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Jak t'uhýk obecný (*Lanius collurio*) rozpoznává nepřátele

Disertační práce

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■ Annotation

This study investigates two questions about anti-predator behaviour of the red-backed shrike. 1) Is the red-backed shrike able to assess the differing dangers represented by various types or species of predators? 2) How does the red-backed shrike recognize the predator? We found, that the red-backed shrike (*Lanius collurio*) adjusts its anti-predator behaviour by assessing the potential threat to themselves from different predator species and by assessing the chance of a successful attack. Further, we found that the presence of general raptor salient features is absolutely necessary for proper categorisation of the intruder as a predator, whereas the natural species-specific colouration in itself is an insufficient cue.

■ Prohlášení

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Michal Němec

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Vysoce převládly ty pozitivní.*

*Děkuji svým rodičům a babičce za celoživotní podporu.
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Kapitola 1

Úvod do problematiky
antipredačního chování a
rozpoznávání predátorů ptáky

Michal Němec, disertační práce

Úvod

V době hnízdění vynakládají ptačí rodiče maximální úsilí na úspěšné předání genů do další generace. Proces odchovu mláďat však může být kdykoli ve svém průběhu narušen, či zcela ukončen mnoha negativními vlivy. Těmito vlivy mohou být například nepřízeň počasí, parazité anebo predace. Právě predace je velmi častou příčinou totálního krachu hnízdění (Martin 1993; Roos 2002; Roos a Pärt 2004). U ťuhýka obecného se podílí až na 46,2 % celkových ztrát (Tryjanowski et al. 2000). Ptáci ovšem mohou predaci různým způsobem čelit – ať už nepřímo, například výběrem vhodného místa k hnízdění (Rauter et al. 2002; Roos a Pärt 2004; Müller, et al. 2004), tak přímo při nastalém ohrožení.

Aktivní obrana potomstva

Prakticky každé zvíře, které ve své blízkosti objeví a identifikuje predátora, se snaží uniknout nebo ubránit (Krebs a Davies 1993). Útěk od predátora je pro pohyblivé živočichy ve většině případů nejspolehlivějším řešením situace (Caro 2005). Takovou možnost však nemá ptačí potomstvo na hnízdě (vejce či altriciální mláďata), které až na výjimky – např. vyskočení z hnízda (Redondo a Carranza 1989; Goławski a Meissner 2007), mířená defekace (Tillmann 2009) či jiný zápach (Hagelin a Jones 2007), nebo batesovské mimikry (Londoño et al. 2015) – nedisponuje žádnými obrannými či únikovými prostředky. Efektivní antipredační chování hnízdících ptáků je tedy jedním z nezbytných předpokladů pro přežití vajec a altriciálních mláďat (Redondo 1989). Každé chování, které vede k redukci predace hnízd (pokud jej ovšem rodiče přežijí) zvyšuje fitness jedince (Knight a Temple 1986). Nebezpečí hrozící ze strany predátorů však soustavně ovlivňuje téměř veškeré jednání potenciální kořisti, od potravního chování až po výběr partnera, protože kořist přizpůsobuje své chování tak, aby snížila riziko predace (Lima a Dill 1990).

Primární snahou většiny ptáků je, aby predátor potomstvo vůbec neobjevil. Tato snaha však nebývá sama o sobě dostačující. Jakober a Stauber (2002) uvádějí, že pouze 16 % hnízd ťuhýka obecného je důkladně ukrytých, zatímco 47 % hnízd je z okolí snadno viditelných. Poměr špatně ukrytých hnízd se zvyšuje při náhradním hnízdění. Autoři se domnívají, že ťuhýci neukrývají svá hnízda lépe většinou kvůli prostému nedostatku

vhodnějších hnízdních keřů. V situaci, kdy se predátor pohybuje v dosahu potomstva, ale o své potenciální kořisti neví, mohou rodiče stále ještě čekat a doufat, že jej neobjeví. Pokud však predátor hnízdo najde, zbývá dospělým ptákům poslední a jediná možnost jak zachránit potomstvo – pokusit se predátora zahnat či jinak odradit od útoku.

Taková forma antipredačního chování, při které se potenciální kořist predátorovi snaží různými způsoby znepříjemnit pobyt ve svém teritoriu, bývá označována termínem mobbing – obtěžování (Hartley 1950). Vyskytuje se především u ptáků a savců při obraně mláďat a jeho účelem je odradit, zastrašit nebo silou vyhnat predátora z vlastního teritoria (pro review viz Caro 2005). Kromě odpuzení predátora funguje mobbing také jako varování konspicivních (především mláďat a partnera), eventuálně heterospicivních jedinců (Curio et al. 1978; Templeton a Greene 2007).

Podle razance s jakou obránce proti predátorovi zasahuje lze mobbing dělit na pasivní a aktivní (Shields 1984; Winkler 1994). Mezi pasivní mobbing můžeme u ptáků počítat některé varovné hlasové projevy – alarm calls (Vieth et al. 1980; Naguib et al. 2009), výstražné postoje, jako je čepýření, zvednutí chocholky, podřepování, podupávání, vzpřímený postoj, nápadné pohyby křídel a ocasu apod. (Ash 1970; Kumar 2003; Griffin et al. 2005), a dále také shlukování do hejn a kroužení ve větší vzdálenosti od predátora (Shields 1984; Conover 1987). Aktivním mobbingem ptáků se většinou rozumí přelety kolem predátora nebo jeho napadání formou náletů, při nichž se může obránce s predátorem i fyzicky střetnout (Ash 1970; Curio 1975; Kruuk 1976; Shields 1984; McLean et al. 1986). Na význam aktivní obrany hnízd bylo poukázáno v mnoha experimentálních studiích, kde bylo ověřeno, že aktivnější/agresivnější rodiče byli při hnízdění úspěšnější (např. Knight a Temple 1986; Remeš 2005; konkrétně u ťuhýka obecného (Tryjanowski a Goławski 2004; Müller, et al. 2004; Goławski a Mitrus 2008).

