (e.g. Quesada & Senar 2007).

19 The black badge is covered by completely black feathers, whereas the total badge involves

20 feathers with black bases and white tips, which gradually wear off (Møller & Erritzoe 1992).

21 The area of the total badge and the area of the black badge were highly correlated (correlation,

22 n = 19, r² = 0.866, p << 0.001) (see also Griffith et al. 1999; Gonzalez et al. 2001). Griffith et

23 al. (1999) found that the measure of the total badge was more repeatable than the black badge.

24 Therefore we used area of the total badge (further on reported as badge size) in statistical

1   analyses. Average total badge area (± SE) of 19 males was 483.84 ± 15.14 mm² (range 350–

2   628 mm²). All the measurements were done by the same person (A.K.).

3

4   Statistical analyses

5   We compared nest defence behaviour (time spent reacting, number of approaches with alarm

6   calls, mean distance from the predator, and risk index values) of males and females within the

7   breeding pairs by Wilcoxon matched-pairs tests. Number of approaches without alarm calls

8   and number of attacks were not compared because these were rather rare. To limit the overall

9   error in the set of tests to 5% we used the Bonferroni correction (α = 0.0125 in individual

10   tests). We analyzed the factors influencing the defence behaviour separetely for males and

11   females. The intensity of nest defence was expressed as risk index value (RI). To find out

12   whether RI values were influenced by brood value and/or the quality and behaviour of the

13   parents and their partners we conducted analyses of covariance (ANCOVAs) with year as

14   categorical factor and laying date, brood size, nestling age, mean nestling condition per brood,

15   parent condition, partner's risk index and badge size (only in case of males) as continuous

16   predictors. The laying dates were expressed as a number of days from 1st April till the layig of

17   the first egg. To control for annual differences in timing, we set the median laying date of the

18   population for each year to zero and calculated the realtive laying date for each brood as the

19   deviation from "time zero" (after Rossmanith et al. 2007). We used forward stepwise variable

20   selection based on Mallows C_p statistics to find a minimal adequate model which best

21   explained the variation in RI values without incorporating unnecessary non-significant

22   variables. Due to missing data about condition of several individuals, we cannot include the

23   partners´condition into full model and its effect on RI values was tested separately using

24   simple regression.

1   All dependent variables were normally distributed, except for the female risk index, which

2   had gamma distribution and was analysed in corresponding GLM with log-link function. All

3   statistical tests were performed using S-PLUS 4.0 software (MathSoft 1997).

4

5   Results

6   Mean laying date (± SE) at the 19 nests was 39.05 (± 4.74) days and average brood size was

7   3.32 (± 0.23) nestlings. Average weight of 10 days old nestlings in the nest was 23.37 g (±

8   0.87) and average tarsus length was 20.3 mm (± 0.3). Average condition of nestlings was not

9   affected by laying date (simple regression: $F = 0.54$, $df = 1, 17$, $p = 0.473$).

10   Males spent longer time reacting than females, which resulted in higher risk index of males,

11   while the mean distance from the predator did not differ between the sexes (Table 1). The

12   number of males´ and females´ approaches with alarm calls did not differ after the application

13   of Bonferroni correction (Table 1).

14   Females´ risk indeces did not relate neither to their condition nor the value of their broods

15   (Table 2). Males´ risk indeces increased significantly with their badge size (Pearson´s r =

16   0.537; Table 2, Fig. 1) and decreased marginally with laying date (Pearson´s $r = -0.395$; Table

17   2).

18   The risk index was not related to the partner´s risk index in either sex (Table 2) and females´

19   risk indeces were not affected by the badge size of their partners (Table 2, Fig. 1). Partner´s

20   condition had no effect on risk index in males (simple regression: $df = 1, 14$, $F = 0.005$, $p =$

21   0.946) nor in females (simple regression: $df = 1, 14$, $F = 1.856$, $p = 0.195$).

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1 Discussion

2 In this study we investigated nest defence behaviour of House Sparrows in respect to parental

3 quality (condition, male badge size) and the current value of their broods. In females neither

4 parameters of brood quality nor their own condition predicted their nest defence intensity.

5 In males the laying date was the only brood value variable which tended to affect their nest

6 defence intensity, but this effect was only marginally significant. The broods laid later in the

7 breeding season tended to be defended less intensely than the sooner broods. Thus the "value

8 of offspring hypothesis" (Andersson et al. 1980, Clutton-Brock 1991) was only partially

9 supported. Our results could further partially support the "relative offspring survival

10 probability hypothesis" (Curio et al. 1984), which predicts that sooner broods have higher

11 probability to survive than later broods and consequently are of greater value for the parents.

12 It is in contrast with "renesting potential hypothesis" (Montgomerie & Weatherhead 1988),

13 according to which the parents should increase their investment with the progress of the

14 breeding season, because their renesting potential decreases. As also both previous studies of

15 House Sparrow nest defence (Reyer et al. 1998, Kopisch et al. 2005) failed to reveal a

16 relationship between brood value and nest defence, we can only speculate that parents base

17 their estimates of brood value on other aspects, which were not investigated so far.

18 Concerning male quality parameters tested, there was no effect of condition on nest defence,

19 but risk index increased with badge size. More intense reaction of larger-badged males agrees

20 with finding of Reyer et al. (1998). They reported that risky approach to the predator

21 increased from small- through medium- to large-badged males. They explained this

22 relationship by higher possible confidence of paternity of larger-badged males, which could

23 contribute to their motivation to defend the nest more intensely. However, the recent meta-

24 analysis (Nakagawa et al. 2007a) did not support the relationship between badge size and

25 cuckoldry. Moreover, studies of other passerines, where the genetic fathers of the nestlings

11

1   were known, found no effect of paternity on male nest defence (Lubjuhn et al. 1993, Griggio

2   et al. 2003, Rytkönen et al. 2007).

3   The explanation for male nest defence intensity increasing with badge size can reside in the

4   fact that birds with larger badges are in better physical condition (Veiga & Puerta 1996) and

5   can afford higher energy expenditure as well as better avoid the risk of injury. The same

6   conclusion was reached by Hogstad (2005) who found that Fieldfares *Turdus pilaris* in better

7   condition were more aggressive towards the predator exposed near the nest. However, in

8   House Sparrow the condition was found to correlate with the badge size only weakly

9   (Nakagawa et al. 2007a) and its effect on nest defence intensity was not found in our

10   population.

11   Larger-badged sparrows also are older (Nakagawa et al. 2007a, b). Owing to this finding our

12   result may just represent a relationship originating from the fact that older birds respond more

13   strongly than young birds due to their experience with a predator (Smith et al. 1984). In our

14   study the predator species was resident and often observed in the vicinity of the nest boxes

15   providing the opportunity for young sparrows to learn to recognise it as a threat early in their

16   life via social learning from their parents (Curio et al. 1978). Although we did not know the

17   age of the parents, most other studies of passerines have not found relationship between age

18   and nest defence (e.g. Winkler 1992, Hatch 1997).

19   Males with larger badges possess higher testosterone plasma levels mediating increased

20   aggressiveness, fighting ability and dominance status (Jawor & Breitwisch 2003, Senar 2006,

21   Ducrest et al. 2008, Buchanan et al. 2010). Higher circulating levels of testosterone arise from

22   pleiotropic effects of the genes regulating melanogenesis (Ducrest et al. 2008), further

23   including higher sexual activity, lesser sensitivity to stress, better antibody response and

24   higher metabolic rate (reviewed by Ducrest et al. 2008). These aspects might be also

25   associated with higher nest defence intensity. While for other males the melanin ornament is a

1   useful signal for decisions whether or not to engage in antagonistic interactions, the females

2   could rather use the information on ability of the male to behave aggressively also towards the

3   nest predators. In our study males defended the nest more vigorously than their females,

4   which is in opposite with the results of Reyer et al. (1998). The usually mentioned

5   explanations for sex differences in defence as different body size, ability to raise offspring

6   alone, renesting potential or mortality (Montgomerie & Weatherhead 1988, Westneat &

7   Sargent 1996) do not seem to be plausible in House Sparrow (discussed in Reyer et al. 1998).

8   However females of this species usually spent more time incubating (Hoi et al. 2003, Bartlett

9   2005, Hořáková, unpubl. data) and achieve higher feeding frequency than males (Voltura et

10   al. 2002, Hoi et al. 2003, Hořáková, unpubl. data). Thus it could be possible that there is a

11   division of labor, when females and males contribute disproportionally in different

12   components of care, resulting in equal shares of both sexes in general level of care as

13   predicted in species with biparental care.

14   However, females mated to larger-badged males did not lower their investment, as was the

15   case in study of Reyer et al. (1998). Their study was carried out in the university campus,

16   where the predation pressure could be lower than at our rural study site. Further the authors

17   used mustelid predators, which threaten also the adult birds unlike the Black-billed Magpie,

18   which predates only the eggs and nestlings. We suppose these different conditions might

19   affect the nest defence behaviour of females.

20   In our experiments the females of larger-badged males did not invest more in nest defence as

21   predicted by the "differential allocation hypothesis" (Burley 1986). So in our population the

22   benefit for these females was above-average intensity of nest defence performed by their

23   partners and thus better protection of their nests. The value of nest defence to female is the

24   protection of her offspring. Even though we did not observe different predation rates of nests

25   in respect to badge size, studies of other passerine species confirmed that successful nests

1   were defended more aggressively than nests that failed (Knight & Temple 1988, Weatherhead

2   1990).

3   Since nest defence can affect the breeding success (Knight & Temple 1986), we hypothesize

4   that the badge size may be a valuable signal of investment in this component of parental care

5   used by females in mate choice, especially in areas under high predation risk, where the

6   benefits from increased nest defence may exceed the benefits from increased food-

7   provisioning. To corroborate this assumption it would be necessary in the future to conduct

8   nest defence experiments in birds with manipulated badge sizes while controlling for other

9   possible effects as brood value or testosterone level.

10

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25

1   Summary

2   Parental investment may be affected by two main factors – the value of nestlings to parents

3   and quality of the individual parent. We investigated experimentally provoked nest defence

4   relative to these factors in a nest-box population of House Sparrows *Passer domesticus*. In

5   males the black throat patch of feathers (badge) serves as a signal of social status and age and

6   probably reflects condition. Because previous studies of information content of this ornament

7   have largely omitted nest defence, we included the badge size as a parameter of male quality.

8   We presented a mounted Black-billed Magpie *Pica pica*, a predator of eggs and nestlings, to

9   19 pairs of sparrows during the breeding seasons 2005-2006. To assess the intensity of

10   individual defence we used the „risk index" increasing with time spent reacting and riskiness

11   of the reaction (frequency of approaches with and without alarm calls and attack flights),

12   while declining with the distance from the predator. Males defended their nests more

13   vigorously than their females (Table 1) and increased the intensity of nest defence with their

14   badge size (Table 2, Fig. 1). We found no factors explaining the variability in female nest

15   defence, as they did not adjust their investment neither to brood value nor their own condition

16   (Table 2). Males adjusted their nest defence to the brood value only marginally, tending to

17   defend early broods more vigorously than broods laid later in the season, but not in respect to

18   other brood parameters (Table 2). Therefore the "brood value hypothesis" was only partially

19   supported. Neither males nor females adjusted their nest defence to the quality or parental

20   investment of their partners (Table 2), so we could not support the "differential allocation

21   hypothesis" in this species. Because of more intense reaction of larger-badged males we

22   suggest that the badge predicts the male investment in nest defence. We further hypothesize

23   that the melanin-based ornament could be used as a signal of this component of parental care

24   by females. This could be true mainly in sites under high predation pressure, where male

25   contribution to nest defence may affect the female breeding success.

1   Table 1

2   Comparison of male and female nest defence variables. Bonferroni correction was applied for

3   the four variables of nest defence, $p \leq 0.0125$ are in **bold**. Descriptive statistics (mean ± SE)

4   and Wilcoxon matched-pairs test results are given (n = 19).

5

Variable	Males	Females	Z	p
Time spent reacting (s)	456.95 ± 65.70	224.63 ± 66.26	2.576	**0.010**
Number of approaches with alarm calls	5.47 ± 0.82	3.42 ± 0.95	2.249	0.025
Mean distance (m)	2.59 ± 0.18	2.97 ± 0.3	0.776	0.438
Risk index	744.34 ± 105.37	324.54 ± 108.91	2.857	**0.004**

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1   Table 2

2   Results of analyses of covariance (ANCOVAs) of an effect of year of study, laying date,

3   brood size, nestling age and condition, males' badge size, parents' own condition and their

4   partners' risk index on the value of risk index of male and female House Sparrows.

5   Significant tests (α = 0.05) are in **bold**. Full model includes all response variables, minimal

6   adequate model is a result of forward variable selection.

7

ANCOVA (n=16)	Male			Female		
Variables	df	F	p	df	F	p
Full model						
Year	1,14	0.033	0.861	1,14	1.522	0.257
Laying date	1,13	3.471	0.105	1,13	0.386	0.554
Brood size	1,12	0.005	0.945	1,12	0.078	0.788
Nestling age	1,11	0.755	0.414	1,11	0.409	0.543
Nestling condition	1,10	0.524	0.493	1,10	0.308	0.596
Parent condition	1,9	0.953	0.362	1,9	0.604	0.463
Partner´s risk index	1,8	2.591	0.152	1,8	4.245	0.078
Male badge size	**1,7**	**6.462**	**0.039**	1,7	0.906	0.373
Minimal adequate model						
Male badge size	**1,14**	**6.060**	**0.029**			
Laying date	1,13	3.991	0.067			

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Fig. 1 Risk index of reactions to a stuffed Black-billed Magpie of 19 House Sparrow males (black dots, solid line) and 19 females (open squares, dashed line) in relation to the black area of male badge.
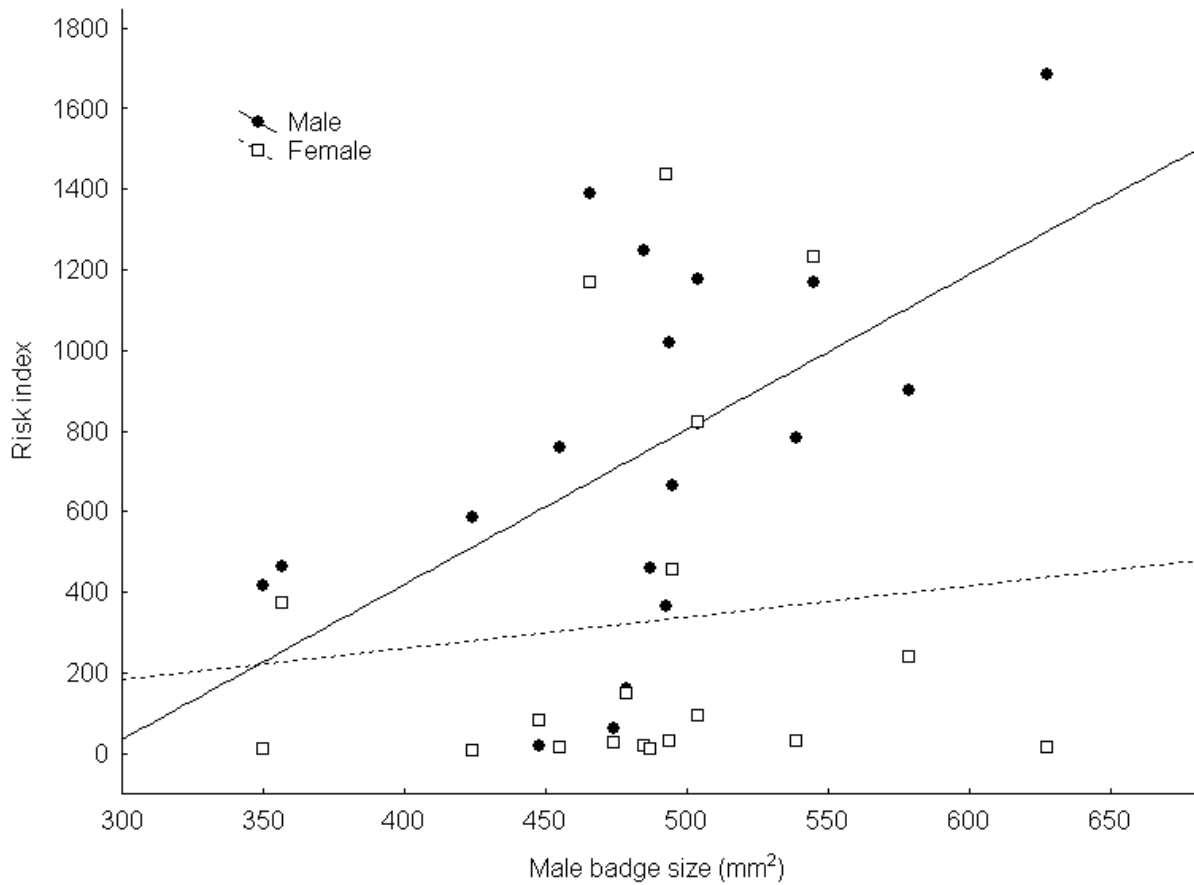
Příspěvek II

Klvaňová A. & Exnerová A.

Mobbing strategy during the breeding season in colonial house sparrow *Passer domesticus*

varies with predator type.

(*submitted*)

1 Mobbing strategy during the breeding season in colonial house sparrow *Passer domesticus*

2 varies with predator type

3

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1   Abstract

2   We investigated mobbing behaviour in house sparrows under different level of threat to test

3   hypotheses on the function of this anti-predator strategy. We exposed three different stuffed

4   predators to induce mobbing reaction in 10 separately breeding colonies. To assess mobbing

5   intensity we used the „risk index" increasing with time spent reacting and riskiness of reaction

6   (number of approaches and attacks), while declining with increasing distance from the

7   predator. The birds reacted simultaneously in a group and discriminated between the

8   predators. They increased the intensity of reaction with decreasing level of threat from

9   sparrowhawk through little owl to black-billed magpie. The results support the "parental care

10 hypothesis" as the nest predator was mobbed most intensely. Males mobbed the magpie

11 more intensely than females, while the sparrowhawk and the little owl were mobbed with

12 same intensity by both sexes. Male mobbing intensity towards magpie and little owl increased

13 with size of the mobber´s badge - a breast patch, which signals dominance and was previously

14 proposed as a signal of nest defence. However, sparrowhawk was mobbed independently on

15 badge size. The "signalling hypothesis" appears to be plausible but this function of mobbing is

16 affected with level of threat posed by the predator.

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22 Introduction

23 Colonial breeding in birds involves several advantages including collective nest defence during

24 the breeding season and thus better protection from predators (Lack 1968; Krebs and Davies

25 1993). In the colony, the approaching predator is detected sooner thanks collective vigilance

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1   (Elgar 1989). The risk taken by a single bird while facing the predator is diluted among all

2   colony members (Hamilton 1971; Brown and Hoogland 1986; Cresswell 1994). As predation is

3   one of the most common causes of nesting failure in birds (Ricklefs 1969), to avoid it is a key

4   parental strategy enhancing the breeding success (Montgomerie and Weatherhead 1988).

5   Intensive nest defence usually results in higher fledging success (e. g. Wiklund 1990;

6   Tryjanowski and Goławski 2004; Hogstad 2005), even if some authors did not support this

7   conclusion (Hatch 1997; Arnold 2000). Mobbing is a special type of antipredator behaviour,

8   when several individuals join the group and approach the predator, typically flicking their

9   wings and tails while uttering specific alarm calls (Curio 1978). This behaviour significantly

10   reduces the risk of predation (Pettifor 1990; Pavey and Smyth 1998), but involves several costs,

11   too. It is time and energy consuming (Biermann and Robertson 1983; Winkler 1994), may

12   result in the mobber´s injury or even be lethal (Myers 1978; Poiani and Yorke 1989; Motta-

13   Junior 2007). In addition, it helps the predator to localise the nest (McLean et al. 1986).

14   Regarding a plenty of hunting techniques and prey specializations in different predators it is

15   adaptive for the birds to adjust their mobbing strategy to the level of threat which a particular

16   predator poses (Kruuk 1964; Andersson et al. 1980) either to them (Buitron 1983; Dale et al.

17   1996) or to the nest (Ghalambor and Martin 2000). Other potential effects on mobbing

18   intensity during the breeding season include sex of the mobber and season stage. Balancing

19   the costs and benefits of defence strategy may result in different behaviour of males and

20   females because of different investment, certainty of paternity, body mass, aggressiveness or

21   conspicuousness (Montgomerie and Weatherhead 1988; Kotiaho 2001). The cues of nest

22   defence may also vary in the course of the breeding season due to changing renesting

23   potential or offspring quality in sense of parental investment theory (Montgomerie and

24   Weatherhead 1988).

1   Ostreiher (2003) resumed a number of hypotheses stated to explain the adaptive value of

2   mobbing either as altruistic behaviour (e. g. Curio 1978; Pavey and Smyth 1998), part of

3   parental care (e. g. Curio 1978) or selfish behaviour (e. g. Slagsvold 1984).

4   Mobbing in house sparrow *Passer domesticus*, L. was described several times (Wilson 1978;

5   Cramp and Perrins 1994). As a multi-brooded colonial passerine showing conspicuous sexual

6   dimorphism it is an ideal model species for testing hypotheses on mobbing behaviour during

7   the breeding season. Moreover the males bear black melanin-based throat patch of feathers,

8   so called badge, which serves as a known signal of dominance (Nakagawa et al. 2007) and

9   enables to distinguish the social status of the bearer. In previous study of another house

10   sparrow colony we showed that males defended the nest predator more intensely than

11   females and increased the defence intensity with their badge size, but irrespective to the

12   season stage (Klvaňová et al. in press). The aim of present study was to test whether the

13   mobbing strategy is stable or it varies under different threat associated with predator type

14   while controlling for the effect of sex of the mobber and stage of the breeding season. We

15   considered two, not mutually exclusive, hypotheses explaining mobbing behaviour in colonially

16   nesting house sparrows. First, if mobbing is rather a part of parental care, sparrows mob the

17   predators to drive them away from the nest (Curio 1978). Prediction derived from the

18   "parental care hypothesis" was that both parents should mob more intensely the nest

19   predator than the predator of adults. Alternatively, if mobbing is rather a selfish behaviour,

20   sparrows mob to advertise their social status to other males (Slagsvold 1984; Moholt and Trost

21   1989; Dugatkin and Godin 1992). Under the "status signalling hypothesis" we predicted that

22   males should mob more intensely than females, but regardless the season stage and predator

23   type. Additionally we predicted that males with larger ornaments, i. e. dominant individuals,

24   mob all predators more intensely than less ornamented ones.