Faktory ovlivňující formu a intenzitu aktivní obrany potomstva

Mobbing je považován za energeticky velmi nákladnou aktivitu a představuje tedy pro obránce značnou investici (Curio 1978; Greig-Smith 1980; Dale et al. 1996; Scheuerlein et al. 2001). Predátor je obvykle větší a těžší než kořist a jeho zahnání je tudíž velmi náročné. Kromě toho mobbing bránícího ptáka připravuje o čas, který by mohl věnovat sběru potravy a další péči o mláďata (Dale et al. 1996). Výsledek střetu je přitom nejistý. Mobbing je velmi nebezpečnou aktivitou, při které obránce riskuje zranění či smrt (Dale et al. 1996; Scheuerlein et al. 2001). Smrt obránce by pak byla fatální i pro mláďata, neboť by se o ně neměl kdo starat. Bránící jedinec by tedy měl před zásahem vážit míru nákladů a rizik vůči hodnotě možného zisku.

Poměr mezi náklady a ziskem při aktivní obraně hnízda byl mnohokrát studován. Nejdůležitějším faktorem ovlivňujícím formu a intenzitu mobbingu je pravděpodobně typ vetřelce. Povaha antipredačního chování je pochopitelně zásadně ovlivněna tím, proti jakému nepříteli je namířena – zda jde o hnízdního parazita, predátora mláďat či dospělců apod. Velmi často záleží na tom, zda nebezpečí přichází ze země nebo ze vzduchu (viz následující kapitola). Významná je rovněž vzdálenost predátora od hnízda (Greig-Smith 1980; Klump a Curio 1983; Regelmann a Curio 1983; Hogstad 2004; Kleindorfer et al. 2005).

Ve většině studií bylo potvrzeno, že ptáci vynakládají na zahnání predátora tím větší úsilí, čím vyšší je hodnota obsahu hnízda. Se zvyšujícím se počtem a/nebo stářím mláďat se tedy zvyšuje i intenzita mobbingu (Dale et al. 1996; Tryjanowski a Goławski 2004; Goławski a Mitrus 2008; Antczak et al. 2009). Například u poštolky obecné (*Falco tinnunculus*) či sýce rousného (*Aegolius funereus*) však nebyla souvislost mezi intenzitou obrany a velikostí snůšky prokázána (Hakkarainen a Korpimäki 1994; Carrillo a Aparicio 2001). Množství potomstva má ovšem vliv také na kondici rodičů a tedy i na množství sil, které jsou schopni do obrany investovat. Velký počet mláďat proto může za určitých okolností intenzitu mobbingu naopak snížit (Greig-Smith 1980).

V průběhu hnízdní sezóny se postupně zvyšuje intenzita mobbingu, neboť s blížícím se koncem období příhodného k hnízdění klesá ptákům

šance, že by byli schopni po ztrátě aktuálního potomstva založit a vyvést potomstvo nové (Regelmann a Curio 1983; Rytkönen et al. 1993; Carrillo a Aparicio 2001).

Na intenzitu mobbingu má u většiny ptáků velký vliv pohlaví (Knight a Temple 1986b; Rytkönen et al. 1993; Dale et al. 1996; Kis et al. 2000; Carrillo a Aparicio 2001). Často se přitom vedoucí role během hnízdní sezóny obrátí. Zpočátku do obrany vkládá více úsilí samice, protože investovala do potomstva více, ale v období krmení mláďat, pokud se jej účastní, začne být aktivnější samec (Rytkönen et al. 1993). Například u bramborníčka černohlavého (*Saxicola torquata*), ani u čížka žlutého (*Carduelis tristis*) ale rozdíl nalezen nebyl, a to ani ve fázi inkubace, ani ve fázi krmení mláďat (Greig-Smith 1980; Knight a Temple 1986b).

Další významnou okolností je také zkušenost mobbujícího ptáka (Csermely et al. 2006; Čapek et al. 2010; Burtka a Grindstaff 2013). Na rozdíl od jedinců pocházejících z přírody nebyly naivní sýkory koňadry (*Parus major*) schopny poznat nebezpečného krahujce obecného, *Accipiter nisus* (Kullberg a Lind 2002). Curio (1978) soudí, že se mladí ptáci učí rozpoznávat a reagovat na predátory od svých rodičů. Naopak Veen et al. (2000) poukazují, že populace rákosníků seychelských (*Acrocephalus sechellensis*), která nemá zkušenost s predátorem vajec snovatcem seychelským (*Foudia sechellarum*), na něj přesto reaguje stejně jako jiná populace téhož druhu, která s ním zkušenost má. Je také známo, že úspěšné předchozí pokusy obránců o mobbing mohou vést k následné silnější reakci a vice versa (Greig-Smith 1980; Knight a Temple 1986b; Clode et al. 2000).

Faktorů ovlivňujících povahu a intenzitu mobbingu je ještě mnohem více. I při zevrubném výzkumu, který hodnotil vliv 16 proměnných na povahu antipredačního chování, zůstalo 43 % variability nevysvětlených (Regelmann a Curio 1983). Stejný výzkum navíc odhalil, že některé faktory (konkrétně stáří a počet mláďat a pohlaví rodiče) působí aditivně.

Variabilita v aktivní obraně proti různým typům predátorů

Ptačí vejce a mláďata ohrožuje mnoho skupin predátorů (z ptáků například draví ptáci a krkavcovití, dále šelmy a jiní savci, také hadi), které se liší loveckými technikami a schopnostmi (vzdušný vs. pozemní predátor apod.). Rovněž pro rodiče představují různí predátoři různý typ a míru rizika. Při aktivní obraně by měli rodiče všechny tyto aspekty zohlednit (Altmann 1956; McLean a Rhodes 1991).