25

4

1   Materials and methods

2   The experiments were carried out in two breeding seasons from April to July 2002 and 2003.

3   We observed ten separate house sparrow colonies of 6-8 pairs nesting on buildings in different

4   districts of Prague, Czech Republic (49°88'N, 14°47'E). The colonies were distant from each

5   other and did not communicate during the breeding season. We chose localities which

6   resembled each other in immediate surroundings of the colony. There was a similar offer of

7   perches (i.e. twigs, fences, wire and so on) in the equivalent distance from the nests. Owing to

8   this experimental design all the birds had equal opportunity to react to the predator. The birds

9   were not trapped. We estimated the breeding status visually by observation the parents

10   provisioning their young. We conducted the trials when the parents were feeding either their

11   first broods (25 April–28 May; 15 trials with 5 colonies), or the second broods (18 June–27 July;

12   15 trials with another 5 colonies).

13   We used three mounted predators of different threat to induce the mobbing reaction. Each

14   predator was exposed to every observed colony only once in random order, which resulted in

15   30 trials. As the most dangerous predator we considered the female sparrowhawk *Accipiter*

16   *nisus*, which threat primarily the parents (Gotmark and Post 1996), but occasionally it was

17   observed to pull out young from the nest hole (Klvaňová and Hořáková, personal observation).

18   The little owl *Athene noctua* also poses a threat both to fledglings and adults (Angelici et al.

19   1997) but during the day it is passive and stressed by mobbing (Flasskamp 1994), and so is less

20   dangerous. The black-billed magpie *Pica pica*, predator of nests and fledglings (Tatner 1983),

21   does not threaten the adult birds and thus represents the lowest risk for adults. Before each

22   trial we watched the colony for 15 min to make sure that majority of the flock was present,

23   birds were feeding the young and no disturbing event (e.g. distraction by people, predator

24   attack) had happened. Each predator model was fixed facing the building the nests were

25   placed on, in constant distance of approximately 5 m from the nests. As soon as the predator

5

1   was detected by a colony member, we began to record the mobbing reaction for 25 min. To

2   minimize the possible effect of habituation the next trial with the same colony followed after

3   at least 3 days.

4   All trials were recorded with a VHS videocamera JVC from a hiding place distant at

5   least 5 m from the model. During the trial colony members were alternately changing their

6   roles. The active mobbers approached the predator with alarm calls and flew over it, while the

7   passive mobbers called from distant hidden place in a group, where it was not possible to

8   count their number or determine their sex exactly. Therefore only the reactions of active

9   mobbers were analysed. We noted the following variables for each mobbing reaction observed

10 during the trial:

11 *Sex* of the mobbing bird.

12 *Type (rank value) of the reaction*. We distinguished three types of reaction - silent approach

13 (rank value 1), more risky approach with alarm calls (rank value 2) and attack, characterised by

14 straight flight towards the predator (rank value 3).

15 *Time reacting* (s) the active bird spent in view (< 5 m from the model).

16 *Distance* (m). We estimated the distance between the bird and the predator model from 1 to 5

17 m (to the nearest 1 m) each 10 s of the bird´s reaction. From these distancies (1-5) we

18 calculated mean distance during performance of each type of behaviour (approach or attack)

19 for each bird.

20 To assess the intensity of mobbing reaction we used the „risk index" (RI):

21                                  $RI = R (tr/dr)$.

22 The value of RI increases with time spent reacting (tr) and rank value of the reaction (R), while

23 it declines with the distance from the predator (dr) (modified after Windt and Curio 1986; see

24 also Brunton 1990).

6

1   Because the birds were not marked, we were not able to distinguish them on individual basis.

2   Thus we considered the mean male and female RI (sum of RI of all reactions performed by

3   males/females during one trial divided by the number of male/female mobbers). The number

4   of mobbers was the highest number of birds observed mobbing simultaneously during the

5   trial.

6   Badge measurements

7   The active mobbers were recorded in detail using a camera with long focal-length zoom lens

8   (see also Bartlett et al. 2005). The videorecords of each trial were played in ATI Multimedia

9   Player on a standard videorecorder connected to PC. The birds were photographed during

10 their reaction in zoomed detail in a frontal view facing the observer using Photoshot function.

11 Our trials took place in the advanced phase of the breeding season, when majority of white

12 feather tips are worn off and the badge has its final size (Møller and Erritzoe 1992). We

13 categorized the males within each colony as small-, medium- or large-badged according to the

14 visually estimated black feather patch size relative to other male colony members (after Reyer

15 et al. 1998; see also Møller 1987). To prevent pseudoreplication we considered only the first

16 reaction of male from each category in a trial, because we were not able to distinguish the

17 individuals within a badge-size category during analysing the records of trials perfectly. Thus

18 we considered only three male reactions from each trial for the analysis of the effect of the

19 badge size on male mobbing.

20 Statistical analyses

21 The intensity of mobbing was expressed as sex-specific risk index value (RI). To find out

22 whether intensity of mobbing reaction was influenced by stage of the breeding season, sex of

23 the mobber and predator type, while controlling for the effect of the year, we conducted

24 repeated-measures analyses of variance (ANOVA) with predator type as repeated within-

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1   subject effect. Risk index values were normally distributed. Differences between the three

2   predator types were tested by Fisher´s Least Square Difference test.

3   To find out whether the effect of male mobber´s badge size on his mobbing intensity was

4   stable we conducted analyses of variance (ANOVA) separately for each predator species. The

5   male risk index values had gamma distribution and were analysed in corresponding GLM with

6   log-link function.

7   Statistical tests were performed using STATISTICA 6.0 (StatSoft, Inc. Tulsa, USA) software.

8

9   Results

10   House sparrows reacted to all exposed mounted predators in a group. Mean number (± SE) of

11   active mobbers in a trial differed between the predator types. The largest proportion of colony

12   members reacted towards magpie - 79% (± 6), towards little owl it was 50% (± 7) and towards

13   sparrowhawk 35% (± 6). During the trial active mobbers occurred on exposed perches being

14   potentially visible for the predator and performed typical movements: spreading and flicking

15   their wings and tails, alternately approaching and retreating the predator, occasionally flying

16   straight towards it but they never performed any physical contact with it. The risk index

17   differed with sex of the mobber and predator type (Fig. 1), but not in respect to the year or

18   stage of the breeding season (Table 1). Approaching the magpie, the sparrows risked

19   significantly more than in reaction to sparrowhawk (Fisher LSD post hoc test: $P < 0.001$, df =

20   24) and little owl (Fisher LSD post hoc test: $P = 0.011$, df = 24). The sparrowhawk was mobbed

21   yet less intensely than the little owl (Fisher LSD post hoc test: $P = 0.013$, df = 24). Although the

22   interaction of predator type x sex was not significant, based on post hoc tests we found that

23   only in trials with magpie mobbing by males was more intense than by females (Fisher LSD

24   post hoc test: $P = 0.003$, df = 36), while the sparrowhawk (Fisher LSD post hoc test: $P = 0.883$,

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1   df = 36) and the little owl (Fisher LSD post hoc test: P = 0.180, df = 36) were mobbed with the

2   same intensity by both sexes.

3   Further we examined the relation between badge size and mobbing intensity of males to

4   individual predators separately. Risk index of reaction increased with badge size in trials with

5   magpie (ANOVA: Wald. Stat. = 11.37, df = 2, 29, p = 0.003) and little owl (ANOVA: Wald. Stat. =

6   16.90, df = 2, 29, p < 0.001), whereas sparrowhawk was mobbed independently on badge size

7   (ANOVA: Wald. Stat. = 1.99, df = 2, 17, p = 0.370).

8

9   Discussion

10   During experimental exposure of different mounted predators to breeding colonies, house

11   sparrows reacted in all trials as a simultaneously mobbing group. The birds were alternately

12   changing their roles of active and passive mobbers as was described also in other mobbing

13   species, e. g. barn swallow *Hirundo rustica* (Shields 1984). This is in a sharp contrast with the

14   previous studies of house sparrow´s nest defence, where the predator models were placed

15   facing a nest box or directly on it and only the nest owners reacted as active mobbers (Reyer et

16   al. 1998; Klvaňová et al. in press). Regarding this discrepancy, we assume that the decision

17   whether to join mobbing depends also on predator´s distance from the nest. The importance

18   of predator distance was highlighted in previous studies - however, it usually had a negative

19   effect - the mobbing intensity increased near the nest, because it was already detected by the

20   predator (Zimmermann and Curio 1988; Kleindorfer et al. 2003). Placing the predator model

21   on the nest box probably represented a situation when it already chose the prey and thus only

22   the nest owners were motivated to defend. Conversely, when the predator was placed 5 m

23   from the colony, all the nests had the same probability to be chosen and predated and thus all

24   the breeding birds had the same motivation to mob the predator. Thus we assume that in the

25   latter case it was rather a group of selfish pairs defending their own offspring than a social

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1   group of altruists putting themselves into risk of predation for the benefit of whole colony.

2   Horn (1968) proposed a similar conclusion for group mobbing in colonial Brewer´s blackbird

3   *Euphagus cyanocephalus*, and explained it by overlap of the average radius each bird defends

4   around its nest.

5   The type of the predator appeared to be an important aspect in sparrows´ decisions on

6   mobbing behaviour. The number of mobbers as well as the mobbing intensity decreased as the

7   risk of injury or death increased. Our results support the hypothesis that the birds adjust their

8   defence strategy to the potential threat posed by different predators (Pettifor 1990; Shedd

9   1982). The predator of eggs and nestlings, represented by the magpie, was mobbed with the

10   highest intensity. The black-billed magpie invaded cities of Central Europe including Prague

11   during recent two decades (Fuchs et al. 2002). It preys on eggs and nestlings of small

12   passerines but does not threat the adults (Cordero 1991). The more risky reaction to the nest

13   predator than to the predator of adults was observed also in the colonies of gulls *Larus* spp.

14   and terns *Sterna* spp. (Clode et al. 2000) or red-winged blackbirds *Agelaius phoeniceus* (Knight

15   and Temple 1988) and supports the hypothesis, that mobbing is a part of parental care

16   because its main beneficiary is the offspring. Sparrows distinguished not only the predators of

17   the nests and adults but also between the two adults´ predators. This ability was shown also in

18   other prey species, e. g. the great tits *Parus major* (Curio et al. 1983). Variability in perceived

19   risk was probably caused by different hunting technique of the two raptors (Bildstein 1982;

20   Pettifor 1990). The little owl belongs to important house sparrow´s predators (Cordero 1991).

21   Although recently it has almost disappeared from Prague (Fuchs et al. 2002) it was still

22   perceived as dangerous by sparrows. Despite its nocturnal activity and stress caused by

23   mobbing (Flasskamp 1994), it may probably injure the mobbing adults as it was described in

24   other owl species (Motta-Junior 2007), and therefore was mobbed less intensely than the

25   magpie. However, due to the owl´s reduced ability of orientation during the day it is less likely

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1   to catch the flying prey than is the sparrowhawk, which was mobbed with the lowest intensity.

2   House sparrows form a notable proportion of the food of this raptor (Cramp and Perrins 1994)

3   and to harass it apparently incur the highest risk.

4   Males mobbed generally more intensely than females which was pronounced in reaction to

5   the least dangerous predator, the magpie, while the owl and the sparrowhawk were mobbed

6   equally by both sexes as in other species with biparental care (Greig-Smith 1980; Buitron 1983;

7   Knight and Temple 1986). Lotem et al. (1998) proposed that there may be an overlooked

8   signalling component of nonsignalling behaviour, e. g. parental care behaviour. If this was true

9   in house sparrows mobbing, 1) its intensity should be considerably higher than could be

10   explained if it was performed solely to drive the predator away and 2) the level of

11   exaggeration of mobbing intensity should be related to quality of an individual, as required by

12   a handicap principle (Zahavi 1975; Lotem et al. 1998). We suppose that the latter condition

13   was fulfilled by observed risk index values reached by active mobbers which demonstrates

14   their ability to sustain increased time and energy expenditure. To prove the former condition

15   to demonstrate the signalling effect is more difficult. However, we suggest that this could be

16   indicated by the fact, that only in trials with magpie the males reacted significantly more

17   intensely than females. As the other two predator models were mobbed equally by both sexes,

18   we can regard the intensity of female mobbing as sufficient to distract the predator and the

19   increase in male mobbing to magpie as a surplus intended for other individuals to use as a

20   source of information. Mobbing the magpie could entail well balanced risks and rewards for

21   signalling, because it poses only low risk of injury, but to mob it is still time and energy

22   consuming.

23   Furthermore, we found that the relation between mobbing intensity and badge size (Reyer et

24   al. 1998; Klvaňová et al. in press) varied with different predator species. The effect of badge

25   size on mobbing intensity was apparent in reaction towards magpie and little owl, but not to

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1   sparrowhawk. We conclude that dominant males defended more intensely against both nest

2   (magpie) and adult (owl) predators, but if the risk of injury or death for adults was too high

3   (sparrowhawk), the differences between larger- and smaller-badged males disappeared.

4   However, this outcome may be influenced by relatively low sample size in reaction to

5   sparrowhawk, which was caused by rather moderate reactions to this predator or passive

6   mobbing in the cover, where it was not possible to record the bird´s badge size. The more risky

7   reaction of males to the nest predator than to the predator of adults was observed also in red-

8   winged blackbirds (Knight and Temple 1988). The most aggressive males had also the best

9   mating success (Knight and Temple 1988).

10   We assume that mobbing the predator could serve also as self-advertisement. However, we

11   cannot distinguish exactly whether the males were signalling rather the social status to other

12   males or parental quality expressed as the ability to defend the nest to the current and

13   potential mates, because both male and female colony members joined the mob and

14   represented the audience. Nevertheless, the status-signalling component in mobbing

15   behaviour could be supported by the fact that its intensity did not differ during the breeding

16   season. As house sparrows are sedentary and occupy the same home ranges almost year

17   round (Anderson 2006), it appears adaptive to signal the social status to colony members at

18   each season stage.

19   It was previously suggested that in social species colony members could demonstrate their

20   dominance and quality towards conspecifics through mobbing ability (e.g. Maklakov 2002),

21   perhaps helping to obtain extra-pair copulations (Slagsvold 1984). However the willingness to

22   do so appears to decrease with the actual danger posed by the predator as the benefits from

23   this behaviour diminish.

24   Based on our results we conclude that mobbing in house sparrows is mainly a part of parental

25   care which probably contains a signalling component. We further corroborate the importance

1   of predator species used in experimental studies of nest defence (Clode et al. 2000) as well as

2   the distance of the model from the nest (Kleindorfer et al. 2003).

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1   Table 1 Effects of predator type, stage of the breeding season and sex of the mobbing house

2   sparrows on the risk index of the reaction towards the stuffed black-billed magpie, little owl

3   and sparrowhawk. Year was entered as a random variable into the model. Results of repeated

4   measures analysis of variance (ANOVA) are given; $p \leq 0.05$ are in bold. All interactions were

5   non-significant (all $p > 0.09$).

6

| Variables	df	F	p
Predator type	2, 19	15.195	**0.00005**
Season stage	1, 19	0.117	0.739
Sex	1, 19	9.043	**0.011**
Year	1, 19	0.079	**0.784**

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1 Fig. 1 Box and whiskers plot of the mobbing intensity expressed as risk index reached by

2 breeding male (white boxes) and female (black boxes) house sparrows in reaction towards

3 stuffed predators of different threat. Boxes indicate mean ± SE, whiskers indicate ± 95%

4 confidence interval.

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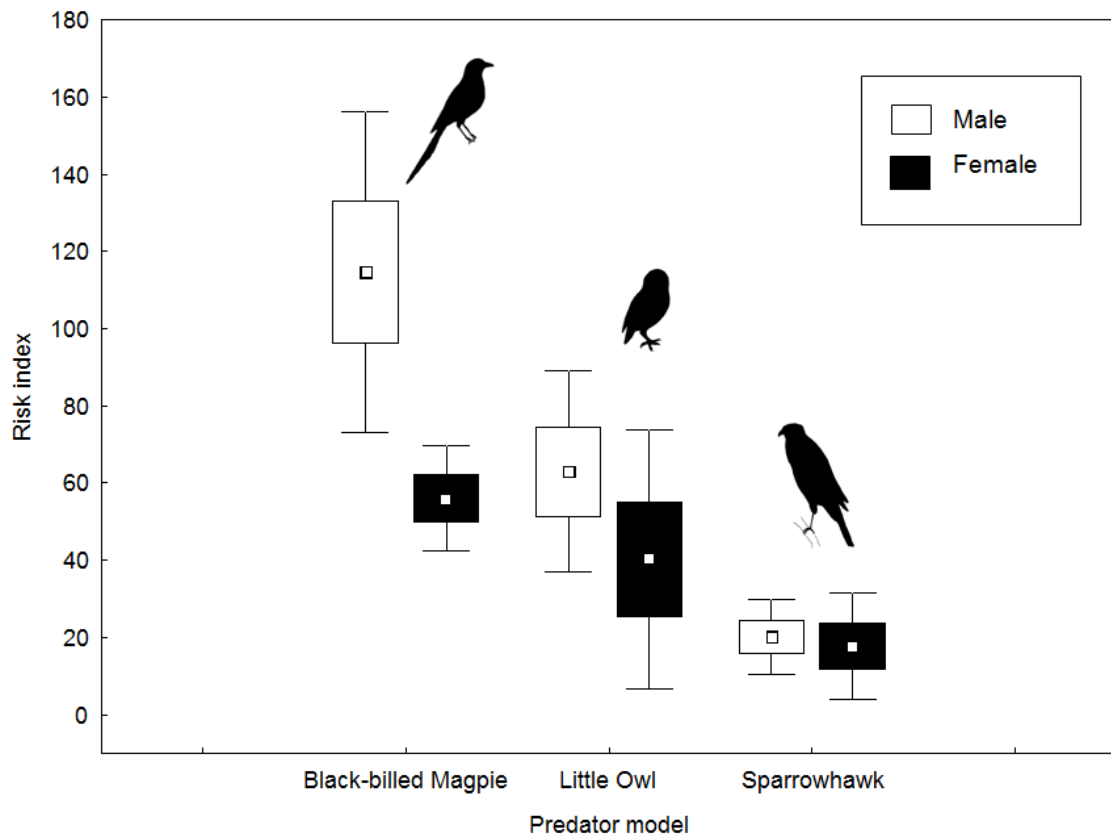
1   Fig. 2 Box and whiskers plot of the mobbing intensity expressed as risk index of male house

2   sparrows in reactions towards stuffed predators of different threat in respect to the badge size

3   of the mobber; white boxes are for large-badged, shaded boxes for medium-badged and black

4   boxes for small-badged males. Boxes indicate mean ± SE, whiskers indicate ± 95% confidence

5   interval.

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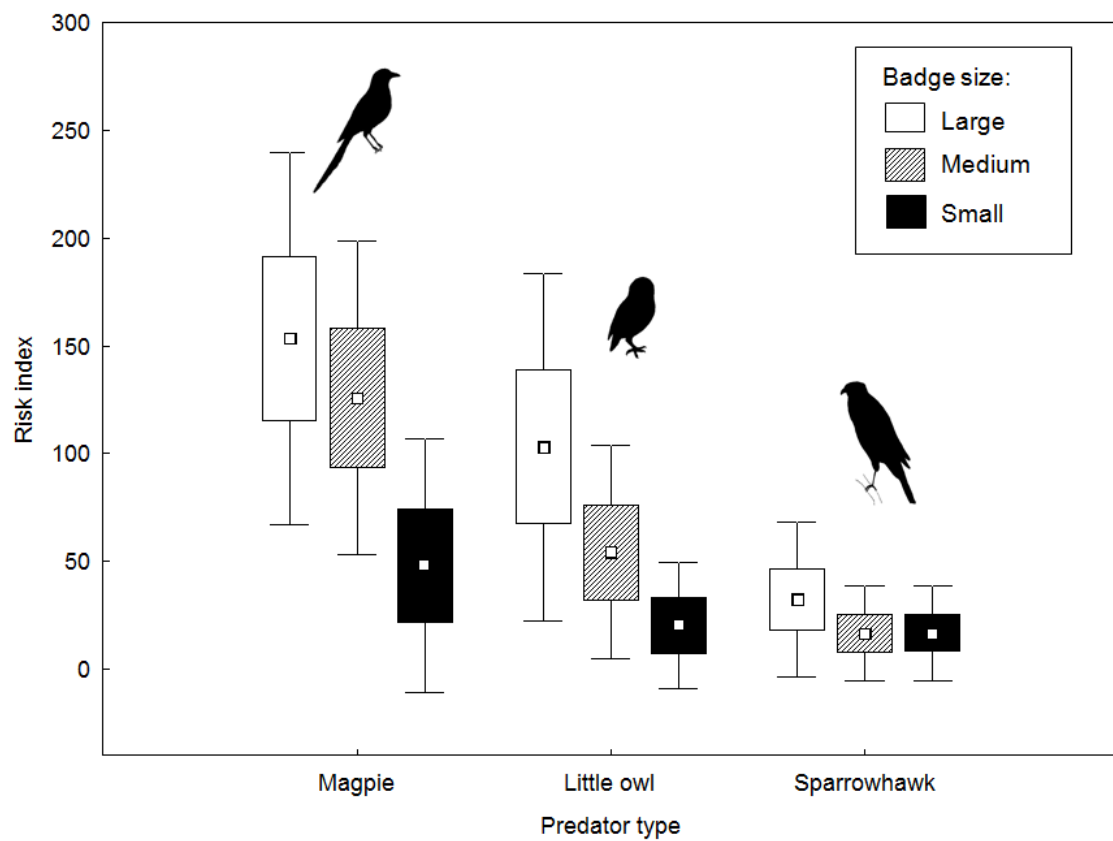
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Příspěvek III

Klvaňová A., Lusková M., Hořák D. & Exnerová A.

Total amount of food and diet composition affects nestling condition

in House Sparrows *Passer domesticus.*

(*submitted*)

1   Total amount of food and diet composition affects nestling condition in House Sparrows *Passer*

2   *domesticus*

3

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9

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1   Summary

2   Capsule

3   The nestlings of House Sparrows fed by higher amount of food and animal component in the diet

4   reached better condition.

5   Aims

6   To investigate what foods are important to nestlings of different age in rural environment of central

7   Europe and whether the diet affects the condition of the nestlings.

8   Methods

9   We analysed 210 faecal samples from 106 nestlings of 31 broods to evaluate nestling diet during the

10   breeding seasons 2008 and 2009 in a nest-box colony on a farmstead in south Bohemia.

11   Results

12   Faecal sacks contained 362 identifiable animal food objects belonging to five arthropod orders. The

13   nestlings were fed primarily by beetles (mainly Scarabeidae) and Diptera (mainly muscids and

14   tipulids). The total amount of food provided by parents to a particular nestling was higher in older

15   nestlings due to increase in total mass of plant component, while total mass of animal component

16   did not differ between age categories. The total amount of food, mass of animal component and

17   marginally the abundance of Coleoptera in the diet of older nestlings were positively related to

18   nestling body condition.