Mnohokrát bylo prokázáno, že ptáci rozpoznávají predátory od neškodných zvířat nebo dalších indiferentních objektů (pro review viz Caro 2005). Například lejscí černohlaví (*Ficedula hypoleuca*) reagovali odlišně na ťuhýka obecného a mandelíka hajního, *Coracias garullus* (Curio 1975), kuřata (*Gallus gallus*) rozlišovala mezi poštolkou a kivim, *Apteryx* spp. (Scaife 1976). Straky reagují jinak na krkavcovité a jinak na dravce (Buitron 1983). Strnádky růzovozobé (*Spizella pusilla*) jednoznačně odlišovaly predátora hnízd, sojku chocholatou (*Cyanocitta cristata*), od neškodné kontroly, strnadce liščího (*Passerina iliaca*), během inkubace i odchovu mláďat (Burhans 2001). Ťuhýci obecní rozlišovali mezi dravci a neškodným holubem (Strnad et al. 2012). Sýkory koňadry byly schopny rozlišit dravce od křepelky (Kullberg a Lind 2002), resp. od holuba a drozda (Tvardíková a Fuchs 2012).

Opakovaně byly zjištěny také rozdíly v reakcích ptáků na predátory dospělců a predátory hnízd. Břehouši černoocasí (*Limosa limosa*) a čejky chocholaté (*Vanellus vanellus*) napadali většinu vran černých (*Corvus corone*) a volavek popelavých (*Ardea cinerea*). Poštolky však byly napadány jen pokud hnízdící ptáci pečovali o mláďata. Pokud měli teprve vejce, poštolky tolerovali (Green et al. 1990). Dale et al. (1996) instalovali během nepřítomnosti obou rodičů lejskům černohlavým k hnízdu vycpaného krahujce obecného, strakapouda velkého (*Dendrocopos major*) a drozda kvíčalu (*Turdus pilaris*). Lejscí nikdy nezaútočili na krahujce, obtěžovali, či přímo útočili na datla, ale nikdy nevykazovali známky vzrušení v přítomnosti drozda. Autoři dále měřili čas, který uplynul od doby, kdy rodiče vyletěli z hnízda do doby jejich návratu. Zjistili, že ač byl u krahujce čas vždy delší než u drozda, významně záleželo také na věku mláďat a jejich kondici. Arnold (2000) instalovala poblíž hnízd kooperativně hnízdící

květosavky křiklavé (*Manorina melanocephala*), která žije v stabilních skupinách společně mobbujících jiné ptačí druhy, jednu ze tří vycpanin: holuba amboinského (*Macropygia amboinensis*), vránu australskou (*Corvus orru*) či raroha proměnlivého (*Falco berigora*). Proti vráně vystupovali jen odvážnější jedinci, na holuba a raroha se shromáždilo obránců více. Ve studii Ghalambor a Martin (2000) krátkověcí brhlíci běloprsí (*Sitta carolinensis*) i dlouhověcí brhlíci američtí (*Sitta canadensis*) rozpoznávali krahujce amerického (*Accipiter striatus*) jako predátora dospělců a střízlíka domácího (*Troglodytes aedon*) coby predátora vajec. Krátkověcí brhlíci ale vykazovali silnější reakci na predátora vajec, zatímco dlouhověcí brhlíci reagovali silněji na predátora dospělců. Autoři to vysvětlují jejich rozdílnou ochotou riskovat smrt svou, či svého potomstva, a dávají to do souvislosti s jejich rozdílnou mírou investic do stávajícího potomstva a do svého budoucího přežití. Amat a Masero (2004) sledovali, jak inkubující kulíci mořští (*Charadrius alexandrinus*) reagují na ptáky létající cca 50 m od jejich hnízd, především na dravce (*Falco tinnunculus*, *F. peregrinus*, *Milvus migrans*, *Hieraaetus pennatus*, *Circus pygargus*, *C. aeruginosus*), ale i na potenciálního predátora hnízd, (rybáka bahenního, *Gelochelidon nilotica*). Objevil-li se některý z dravců, dospělí kulíci ulétali pryč, zatímco rybáky občas pronásledovali nebo situaci kolem svých hnízd alespoň znedaleka pozorovali.

Některé práce popsaly, že hnízdící ptáci rozlišují mezi hnízdními predátory a hnízdními parazity. Neudorf a Sealy (1992), například, sledovali reakce vlvovce červenokřídleho (*Agelaius phoeniceus*), drozdce černohlavého (*Dumetella carolinensis*), trupiála baltimorského (*Icterus galbula*) a brkoslava amerického (*Bombycilla cedrorum*) na atrapu hnízdního parazita, vlvovce hnědohlavého (*Molothus ater*), predátora hnízd, vlvovce nachového (*Quiscalus quiscula*) a neškodného strnadce liščího (*Passerella iliaca*). Zjistili, že vlvovec červenokřídly, který jako jediný z uvedené čtveřice ptáků vejce vlvovce hnědohlavého neodmítá, proti němu reagoval agresivně. Naopak zbylé tři hostitelské druhy, které vejce vlvovce hnědohlavého nepřijímají, na něj reagovaly neagresivně, stejně jako na neškodného strnadce. Všechny testované druhy, s výjimkou brkoslava, který nebyl agresivní k žádné atrapě zřejmě kvůli dobrému ukrytí svých hnízd, považovaly vlvovce nachového za predátora potomstva a útočili na něj. Autoři proto soudí, že minimálně tyto tři agresivní

hostitelské druhy dokážou rozlišit specifické problémy, které přináší ten který vetřelec. Také lesňáčci žlutí (*Dendroica petechia*) rozlišují mezi nebezpečím plynoucím z hnízdního parazitismu a predace jejich potomstva. Na vlhovce hnědohlavého reagovali intenzivněji během fáze inkubace vajec, naopak na vlhovce nachového během fáze péče o mláďata (Gill a Sealy 1996).