19   Conclusions

20   To compensate increasing demands of older nestlings the parents increased the mass of plant

21   material in the diet. This might be caused either by some upper limit to which they are able to catch

22   invertebrate prey, or by growing nestlings´ preferences for plants. The effect of food amount and

23   animal component in nestling diet on their condition stressed the importance of arthropods for

24   breeding success.

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2

1   Introduction

2   Common factors influencing breeding success are resource availability and weather conditions (Lack

3   1954). In birds, food supply during the breeding season is a particularly important determinant of

4   fledgling condition and survival (e. g. Anderson 1977, Hochachka & Smith 1991, Naef-Daenzer &

5   Keller 1999, Rossmanith *et al.* 2007). Nutrition at the nestling stage may affect fitness later in the life

6   of the birds (Metcalfe & Monaghan 2001). Low-quality diet poor in nutrients may reduce growth

7   rates in the nestlings of passerines (Johnston 1993, Birkhead 1999). Variable proportions of different

8   prey types (Wright *et al.* 1998) or the presence of particular key prey in the nestling diet is likely to

9   affect the reproductive performance. Thus, caterpillars are important components in the nestling

10   diet of the Lesser Spotted Woodpecker *Dendrocopos minor*, positively affecting their body mass

11   (Rossmanith *et al.* 2007), insect larvae increase the condition in young Skylarks *Alauda arvensis*

12   (Donald *et al.* 2001) and lipid-rich fish are needed for successful recruitment in young Red-legged

13   Kittiwakes *Rissa brevirostris* (Kitaysky *et al.* 2006). Finally, in the Blue Tits *Cyanistes caeruleus* the

14   presence of spiders in the nestling diet influence risk taking behaviour and performance in spatial

15   learning task via high levels of amino-acid taurine (Arnold *et al.* 2007).

16   As the breeding success determines population stability (Haig *et al.* 1993) its reduction may cause the

17   decline of a population, too (Vincent 2005, Baillie *et al.* 2007, Peach *et al.* 2008). In House Sparrows

18   *Passer domesticus,* L. reduced breeding success may be caused by low chick condition resulting from

19   their starvation due to lower availability of invertebrate food (Mitschke *et al.* 1999, Vincent 2005).

20   Peach *et al.* (2008) showed that low reproductive output in a British population was associated with

21   high proportions of vegetable material in nestling diet and low aphid (Aphidoidea) densities within

22   the home ranges of their nests. This way the lack of appropriate nestling food might contribute to

23   the large decline of House Sparrow populations, which they have experienced during last decades in

24   many European countries (e.g. PECBMS 2010). The factors determining this negative population

25   trend have been widely discussed (Siriwardena *et al.* 2002, Anderson 2006) including agriculture

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1   intensification (Hole *et al.* 2002), predation risk (MacLeod *et al.* 2006), air pollution (Peach *et al.*

2   2008) and general habitat changes (Summers-Smith 1999).

3   Nestling food of House Sparrows comprises only invertebrates during first three days of life

4   (Summers-Smith 1963). Since then the proportion of animal component decreases gradually and

5   after fledging the diet becomes almost entirely vegetable (Mueller 1986). The studies of food

6   composition (reviewed in Anderson 2006), based mainly on analyses of faeces or neck collar samples,

7   showed, that the animal material consists mainly of insects and in a lower rate also of spiders. Most

8   common insect groups are beetles, caterpillars, flies, and grasshoppers and crickets, sometimes

9   accompanied by aphids and ants. The plant material consists mostly of various grains and seeds. The

10   composition of nestling food changes geographically and seasonally with the availability of particular

11   prey species (e.g. Encke 1965, Anderson 1984).

12   Published studies on diet composition of European House Sparrow nestlings come from Bulgaria

13   (Simeonov 1964), Germany (Encke 1965, Mitschke *et al.* 1999), Great Britain (Seel 1969, Vincent

14   2005) Romania (Ion 1971) and Poland (Wieloch 1975). In the Czech Republic the food of nestlings

15   was not studied and other diet analyses from Central and East Europe have arisen several decades

16   before the population started to decline. In this paper, we aimed to explore what foods are today fed

17   to nestlings in a Central European rural environment. We investigated the influence of food amount

18   and diet composition on nestling prefledging condition to reveal, if these factors might affect the

19   breeding success also in this region.

20

21   Materials and Methods

22   *Study area and population*

23   Our study was conducted on the farmstead in Veselí nad Lužnicí, Czech Republic (49°11'N, 14°41'E).

24   Habitat composition was mapped within a 200 m radius of the buildings with nest boxes, because

25   adults usually do not forage farther from their nests (Summers-Smith 1963; personal observation on

4

1   study site). Almost half of the surrounding area was composed by grassland (47%), over one-third

2   was built-up or covered by concrete (22%) and dung-yard (11%). Another 10% consisted of broad-

3   leaved trees. Shrubs and arable farmland provided both 4% of the radius, although the fields were

4   found on much larger area around the farm. Remaining 3% consisted of the coniferous trees. Settled

5   area was situated in the minimal distance of 300 m. In 2004, we erected 50 nest boxes (25 x 15 x 15

6   cm) on the farm buildings 4-5 m above ground level. For this study we gathered data on 31 broods

7   during the breeding seasons 2008 and 2009 (16 broods each year). The nest boxes were monitored

8   every other day for signs of nesting. Once egg laying had begun, we checked the nests to ensure the

9   date of hatching. To control for annual differences in timing, we set the median laying date of the

10   population for each year to zero and calculated the relative laying date for each pair as the deviation

11   from "time zero" (after Rossmanith *et al.* 2007). When the nestlings reached 10 days, they were

12   ringed with aluminium rings and marked with unique combination of plastic colour rings. Each

13   nestling was weighed using spring scale to the nearest 0.1 g and its left tarsus and wing length were

14   measured to the nearest 1 mm. To estimate body condition of nestlings we used the residuals from

15   linear relationship between the logarithm of tarsus length and the logarithm of body mass ($F_{1,104}$ =

16   40.2, p < 0.0001, R^2 = 0.28; Bradbury *et al.* 2003, Schulte-Hostedde *et al.* 2005).

17   *Diet analysis*

18   We used faecal samples to evaluate nestling diet (Moreby & Stoate 2000), although we are aware of

19   several problems associated with this method. Some items cannot be detected in the sample

20   because their high digestibility (Ralph *et al.* 1985). Therefore, especially invertebrates with few hard

21   body parts, such as aphids or ants, are probably underestimated. However, this bias is not always

22   remarkable (Poulsen & Aebischer 1995, Moreby & Stoate 2000) and this method is almost stressless

23   for the nestlings (Brickle & Harper 1999). Our aim was to test an effect of nestling food on their body

24   condition rather than to describe composition of their diet in detail. We took food samples from all

25   nestlings twice during the breeding attempt: at the nestling age of 4-6 days (younger age) and 9-11

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1   days (older age). Nestlings commonly produced faecal sacs when handled. We analyzed 210 faecal

2   sacs (112 from 54 nestlings in 2008 and 98 from 52 nestlings in 2009). In these 362 food objects were

3   recognized. As a food object any arthropod body part was considered.

4   After collection, fresh droppings were conserved in vials of 70% ethylalcohol. Data were pooled

5   within broods for analysis to avoid pseudo-replication. For examination, the contents of each faecal

6   sample were deposited into a petri-dish. The underside of the dish was scored with radial lines at 10°

7   intervals giving 36 equal segments. The contents of each faecal sample were placed on the dish with

8   a small amount of ethanol, spread evenly across the 36 segments and inspected at 30 x magnification

9   using a binocular microscope. By rotating the dish through 360° it was possible to search the entire

10   contents and the food objects found in each section were recorded (following Green & Tyler 1989,

11   Vincent 2005).

12   First we separated the animal and plant fractions. Plant material was dominated by soft, easily

13   digestible cereal grains, which did not allow quantifiable comparison with arthropod remains.

14   Therefore, we weighed both animal and plant component of each sample. For comparison of these

15   two components we considered only their weight.

16   For identification of the arthropods we followed Calver & Wooller (1982) and Ralph *et al.* (1985). The

17   number and type of food objects, such as legs or mandibles were recorded. For each of the main

18   arthropod groups encountered the following body parts were counted (after Vincent 2005):

19   Coleoptera (beetles) – head, mandibles, legs, elytrae; Diptera (flies) – heads, wings, legs;

20   Heteroptera: head, wings, legs; Cicadomorpha: head, wings, legs; larvae: head; Araneae (spiders) –

21   head, chelicerae, leg tips.

22   Identifiable parts were then matched to approximate the number of individuals occurring in each

23   sample (e.g. two mandibles and/or up to six legs represented one beetle). As the majority of

24   arthropod pieces were too fragmented to be counted and identified, we calculated percent

25   composition of the contents from the identifiable material only. These percentages are not true

6

1   representations of the diet composition of House Sparrows nestlings but are proportions of the

2   identified material that remained intact throughout the digestive process. We identified arthropods

3   to the lowest taxonomic level possible. To assess the relative abundance of individual taxa we

4   followed Calver a Wooller (1982). The most abundant arthropods were summed into three

5   categories for statistical analyses. These were Coleoptera adults, Diptera adults, and Larvae

6   (Scarabeidae and Diptera).

7   We measured the frequency (%) with which each taxon occurred in each faecal sample, and we

8   calculated abundance of individual taxa relative to the other taxa detected (%).

9   In contrast to animal remains, abundance of plant parts in samples could not be accurately estimated

10   due to digestion. Therefore we weighed the dry plant parts on analytical balance.

11   *Statistical analyses*

12   We employed common statistical procedures such as ANOVA and linear regression to test

13   hypotheses. For testing age differences in food composition and effects of food composition on body

14   condition we used simple mixed effect models and random factors to rule out repeated measures

15   and pseudo-replications. Group data are presented as mean ± SE.

16   First, we tested the relationship between age categories of the nestlings and total mass of food

17   provided by parents to one nestling. We built up a simple linear mixed effect model containing total

18   mass of food as dependent variable, age categories as factor and nest identity (to filter out repeated

19   measures) nested within years as random factors.

20   Further, we looked for differences in abundance of three major categories of animal diet (i.e.

21   Coleoptera adults, Diptera adults, and Larvae) between two age categories of the nestlings. For each

22   animal diet category, we calculated an average number of individuals of given group of arthropods

23   per nestling in the nest. We tested the effect of nestling age separately on abundance of each of

24   three animal diet categories. Employed linear mixed effect models contained age category as a factor

25   and nest identity nested within years as random factors.

7

1   At older age the body mass estimates were taken from each nestling. Therefore we were able to test

2   whether food composition and total mass of food during the development of nestlings influenced

3   their prefledging body condition. The relationship between food composition and condition was

4   tested separately for younger and older nestlings. We built up linear models with condition as

5   dependent variable and food composition characteristics and year as independent variables/factors.

6   All statistical tests were performed using in R 2.12.0 (R Development Core Team 2010).

7   Results

8   We investigated diet composition and its effect on nestling condition during two breeding seasons in

9   2008 and 2009. Between years, relative timing of breeding was not significantly different (main

10   effects ANOVA, F = 0.148, df = 1, 29, p = 0.704). Within both years, the beginning of egg laying in the

11   first breeding attempt ranged from 19 April to 31 May with median date on 29 April; in the second

12   breeding attempt it ranged from 16 May to 15 June with median date on 3 June.

13   We gathered data on 22 first broods and nine second broods. Mean nestling body condition did not

14   differ between the breeding attempts (F = 0.102, df = 1, 29, p = 0.752), neither between the years (F

15   = 2.730, df = 1, 29, p = 0.110). Consequently we pooled data from both years and breeding attempts

16   for analysis of the nestling condition.

17   Successful nests produced on average 3.45 ± 0.19 fledglings (range = 1–5, n = 31). Relative laying date

18   influenced neither the number of fledglings (r^2 = 0.029, p = 0.363, n = 31), nor mean nestling body

19   condition per brood (r^2 = 0.069, p = 0.152, n = 31).

20

21   Nestling diet

22   Nestling diet consisted of both animal and plant component. Samples containing exclusively plant

23   material were gathered only from nestlings older than nine days (21 samples in 2008, eight samples

24   in 2009). Plants comprised 56.3% of mean sample weight. Identifiable plant remains were mostly

25   represented by Poaceae (approximately 90%) in the form of seeds, fragments of stalks and spikelets

     8

1   of millet *Panicum miliaceum* and wheat *Triticum* spp. Remaining 10% comprised seeds of Poppy

2   *Papaver somniferum* (Papaveraceae), Flixweed *Descurainia sophia* (Brassicaceae), Stinging Nettle

3   *Urtica dioica* (Urticaceae) and unclassified species of Fabaceae. Anorganic material (sand) was

4   regularly present in the samples and in one case we also found a piece of gastropod shell.

5   Faecal sacks contained items belonging to five arthropod orders – Coleoptera, Diptera, Heteroptera,

6   Cicadomorpha, and Araneae (Tab. 1). Faeces composition calculated per nest was dominated by

7   adult beetles, mainly of Scarabeidae. Adult Diptera, mainly muscids and tipulids were second most

8   abundant prey. Larvae of the scarabeids and dipterans were the third most abundant prey type in

9   the nestlings´ diet. Other arthropod taxa accounted for less than 5% of all identifiable animal food

10   objects and therefore were summed under category „other arthropods".

11

12   Effect of nestling age on their diet

13   The total mass of food provided by parents to a particular nestling varied significantly between age

14   categories being higher in older nestlings (t = 4.379, df = 23, p < 0.001). This was mostly due to

15   increase in total mass of plant component (t = 4.379, df = 23, p < 0.001) as total mass of animal

16   component did not differ between age categories (t = 0.682, df = 23, p = 0.502). Mean sample weight

17   at younger age was 41.56 mg and animal component comprised 71.15%. Mean sample weight at

18   older age was 77.5 mg and animal component comprised 32.95%.

19   Further, we looked for differences in abundance of three major categories of animal diet (i.e.

20   Coleoptera adults, Diptera adults, and Larvae) between two age categories of the nestlings. For each

21   animal diet category, we calculated an average number of individuals of given group of arthropods

22   per nestling in the nest. We found no significant differences in abundance of any animal diet

23   category: Coleoptera adults - t = 0.164, df = 23, p = 0.871, Diptera adults - t = -0.527, df = 23, p =

24   0.603, Larvae - t = -0.490, df = 23, p = 0.629.

25

9

1   Prefledging body condition vs. food composition at younger age

2   We found no significant relationship between prefledging condition and total mass of food provided

3   to nestlings by parents at younger age ($F_{(1,20)}$ = 0.772, p = 0.390). Neither the mass of plant nor animal

4   diet component influenced condition estimates ($F_{(1,20)}$ = 0.036, p = 0.851 and $F_{(1,20)}$ = 1.414, p = 0.248,

5   respectively). Effect of year and interactions were non-significant in all cases (all p > 0.065). The

6   abundance of three major categories of animal diet at younger age had no significant effect on

7   prefledging condition: Coleoptera adults - $F_{(1,20)}$ = 0.024, p = 0.878, Diptera adults - $F_{(1,20)}$ = 0.426, p =

8   0.521, Larvae - $F_{(1,20)}$ = 2.311, p = 0.144. Effect of year and interactions were not significant (all p >

9   0.15).

10

11   Prefledging body condition vs. food composition at older age

12   We found a significant relationship between prefledging condition and total mass of food delivered

13   by parents to a particular nestling ($F_{(1,20)}$ = 5.642, p = 0.028). Effect of year and year x total interaction

14   were non-significant and eliminated from the model during its simplification (explanatory power

15   remain unchanged, both p > 0.31). Minimum adequate model thus contained only total mass of food

16   ($F_{(1,20)}$ = 5.737, p = 0.026). We found no evidence for an effect of the mass of plant component on

17   condition ($F_{(1,20)}$ = 0.161, p = 0.693). Effect of year and interaction were non-significant (both p >

18   0.41). However, the mass of animal component in the diet was positively and significantly related to

19   condition ($F_{(1,20)}$ = 7.605, p = 0.012). After model simplification, i.e. removing factor year and year x

20   animal interaction, which caused no significant change in model explanatory power (both p > 0.41),

21   the effect of the mass of animal component on condition remained significant (p = 0.011).

22   The abundance of three major categories of animal diet at older age had no significant effect on

23   condition: Diptera adults - $F_{(1,20)}$ = 0.011, p = 0.918, Larvae - $F_{(1,20)}$ = 0.848, p = 0.368. However, the

24   effect of abundance of Coleoptera adults was marginal ($F_{(1,20)}$ = 3.864, p = 0.063). Effect of year and

25   interactions were not significant (all p > 0.19).

1 Discussion

2 This study indicates the importance of food amount and composition for nestling condition. The

3 nestlings were fed by a variety of animal and plant material. Principal diet composition based on

4 faecal analysis was similar as in other parts of house sparrow´s range. The nestlings consumed mainly

5 beetles and dipterans which accounted for almost 83% of animal food. Coleoptera were the most

6 abundant nestling food type in Poland (Anderson 1984) and Bulgaria (Ivanov 1990), too. Also in Great

7 Britain the beetles belonged to the most important prey species (Vincent 2005). However, the beetle

8 families most often encountered in the diet of nestlings were usually Carabidae and Curculionidae,

9 both on rural and urban sites (Vincent 2005, Anderson 2006). In our study the beetles were

10 represented mainly by scarabeids (*Onthophagus* spp., *Aphodius* spp.) which live in the dung and are

11 therefore abundant on the farmstead. The locality is probably also especially suitable for muscids and

12 tipulids, which were the most abundant dipterans, while elsewhere the most frequent dipterans

13 were hoverflies (Syrphidae) (Anderson 2006). Vincent (2005) mentioned also aphids, spiders and ants

14 among the most common prey species in rural habitats (see also Encke 1965, Mitschke *et al.* 1999).

15 In our study we found spiders only in a quarter of all samples and ants and aphids were not detected

16 at all. The lack of these soft-bodied taxa in the faeces might be caused by their high digestibility,

17 however, Vincent (2005) used the same method for diet analysis.

18 The abundance of three major categories of animal diet, i. e. adults of Coleoptera, adults of Diptera,

19 and Larvae, did not differ during the course of nestlings´ development. This result might arise from

20 the fact, that we have not analysed the diet of the nestlings during the very first days of their life,

21 when the difference in diet composition may be more pronounced. Bigger sample size would also

22 allow for finer-scale comparison without combining several taxa to conjunctive categories. Further,

23 because of methodological limitations we cannot exclude that other components, which are hardly

24 detectable in faeces, differed with age of nestlings. For instance, in some passerines a peak in

25 spiders´ abundance in nestling diet was reported during early stages of their development (Cowie &

11

1   Hinsley 1988, Grundel & Dahlsten 1991, Naef-Daenzer *et al.* 2000). It was shown that parents select

2   for spiders because of high content of taurine, an amino acid affecting behavioural characteristics of

3   nestlings, that could impact fitness (Arnold *et al.* 2007). However, because of relatively low

4   abundance of spiders in the diet of nestlings in our study we could not test the age dependance of

5   this prey in House Sparrows. Finally, it is possible that for development of House Sparrow nestlings

6   the presence of animal protein in general is essential rather than presence of some specific

7   invertebrate species. This assumption is in concordance with the general opportunistic nature of

8   sparrows (Anderson 2006). The parents usually feed their young with the locally and temporary most

9   abundant prey, e. g. coprophagous beetles on the farmstead (this study) or aphids and ants in the

10   cities (Mitschke *et al.* 1999, Vincent 2005). Brodmann & Reyer (1999) previously showed that in

11   Water Pipits *Anthus spinoletta* parents searching for nestling food select prey by its size and

12   catchability rather than nutritional value.

13   The older nestlings get more food than the younger ones. The increase in food amount was caused

14   by higher mass of plant component in older nestlings´ diet, while the mass of animal component

15   remained stable across the two stages of development. Thus the proportion of the animal

16   component decreased with age. Increased amount of food delivered to older nestlings is common in

17   birds and reflects higher nutritional demands of growing offspring (Pinowski 1967, Conrad &

18   Robertson 1993). Increased proportion of vegetable material in the diet of House Sparrow nestlings

19   has been reported also from other localities (Wieloch 1975, Summers-Smith 1988, Anderson 2006).

20   During first days of their life the nestlings are fed almost solely by animal diet (Summers-Smith 1963),

21   because they need essential amino acids from animal proteins for their development (Ricklefs 1983,

22   Arnold et al. 2007). At the age of 16-17 days the nestlings´ preferences switch from insects to seeds

23   and the diet gradually becomes almost entirely vegetable (Mueller 1986). Before fledging the

24   nestlings need to gain fat stores, for which the seeds and grain provide suitable resource. House

25   Sparrow parents supply higher nutritional demands of growing chicks by providing them vegetable

12

1 material, mainly seeds, which represent the most abundant food in the study site. The stable amount

2 of animal component fed to the nestlings suggests that there is probably some upper limit of animal

3 prey that the parents are able to catch. Thus, they offset increasing food demands of young with

4 plant material for several reasons: it is abundant, easy to acquire and it corresponds with increasing

5 nestlings´ preferences for plant food.

6 The total amount of food and mass of animal component in the diet that was fed to nestlings in the

7 prefledging period, but not at younger age, were shown to positively affect their condition. The

8 positive effect of the amount of food on body mass of nestlings and on greater fledging success in

9 House Sparrows was previously shown by Anderson (1977) during the local emergence of 13-year

10 periodical cicadas, which represented a super-abundant food. The effect of body mass on fledging

11 success proved Cleasby *et al.* (2010), who found that House Sparrow nestlings of greater mass on day

12 11 were more likely to recruit. The importance of animal component was stressed by Vincent (2005),

13 who found more plant material within the diet of nestlings that subsequently died than in the diet of

14 those that fledged. The shortage of animal prey causes consumption of unsuitable food and/or

15 starvation, which leads to lower breeding success (Seel 1969, 1970, Vincent 2005).

16 None of the three major components of animal diet did influence the nestlings´ quality except the

17 abundance of beetles in the diet of older nestlings, which tended to increase their condition.

18 However, this effect of the beetles might arise just from the mere fact that this prey group

19 represents most of the animal component in the nestlings´ diet at our study site. Although this effect

20 was marginal it shows the same trend as was found in Great Britain, where the abundance of the

21 beetles in nestlings´ diet also increased their condition (Vincent 2005). In the same British locality the

22 abundance of ants had an opposite effect (Vincent 2005) and reduced nestlings´ body mass was

23 associated with low aphid densities in the vicinity of the nests (Peach *et al.* 2008). Although the ants

24 occurred at our study site, we have not detected any in the samples. Therefore it seems apparent

25 that sparrows select the ants as food for their nestlings only in areas where more suitable prey is

1   scarce. Finally, the absence of aphids in our samples shows that their lack not always leads to

2   malnutrition, because sparrows can replace them with alternative prey.