Často je však obtížné dokázat, že obránce vnímá hnízdního parazita jinak než predátora. Intenzita varování strnádky růžovozobé byla silnější na predátora, sojku chocholatou, než na parazita, vlhovce hnědohlavého. Jelikož však strnádky mobbovaly vlhovce s nezměněnou intenzitou i během stádia krmení mláďat, kdy by jim vlhovec již neměl uškodit, nelze s jistotou konstatovat, že jej strnádky vnímaly jako hnízdního parazita (Burhans 2001). K týmž závěrům došli při testování týchž vetřelců (D’Orazio a Neudorf 2008). Střízlík karolinský (*Thryothorus ludovicianus*) strávil více času mobbingem na sojku chocholatou než na hnízdního parazita vlhovce hnědohlavého. Intenzita varování proti oběma vetřelcům ale zůstávala v době inkubace vajec a krmení mláďat stejná. Olendorf a Robinson (2008) nenalezli žádný rozdíl v míře varování, náletů, nejbližším přiblížení ani počtu obránců tyranovce zelenavého (*Empidonax virescens*) proti predátoru hnízd, sojce chocholaté a hnízdnímu parazitovi, vlhovci hnědohlavému.

Testovala se rovněž schopnost ptáků rozlišovat pozemní a vzdušné predátory. Tenkozobec americký (*Recurvirostra americana*) a píslila americká (*Himantopus mexicanus*) reagovali na atrapy savčích predátorů relativně slabě, většinou ve formě kroužení ve vzduchu a pozemního „distraktion display“ (tj. upoutávání pozornosti na sebe např. předstíráním zranění). Mobbování byli savci pouze zřídka. Ptačí predátoři byli naopak mobbování často a obránci se v jejich přítomnosti pohybovali především ve vzduchu, málokdy po zemi (Sordahl 2009). Kleindorfer et al. (2005) zjistili, že rákosníci tamaryškoví (*Acrocephalus melanopogon*), obecní (*A. scirpaceus*) a velcí (*A. arundinaceus*) přizpůsobují své antipredační chování tomu, zda jejich potomstvo ohrožuje pozemní (had, lasice hranostaj, *Mustela erminea*), nebo vzdušný predátor, moták (*Circus aeruginosus*), přičemž velmi záleželo také na tom, v jaké vzdálenosti (1 m nebo 5 m) se tento predátor nachází. Ptáci s hnízdy nízko nad zemí je bránili intenzivněji proti atrapám pozemních predátorů, zatímco ptáci s hnízdy výše nad zemí intenzivněji mobbovali vycpaného motáka. Palleroni et al. (2005) otestovali

vliv velikosti predátora na antipredační chování domácích kurů (*Gallus gallus*) pomocí tří druhů živých dravců – malého krahujce amerického (23 cm), středního jestřába Cooperova (*Accipiter cooperii*, 51 cm) a velkého jestřába lesního (*A. gentilis*, 62 cm). Tito dravci mají stejné tělesné proporce, zbarvení a způsob lovu. Velký dravec je hrozbou pro dospělé, zatímco malý dravec představuje smrtelné riziko pro mláďata. Dravci byli cvičeni, aby doletěli z ruky na strom a poté zpět na ruku. Testovaný pár dospělých kurů s kuřaty byl umístěn do venkovního výběhu. Při přeletu malého dravce měli dospělí kuři nakrčený nebo vzpřímený postoj a sledovali jej, zatímco při přeletu velkého se skrčili a ustupovali pryč.

Jako nejlepší důkaz schopnosti ptáků rozlišit různé typy predátorů posloužila odlišnost varovných hlasů, které kořist za přítomnosti toho kterého predátora vydává, aby varovala mláďata či partnera (Magrath et al. 2010). Intenzita hrozícího nebezpečí může být vyjádřena buď kvantitativní, nebo kvalitativní změnou používaných hlasů (Evans et al. 1993). Japonské sýkory koňadry (*Parus major minor*) reagují různým varovným hlasem na atrapy vrány hrubozobé (*Corvus macrorhynchos*) a užovky japonské, *Elaphe climacophora* (Suzuki 2012). Variabilita varovných hlasů se odráží i v tom, jak na ně reagují mláďata. Kleindorfer et al. (1996) popisují, jak mláďata rákosníka tamaryškového reagují různým způsobem na různé typy varování rodičů. Před vzdušným predátorem zůstávají skrčená ve hnízdě, zatímco před pozemním predátorem skáčou z hnízda ven. Podobně reagují na dva akusticky odlišné varovné hlasy rodičů i mláďata sýkory koňadry japonské. Při varování před vránou hrubozobou, která je může ohrozit venku, se krčí v hnízdní dutině, zatímco při varování před užovkou japonskou, která může do hnízdní dutiny proniknout, mláďata dutinu opouštějí (Toshitaka 2011). Timálie (*Turdoides squamiceps*) sice nemá pro pozemní (kočka) a vzdušné (sova) predátory kvalitativně odlišné zvuky, ale dokáže je rozlišit prostým počtem opakování varovného "cvik". Jednoduché provedení nese informaci o pozemním predátorovi, zatímco vícenásobné opakování kóduje vzdušného predátora (Naguib et al. 2009). Také střízlík karolinský vydává proti přeletujícímu dravci více vysokofrekvenčních hlasů než k pozemnímu predátorovi (Morton a Shalter 1977). U orebice rudé (*Alecrotis rufa*) je četnost varování vzhledem k typu predátora přesně opačná – proti pozemnímu predátorovi

obsahuje hlas větší počet slabik než proti vzdušnému a liší se od sebe také ve frekvenci (Binazzi et al. 2010).

Velmi sofistikovaný je systém mobbingových hlasů sýkor černošedých (*Poecile atricapillus*), jenž umožňuje vyjádřit mnoho podrobností o nebezpečnosti predátora (Templeton et al. 2005). Tyto sýkory disponují dvěma hlavními varovnými hlasy, na které reagují nejen konspecifičtí, ale i mnozí heterokonspecifičtí příjemci. Zatímco tiché “seet” vydávají, když spatří letícího dravce, a příjemci na něj reagují únikem do krytu, hlasitý širokopásmový signál “chick-a-dee” slouží k varování před sedícími dravci či sovami a pobízí příjemce ke kolektivnímu mobbingu proti nim (Ficken et al. 1978; Smith 1991; Templeton a Greene 2007). “Chick-a-dee” je tvořen slabikami, jejichž vzájemný poměr a důraz může být modifikován například podle velikosti predátora. Kompozice jednotlivých slabik a jejich zastoupení zřejmě souvisí i s pocitem strachu, který ptáci pociťují. Pokud se cítí ohroženi, zvyšují podíl prvních slabik “chick” na úkor těch následujících. Protažení poslední slabiky se naopak objevuje při mobbingu. Prostým zvýšením počtu volání “chick-a-dee” je kódována míra bezprostřednosti hrozícího nebezpečí daná jeho vzdáleností (Baker a Becker 2002).

Je ovšem možné, že ptáci nerozlišují přímo typ či druh predátora, ale ovlivňuje je spíše naléhavost nebezpečí a kontext, ve kterém se s ním setkávají (Evans et al. 1993; Leavesley a Magrath 2005; Binazzi et al. 2010). Evans et al. (1993) zjistili, že varování před vzdušným predátorem vydávají kuři domácí i na savce prezentované ve vzduchu a naopak, že varování před pozemním nebezpečím se objevovalo proti vzdušným predátorům v úrovni země. Kleindorfer et al. (2005) popsali, že obrana hnízd tří druhů rákosníků (r. tamaryškový, r. obecný a r. velký) je silnější u hnízd nízko nad zemí. U všech druhů se projevuje navíc interakce mezi typem predátora a výškou hnízda.

Variabilita v aktivní obraně proti různým druhům predátorů téhož typu

Méně známé už jsou rozdíly v reakcích kořisti na predátory téhož typu, lišící se jen detaily potravní ekologie, například preferovanou složkou potravy. Příčina tkví nejspíš v tom, že takové rozdíly jsou většinou malé. Zřejmě nejčastěji se projevují v míře riskování. Regelmann a Curio (1983) popsali, že sýkora koňadra se při obraně hnízda přibližuje na různou vzdálenost ke

krahujci obecnému, puščíkovi obecnému (*Strix aluco*) a kulíškovci perlovému (*Glaucidium perlatum*) v závislosti na tom, zda se jedná o denního či nočního lovce a (v případě obou sov) zda preferuje savce či ptáky. Čejky (*Vanellus* sp.) uplatňují různou varovnou vokalizaci proti podobným vzdušným predátorům, neboť varují častěji proti motákům (*Circus* sp.) než proti orlům jasnohlasým, *Haliaeetus vocifer* (Walters 1990). Poštočky obecné útočily více na jim známou vránu šedou (*Corvus cornix*), než na neznámého krkavce velkého, *Corvus corax* (Csermely et al. 2006).

Přesvědčivý experiment provedli Tvardíková a Fuchs (2011), když v zimním období nabídli volně žijícím sýkorám dvě identická krmítka nedaleko sebe a instalovali u nich různé predátory. Sýkory byly zvyklé navštěvovat obě krmítka, a tak mohly volit místo podle aktuální bezpečnostní situace. Pokud byla k prvnímu krmítku instalována atrapa poštolky obecné nebo krahujce obecného a druhé bylo bez predátorů, sýkory navštěvovaly výhradně druhé krmítko. V případě, že byla u prvního krmítka vystavena poštolka a u druhého krahujec, bylo více navštěvováno první krmítko. Sýkory tedy vždy volily „bezpečnější krmítko“ a byly schopné rozlišit dva podobné predátory, z nichž krahujce vnímali jako nebezpečnějšího.

Malý počet prací testujících schopnost ptáků rozlišit různé druhy predátorů téhož typu nás přivedl k zájmu o tuto problematiku. Náš výzkum začal porovnáním reakce hnízdících ťuhýků obecných na pět vetřelců nacházejících se v těsné blízkosti jejich hnízd: dva predátory dospělců (krahujce obecného a poštolku obecnou), dva predátory hnízdního obsahu (sojku obecnou, *Garrulus glandarius* a straku obecnou, *Pica pica*) a neškodnou kontrolu, holuba domácího, *Columba livia* (Strnad et al. 2012). Ťuhýci mobbovali tři ze čtyř predátorů (krahujce, poštolku a sojku) stejně intenzivně, lišila se však jejich ochota riskovat. Ta klesala od sojky, přes poštolku, po krahujce. Z toho je zřejmé, že ťuhýci rozlišovali krahujce, který je specializovaným lovcem drobných pěvců (Opdam 1978; Kropil a Sládek 1990; Zawadzka a Zawadzki 2001; Bujoczek a Ciach 2009), včetně ťuhýků obecných (Glutz v. Blotzheim et al. 1971) od méně nebezpečné poštolky, která loví především malé savce (Korpimaeki 1986; Van Zyl 1994; Salata-Pilacinska a Tryjanowski 1998). Oba druhy se přitom liší jen zbarvením – velikost i tvar těla, stejně jako přítomnost typických dravčích znaků (např. zahnutý zobák), je totožná (Cramp et al. 1994).

Nejpřekvapivějším výsledkem však byl diametrální rozdíl v reakci ťuhýků na dva ekologicky podobné predátory hnízd – sojku a straku. Zatímco sojka byla intenzivně napadána, chování vůči strace bylo zcela pasivní. To je zvláštní, neboť jak sojka, tak straka jsou všeobecně známé pleněním ptačích hnízd (Groom 1993; Roos a Pärt 2004; Chiron a Julliard 2007). Vysvětlení tohoto jevu se nabízelo trojí. Buď ťuhýci straku nepovažují za nebezpečnou a pasivita je tedy projevem nezájmu, nebo jí naopak považují za velmi nebezpečnou a bojí se jí, popřípadě jde o speciální strategii vedenou snahou neupozorňovat na existenci hnízda. Ta by mohla být účinnější než mobbing, pokud by platil předpoklad, že straky jsou schopny spojit si přítomnost mobbujících ptáků s přítomností hnízda a později se do místa střetu nepozorovaně vracet.