3   Our study brings the first analysis of House Sparrow nestlings´ diet from the Czech Republic, since

4   there only a study of adult sparrows has been undertaken (Ašmera 1962). Description of the diet of

5   sparrows breeding on a farmstead helped to assess contemporary suitability of rural habitats as

6   sources of nestlings´ food and revealed geographic variation in proportions of different diet

7   components. Our results corroborate the importance of animal prey during the whole nesting period

8   for the quality of nestlings. Hence, we assume that even if probable decline of arthropods was not

9   the main cause of the negative population trend of House Sparrows, it might contribute to low

10   reproductive success and weaken the population productivity.

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12   Acknowledgements

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1 Table 1 Animal food in the diet of house sparrow nestlings assessed using faecal analysis; based on

2 210 faecal sacs containing 362 identifiable animal food objects from 106 nestlings from 31 nests.

3

Taxon	Abundance (%)	Frequency (%)	Mean abundance/nest (%)	SD
Total adult Coleoptera	**61.05**	**94.30**	**61.97**	**26.40**
Total Scarabeidae	34.25	75.76	35.36	27.36
Aphodius	15.19	58.62	14.44	16.18
Ontophagus	0.83	5.17	0.80	3.81
Other Scarabeidae[a]	18.23	70.42	20.12	21.31
Carabidae	11.33	48.28	11.96	15.30
Cerambycidae	4.70	24.14	3.68	7.14
Other Coleoptera[b]	10.77	48.28	10.96	16.73
Total adult Diptera	**21.54**	**74.10**	**21.73**	**19.41**
Tipulidae	9.39	48.28	10.00	12.76
Muscidae	7.73	31.03	7.90	16.83
Other Diptera[c]	4.42	24.14	3.83	7.62
Total Larvae	**8.57**	**39.70**	**8.64**	**13.60**
Larvae of Scarabeidae	6.91	32.76	6.48	11.75
Larvae of Diptera	1.66	6.90	2.15	8.68
Other arthropods	**8.83**	**38.00**	**7.67**	**11.74**
Heteroptera	3.31	18.97	3.24	7.67
Cicadomorpha	1.38	6.90	0.94	3.55
Araneae[d]	4.14	24.14	3.49	7.23

4 [a] The group Other Scarabeidae was represented by *Phyllopertha* and other unidentified genera.

5 [b] The group Other Coleoptera was represented by Oedemeridae, Geotrupidae (*Geotrupes* spp.) and

6 other unidentified families.

7 [c] The group Other Diptera was represented by Faniidae, Culicidae and other unidentified families.

8 [d] The group Araneae was represented by *Pardosa* spp. (Lycosidae), *Tetragnatha* spp.

9 (Tetragnathidae) and other unidentified genera.

20

1   **Figure legends**

2

3   Figure 1

4   Average *per capita* amount of food delivered to 4-6 days [younger age] and 9-11 days [older age] old

5   nestlings of House Sparrow *Passer domesticus*.

6

7   Figure 2

8   Average *per capita* amount of plant [open box] and animal [dashed box] components in the diet of 4-

9   6 days [younger age] and 9-11 days [older age] old nestlings of House Sparrow *Passer domesticus*.

10

11   Figure 3

12   The relationship between average body condition (residuals from the regression of body mass on

13   tarsus length) estimate of 9-11 days old nestlings in nests of House Sparrow *Passer domesticus* and

14   average *per capita* amount of food delivered by parents; p = 0.01.

15

16   Figure 4

17   The relationship between average body condition (residuals from the regression of body mass on

18   tarsus length) estimate of 9-11 days old nestlings in nests of House Sparrow *Passer domesticus* and

19   average *per capita* amount of animal food component delivered by parents; p = 0.011.
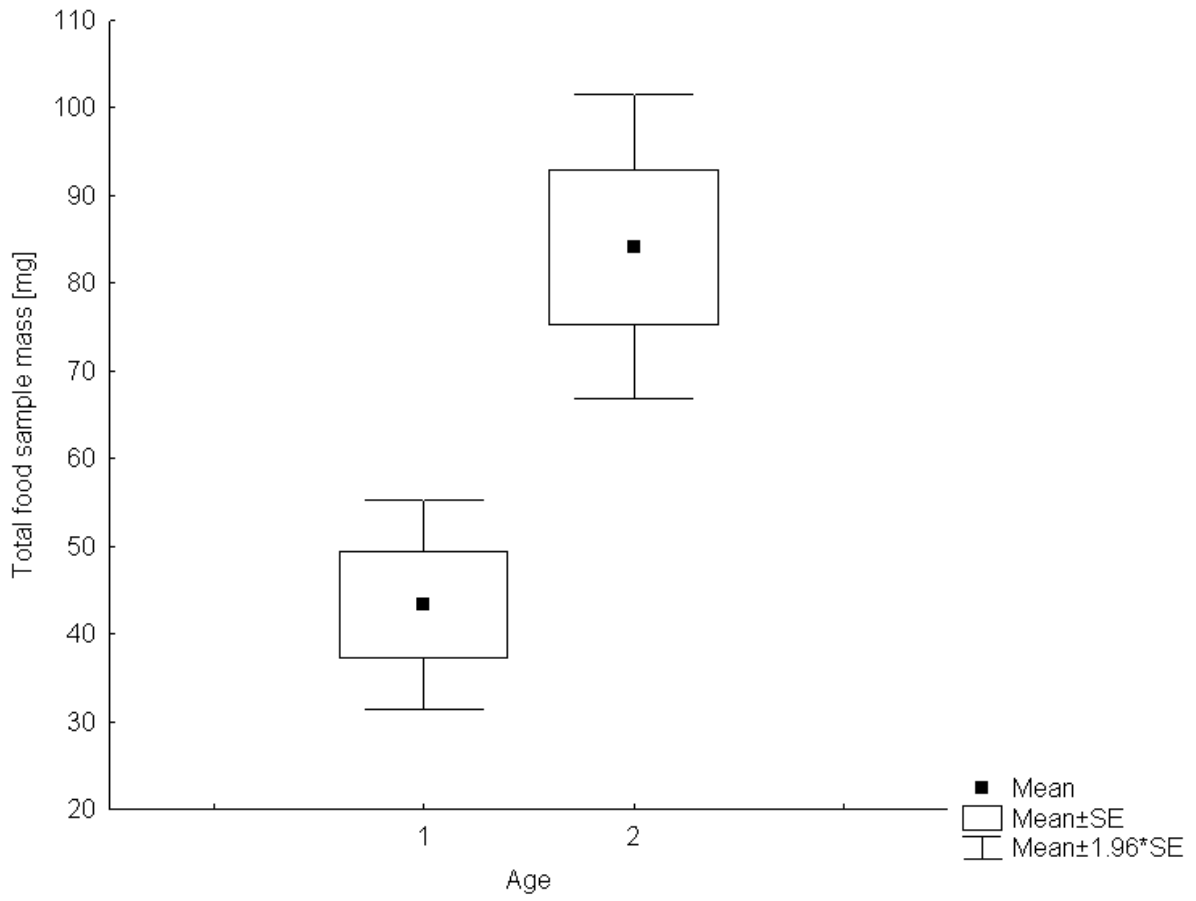
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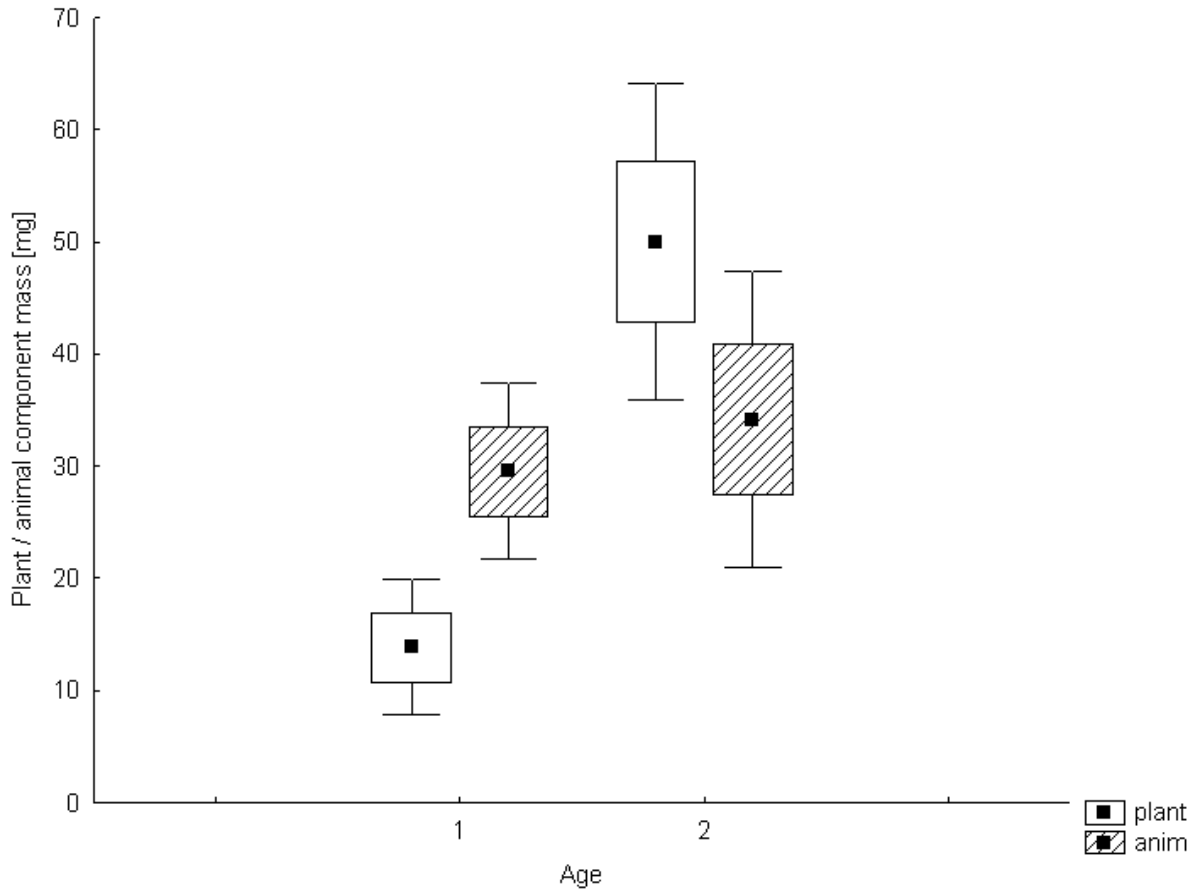
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1   Fig. 1