Toto riziko experimentálně doložili (Krama a Krams 2005), kteří zjistili, že varovné hlasy proti jednomu predátorovi může odposlechnout i jiný predátor, který je následně schopen zaměřit svou pozornost na místo konfliktu. Autoři pracovali s umělými hnízdy v budkách, v nichž byla křepelčí vejce. U poloviny budek 1–2 hodiny před západem slunce třikrát přehráli nahrávku varovné vokalizace lejska černohlavého. Tyto budky pak byly v noci signifikantně častěji predovány kunou lesní (*Martes martes*). Podobným pokusem (Krams et al. 2007) ukázali, že hnízdní budky, u nichž byla před soumrakem přehrávána 15 minutová nahrávka varovných hlasů lejska černohlavého, byly v noci kunou vypredovány častěji, než budky, u nichž byla nahrávka přehrávána jen 2 minuty.

Pokusili jsme se rozdíly v chování ťuhýků vůči strace a sojce objasnit porovnáním reakcí ťuhýků na další krkavcovité (Němec a Fuchs 2014). Pro tento experiment se nám podařilo sehnat vycpaniny všech našich zástupců krkavcovitých, kromě kavky. Porovnávali jsme tedy reakce na sojku obecnou, ořešníka (*Nucifraga caryocatactes*), havrana (*Corvus frugilegus*), vránu (*Corvus corone*) a krkavce velkého. Tyto druhy se liší velikostí svého těla a podílem ptačích vajec a mláďat ve svých jídelničcích. Sojka a ořešník jsou nejmenší, havran a vrána jsou střední velikosti a krkavec je největší. Sojka, vrána a krkavec jsou považováni za běžné pleniče hnízd, zatímco ořešník a havran nikoli. Jako neškodná kontrola sloužil opět holub domácí. Malé druhy krkavcovitých (sojka a ořešník) byly napadány signifikantně intenzivněji než větší druhy (havran, vrána, krkavec) a neškodný holub. Všechny tři větší krkavcovití byli napadáni stejně výjimečně jako holub.

Ťuhýci se současně přibližovali na menší vzdálenost k menším druhům krkavcovitých a k neškodnému holubovi než k větším druhům. Tyto výsledky ukázaly, že ťuhýci přizpůsobují svou antipredační strategii velikosti predátora a nikoli míře specializace predátora na plenění hnízd. Ťuhýci tedy zřejmě váží svou schopnost zahnat vetřelce a vzdávají nesmyslnou agresi proti velkému, neporazitelnému soupeři.

Tyto výsledky sice podporují hypotézu, že absence aktivního mobbingu vůči některým krkavcovitým není projevem nezájmu, nýbrž alternativní antipredační strategií. Jednoznačný důkaz však neposkytují. Ten jsme se pokusili přinést v dalším experimentu (Surová et al. in prep.). Do těsné blízkosti hnízd ťuhýka obecného jsme umísťovali atrapu poštolky obecné – ťuhýkům známého vetřelce, kterého ze svého teritoria intenzivně vyhánějí (Strnad et al. 2012). Do vzdálenosti 10 m jsme navíc ve stejnou dobu instalovali atrapu dalšího vetřelce (straku obecnou, sojku obecnou, holuba domácího). Druhý vetřelec byl instalován vždy v takové poloze, aby „viděl“ poštolku. Při kontrole byla ťuhýkům předložena samotná poštolka. Ťuhýci intenzivně útočili na poštolku, pokud byla u hnízda samotná, nebo pokud byl v povzdálí holub. Pokud byla v povzdálí nainstalovaná sojka, ťuhýci napadali obě atrapy, přičemž poštolku stíhali napadat téměř stejně intenzivně jako v předešlých dvou případech. Pokud však byla v povzdálí instalovaná straka, ťuhýci významně omezili útoky na poštolku, či od nich úplně upustili. Kvůli vzdálenějšímu nebezpečí tedy ťuhýci upustili od eliminace bezprostředního nebezpečí. Z toho vyvozujeme, že si ťuhýk dobře uvědomuje situaci, kdy se „straka dívá“, a že tomu uzpůsobuje své chování. Výsledky této práce zároveň jednoznačně dokazují, že ťuhýci se před strakou snaží neupozorňovat na hnízdo, aby minimalizovali riziko, že straku svým chováním upozorní na jeho přítomnost a ona jej vyplení za jejich nepřítomnosti.

Rozpoznávání a kategorizace predátorů ptáky

Všechny dosud citované práce testovaly, zda jsou ptáci schopni rozlišit různé predátory, ale nezabývaly se tím, jak rozpoznávání konkrétních typů či druhů predátorů probíhá. Že jde přitom o zajímavou problematiku, ukazují i výsledky naší práce porovnávající obranu vůči různým druhům krkavcovitých (Němec a Fuchs 2014). Ťuhýci v našich experimentech reagovali útočně na ořešníka, přestože je nanejvýš pravděpodobné, že s ním nemohou mít zkušenost jako s predátorem potomstva ani dospělců. Vejce a mláďata ptáků se v potravě ořešníka objevují jen vzácně (Hudec 1983) a útoky na dospělé ptáky i savce jsou zcela ojedinělé (Cramp et al. 1994). Ořešník se navíc ani nepodobá ostatním krkavcovitým. Není

Problematikou rozpoznávání jiných živočichů, včetně predátorů, se zabývali již zakladatelé etologie. Nejvýznamnější roli při rozpoznávacích procesech přisuzovali obvykle tzv. "klíčovým znakům". Z původního termínu "spouštěč (Auslöser/releaser)", který reprezentoval stimulus vyvolávající jakoukoli specifickou reakci (Lorenz 1937), odvodil Tinbergen (1948) pojem "sign stimulus" označující signál (část těla či chování) vyslaný jedním zvířetem, který způsobuje typické chování u druhého zvířete. Později byl užíván pojem "key features" (Marr a Nishihara 1978; Bruner a Austin 1986), nebo "salient features" (Schleidt et al. 2011). V češtině se pro tyto nápadné znak ujal termín "klíčové podněty" (Veselovský 2005).