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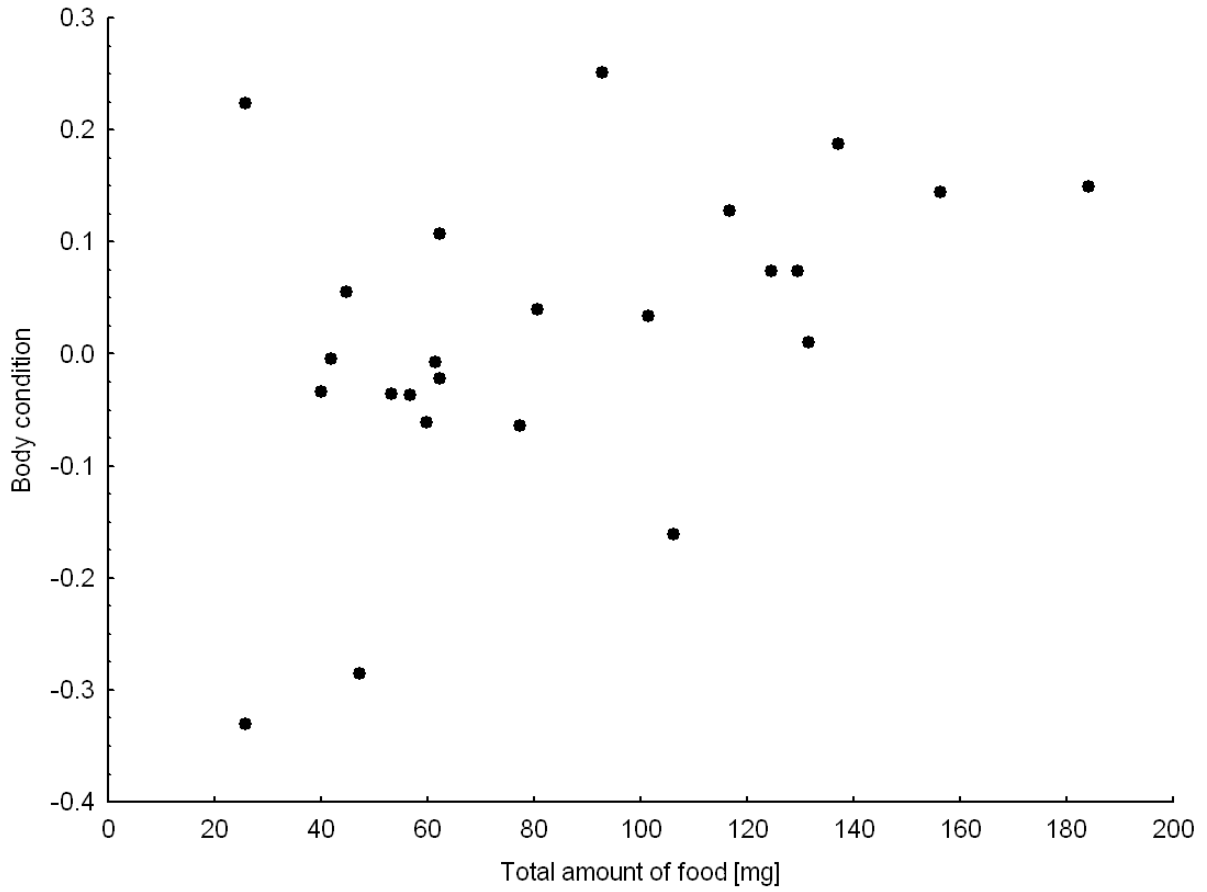10

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1   Fig. 2

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1   Fig. 3

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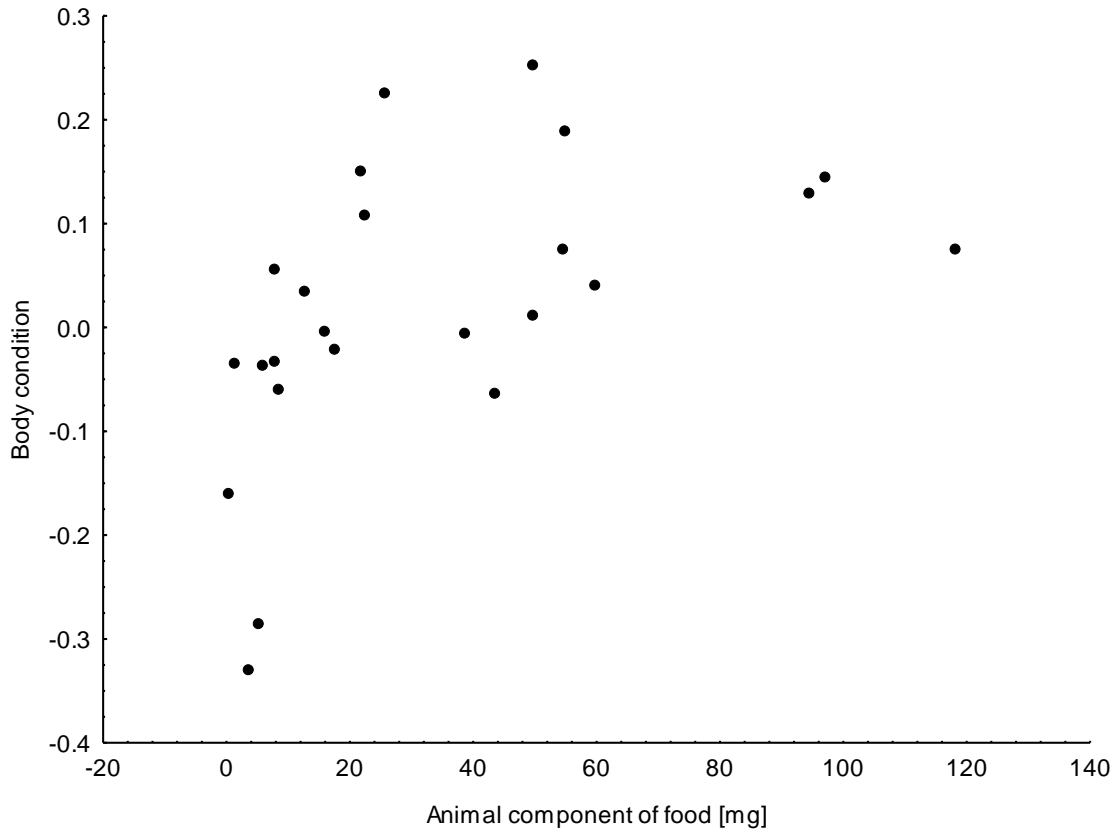10

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1   Fig. 4

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Souhrn poznatků disertační práce

Biparentální péče u vrabce domácího je nerovnoměrně rozdělena mezi oba partnery. Zatímco samice věnovala více času zahřívání mláďat a častěji je krmila, samec více investoval do obrany hnízda. Rodiče přitom nepřizpůsobovali intenzitu obrany hnízda chování svých partnerů, ani parametrům snůšky. Jen samci měli tendenci bránit dřívější snůšky více, jak předpokládá hypotéza hodnoty snůšky. Příspěvek samce ke krmení mláďat pozitivně ovlivňoval jejich hmotnost.

Intenzita obrany hnízda rostla u samců s velikostí melaninového ornamentu, proto předpokládáme, že by ornament mohl sloužit jako signál ochoty samce investovat do obrany hnízda. Potvrzení funkce ornamentu jako signálu rodičovské péče v pohlavním výběru doplňuje závěry recentní metaanalýzy. Naše výsledky ukazují, že velikost ornamentu sice nevypovídá o frekvenci krmení a o čase stráveném zahříváním mláďat, ale koreluje s intenzitou hnízdní obrany, což je složka rodičovské péče, která nebyla metaanalýzou postihnuta. Domníváme se, že tento výsledek není překvapivý, protože korelace velikosti melaninového ornamentu a antipredačního chování je pravděpodobně výsledkem pleiotropního účinku genů řídících melanogenezi, mezi něž patří ovlivnění hladiny testosteronu, který podporuje agresivitu uplatňující se i při obraně hnízda, avšak snižuje intenzitu dalších složek péče, jako jsou právě inkubace nebo krmení mláďat.

Antipredační strategie vrabců není stabilní a mění se s druhem predátora a jeho vzdáleností od hnízda. Obě pohlaví přizpůsobovala intenzitu obrany hnízda míře ohrožení, kterou pro ně daný predátor představoval. Intenzita reakce se snižovala od predátora vajec a mláďat, straky obecné, přes sýčka obecného k nejnižší intenzitě v experimentech s krahujcem obecným. Umístění predátora přímo na hnízdní budku vyvolalo reakci pouze u ohroženého páru, byla-li však atrapa umístěna ve větší vzdálenosti, reagovalo na ni celé hejno tzv. mobingem. Mobující vrabce tak lze považovat spíše za hejno sobeckých rodičů, bránících své vlastní potomky, než skupinu altruistických jedinců, kteří by riskovali v zájmu celé kolonie. V otázce adaptivní hodnoty mobingu jsme proto dospěli k závěru, že toto chování je především součástí rodičovské péče, protože hlavním příjemcem výhod z něj jsou mláďata v hnízdě. Kromě toho je příležitostí pro signalizaci kvality samců, kteří reagovali na predátory s vyšší intenzitou než samice a v závislosti na velikosti ornamentu. Je-li však riziko napadení predátorem vysoké, jako v případě krahujce, stává se mobing pro signalizaci nevhodným, protože na tohoto predátora reagovali samci stejně jako samice, a to opatrně bez ohledu na velikost ornamentu.

Analýzou výkalů mláďat jsme zjistili, že vrabci krmili především brouky a dvoukřídlým hmyzem, a to taxony typickými pro prostředí hospodářského statku. Mláďata, krmená větším množstvím potravy a její živočišné složky a okrajově také větším počtem brouků, dosahovala vyšší kondice. Naše výsledky prokázaly význam živočišné potravy pro reprodukční úspěch vrabců, a podporují tak hypotézu, že jednou z příčin recentního úbytku populací tohoto druhu v Evropě je nedostatek hmyzu v potravě mláďat.

Summary of the thesis

Individual components of parental care are disproportionally distributed among the parents in the House Sparrow. While the female broods the nestlings more often and feeds them more frequently, the male defends the nest more intensely. In an experimental study the parents did not adjust their nest defence intensity to behaviour of their partners, nor to brood parameters. Only males tended to defend the sooner broods more intensely, which is in concordance with the „brood value hypothesis". Male contribution to nestling feeding affected their body mass.

Male nest defence intensity increased with the size of their melanin ornament. Thus, we assume that the ornament could signal male investment in this component of parental care, while it does not correlate with feeding frequency and time spent by incubation. This output is probably caused by pleiotropic effect of genes regulating melanogenesis, affecting e. g. testosterone plasma level, which is associated with increased agression and lower intensity of other components of parental care as nestling provisioning or incubation.

We have also aked the question whether the anti-predator strategy in House Sparrow is stable or depends on the type of the predator. In experiments with three different predator species we showed, that sparrows adjust their nest defence intensity to the potential threat, which individual predator poses. The most risky reactions were performed in experiments with the Magpie *Pica pica.* The intensity of nest defence further decreased in reaction to the Little Owl *Athene noctua* and was lowest to Sparrowhawk *Accipiter nisus*. We also stressed the importance of predator´s distance from the nest. While placed directly on the nest box the predator induced the nest defence only in the threatened pair. However, placing the predator farther from the colony, representing situation, when all nests were threatened, induced mobbing in all colony members. We assume, that the mobbers were rather a group of selfish parents defending their own progeny, than a social group of altruists putting themselves into risk of predation for the benefit of whole colony. Regarding the adaptive value of mobbing we concluded that it is mainly a part of parental care, because the main beneficiaries of this behaviour are the offspring. Further, mobbing is probably an opportunity for signalling, as males mobbed the predator more intensely than females and with respect to their ornament size. However, if the risk of injury is high, mobbing probably becomes not more suitable for signalling as was shown in experiments with Sparrowhawk, when all males reacted with the same low intensity as females and irrespective of their ornament size.

Results of faecal analysis showed that nestlings were fed mainly by beetles and dipterans. The nestling condition was affected by the mass of food and its animal component and marginally also by the amount of the beetles in the diet. Thus, we showed the importance of the animal prey for the reproductive success, which supports the hypothesis, that the shortage of invertebrates in the nestlings´ diet contribute to the recent population decline of House Sparrows in Europe.