Zásadní role klíčových znaků při rozpoznávání predátorů byla poprvé prokázána v experimentech se siluetami dravců. Při nich byly porovnávány reakce bělokura rousného (*Lagopus lagopus*) a kuřat kura domácího (*Gallus gallus*) na siluety ptáků různých tvarů. Zásadní vliv na vyvolání antipredační reakce měla délka krku siluety. Pokud bylo siluetou pohybováno takovým směrem, že byl tvořen dojem krátkého krku vpředu a dlouhého ocasu vzadu, vyvolávala u testované drůbeže útekové chování. Pokud bylo touž atrapou pohybováno v opačném směru a jevila se tedy jako pták s dlouhým krkem a krátkým ocasem, antipredační chování se neobjevilo. Ostatní potenciální znaky, tvary křídel či těla siluety, neměly na reakci testovaných ptáků žádný vliv (Goethe 1937; Krätzig 1940, Lorenz 1940 ex Tinbergen 1948).

Ve své revizi Lorenzových a Tinbergenových experimentů však Schleidt et al. (2011) poznamenávají, že Tinbergen a Lorenz napsali víc prací

o „krátkém kru“, ale kreslili v nich různé obrázky, které si navzájem neodpovídaly – není tedy zcela jasné, co kdy bylo použito. Lonrenz pak podle nich navíc za „spouštěč“ antipredační reakce nepovažoval ani tak „krátký krk“, jako spíš „pomalou relativní rychlost letu“. První, kdo použil model husa/sokol (podle směru letu) byl podle Schleidt et al. (l.c.) Goethe (1937).

V dalších desetiletích studie s tematikou klíčových znaků přibývaly pomalu. Zřejmě nejobsáhlejší výzkum na toto téma provedl (Curio 1975), když testoval intenzitu varovné vokalizace (call-rate) lejsků černohlavých proti modifikovaným atrapám ťuhýka obecného a kulíška nejmenšího (*Glaucidium passerinum*). Nejprve byly prezentovány atrapy samce ťuhýka obecného s barevnými úpravami oční pásky. Nejsilnější varovnou reakci však vyvolávala u lejsků jen atrapa ťuhýka v přirozeném stavu. Kromě atrapy s červeným očním proužkem, která se od té kontrolní signifikantně nelišila, způsobovaly všechny ostatní testované změny velmi výrazný pokles intenzity reakce (oční proužek zelený, bílý proužek na černé hlavě, černý na jednotně bílé hlavě, hlava bez proužku a nakonec hlava bez proužku a bez oka). Dále byl testován vliv kontrastu mezi očním proužkem a zbytkem hlavy – buď byla ubírána barva černého proužku, nebo naopak sycena barva hlavy. Odebírání sytosti proužku nepůsobí v reakci lejsků větší změny. Teprve když proužek zcela splynul s podkladem, vymizela i reakce lejsků. Ztmavení hlavy naopak lineárně zvyšovalo antipredační reakci lejsků až do chvíle, kdy již byla celá černá, to pak reakce lejsků poklesla. Důležitá je také poloha oční pásky. Lejscí reagovali na atrapu, u níž byl oční proužek posunut z čela na týl, dokonce o něco silněji než na kontrolní nezměněnou atrapu. Ostatní modifikace (páska pod krkem, na břiše, vertikálně na temeni) už vyvolávaly jen velmi nepatrné reakce. Následně byly prezentovány atrapy samce ťuhýka s barevně upraveným tělem. Lejscí však reagovali silně pouze na kontrolní nezměněný model. Když byl z ťuhýka sejmut barevný vzor a na bílém těle byl ponechán jen černý oční proužek, reakce lejsků dramaticky poklesla. Žádnou reakci nevyvolávala ani bílá atrapa bez očního proužku a stejně tak bez reakce zůstala i bílá čtverhranná tyčka se stylizovaným jedním nebo dvěma očními páskami, postrádající však ptačí tvar těla.

Na atrapě kulíška testoval Curio (1975) význam očí. Na atrapu s trojúhelníkovitými očima reagovali lejscí téměř stejně silně jako na

kontrolní nezměněnou atrapu. Pokud chybělo jedno oko (bylo zakryto peřím), lejscí atrapu prakticky ignorovali. Když však byly zakryty obě oči, lejscí na atrapu opět reagovali, ale nárůst aktivity nebyl signifikantní. Autor mírný nárůst vysvětluje znovu navrácenou symetrií a dodává, že tvar očí je pravděpodobně méně důležitý než jejich počet.

Další experimenty význam klíčových znaků v různé míře potvrdily. Nice a Pelkwyk (1941) testovali reakci strnadce zpěvného (*Melospiza melodia*) na různě modifikované kartonové modely puštíka proužkovaného (*Strix varia*). Došli k závěru, že z celé atrapy puštíka je sice hlava nejdůležitější, nicméně pouhá nepřítomnost očí strach z atrapy nesnižuje. Význam očí testoval také (Scaife 1976), který při pokusech s kuřaty zjistil, že stresovou reakci (ústup do bezpečí) vyvolávají žluté dravčí oči, a to i pokud jsou umístěny na vycpaném křivím, kterého se kuřata jinak nebojí. Watve et al. (2002) zjistili, že vlha východní (*Merops orientalis*) je schopna posoudit, zda se predátor „dívá“. Je pro ni významné, jaký úhel svírá pohled očí člověka s přímkou vedoucí k jejímu hnízdu, zatímco úhel svíraný mezi tělem a hnízdem význam nemá. Podobné poznatky shromáždili Carter et al. (2008), když otestovali vliv přímého pohledu člověka na krmící se špačky obecné (*Sturnus vulgaris*). Pokud byl pohled „lidského predátora“ odvrácený, špačci se vrátili k hledání potravy a zkonzumovali jí více v kratším čase. Autoři podotýkají, že jedinec, který dokáže správně vyhodnocovat takto jemné detaily, jako je například směr pohledu predátora, získává konkurenční výhodu nad konspicivními jedinci, kteří to nedokážou.

Gill et al. (1997) otestovali klíčový význam zobáku. Připevnili na atrapu vlhovce kravského (*Molothrus cabanisi*) zobák mladého špačka obecného který je, podobně jako zobák vlhovce, tmavý, avšak delší a tenčí. Lesňáček žlutý reagoval mnohem silněji na kontrolní atrapu s původním zobákem. Zobák přitom hraje významnou roli i při výběru sexuálních partnerů. Burley a Coopersmith (1987) zjistili, že samice zebřičky pestré (*Taeniopygia guttata*) tíhnou k samcům s co nejčervenějšími zobáky (uměle přibarvenými), zatímco samci si vybírají samice, jejichž zobák spadá spíše doprostřed fenotypového rámce. Také Patton et al. (2010) došli v laboratorních podmínkách k závěru, že holubi používají zobák jako klíčový znak při výběru sexuálního partnera.

Častými klíčovými znaky jsou nápadné barevné prvky na ptačím těle. Deppe et al. (2003) zjistili, že pokud byly na modelu kulíška amerického

(*Glaucidium gnoma*) přítomny vzory očních skvrn, bránící ptáci se k atrapě neodvažovali přiblížit tak jako k atrapě beze skvrn.

V posledních letech byl opakovaně zkoumán efekt podobnosti zbarvení peří hnízdního parazita (kukačky obecné, *Cuculus canorus*) se specializovaným predátorem dospělých pěvců (krahujcem obecným). Lyon a Gilbert (2013) pozorovali mobbing na kukačku u druhu, který kukačka téměř neparazituje (vlaštovka obecná, *Hirundo rustica*) nebo který ji vůbec nezná (mlynařík americký, *Psaltriparus minimus*). V obou případech si ji podle autorů pletou s krahujcem (či jiným zástupcem rodu *Accipiter*). Liang a Møller (2014) pak zjistili, že vlaštovky brání hnízdo proti kukačce i krahujci víc v Dánsku než v Číně, zřejmě proto, že v Dánsku je krahujec relativně běžnější a představuje tedy známější nebezpečí. Autoři ovšem výsledky vysvětlují tak, že v Číně je více hnízdních parazitů a je tedy pro obránce těžší je rozeznat. Také Langmore et al. (2012) potvrzují, že kukačku se musí ptáci naučit rozpoznávat, neboť sýkory (*Parus major* a *Cyanistes caeruleus*), kukačkou neparazitované, na ni reagují podobně opatrně jako na krahujce.

Nicméně, rákosník obecný, druh, který je kukačkou běžně parazitován, reagoval varovnými hlasy na atrapu kukačky mnohem silněji, než na atrapu krahujce nebo kontrolní čírky obecné (*Anas crecca*), čímž se potvrdilo, že mezi nimi rozlišuje (Welbergen a Davies 2008). Na druhou stranu, podobnost kukačky s krahujcem ji má zřejmě opravdu chránit před napadením ze strany hostitelských ptáků. V další studii bylo manipulováno se zbarvením peří jednotlivých atrap a ukázalo se, že rákosníci obecní si troufají přiblížit na kratší vzdálenost ke kukačce, která nemá vlnkovaná prsa, než ke kukačce, která je vlnkovaná má, čímž se více podobá krahujci (Welbergen a Davies 2011). Také když bylo vlnkování přidáno na kontrolní atrapu hrdličky zahradní (*Streptopelia decaocto*), přibližovali se k ní rákosníci méně, než když vlnkování neměla. Vlnkování však nevyvolává antipredační chování nepodmíněně, neboť se neprojevil žádný rozdíl v přibližování rákosníků k vlnkovanému či nevlnkovanému krahujci (Welbergen a Davies 2011). Autoři předpokládají, rákosníci rozpoznávají krahujce nejspíš podle typických dravčích znaků přítomných na jeho těle.

Také Trnka a Prokop (2012) zjistili, že rákosníci velcí sice napadají kukačku obecnou i krahujce obecného s podobnou intenzitou, ovšem jen tehdy, pokud jim byly obě atrapy prezentovány postupně. Když byly atrapy

obou vetřelců prezentovány simultánně, kukačka pak byla napadána více. Autoři vysvětlují, že jednak kukaččí mimikry nejsou dokonalé, a navíc, že rákosníci velcí jsou díky svým tělesným dispozicím mimořádně agresivní a při obraně hnízda generalizují nebezpečnost na všechny vetřelce.

V dalších experimentech Trnka et al. (2012) zjistili, že pro rozpoznání kukačky rákosníkem velkým mají její žlutá duhovka a žlutý oční kroužek větší význam než vlnkování na břicho. Vysvětlují to tím, že potenciální hostitel hnízdního parazita sleduje většinou shora. Navíc autoři zmiňují, že tentýž podnět může u některé populace rákosníků vyvolat útočnou reakci a u jiné populace naopak útek, v závislosti na tom, jakou zkušenost mají daní jedinci s prezentovanými vetřelci. Trnka a Grim (2013) ještě srovnali reakci rákosníka velkého na šedou a hnědou formu kukačky, na krahujce a na poštolku. Rákosníci provedli více náletů na šedou formu kukačky než na krahujce, z čehož je zřejmé, že mezi nimi rozlišovali. Nerozlišovali však hnědou formu od poštolky. Obě barevné formy kukačky nicméně počtem provedených náletů odlišili od kontrolní neškodné hrdličky divoké (*Streptopelia turtur*). Podle autorů není dynamika kukaččího polymorfismu ovlivněna lokálním výskytem predátorů na lokalitě, ale jde o kontra-adaptaci kukaček k maření adaptace hostitelů na odhalení mimikry.

Ačkoliv ptáci v kognitivních úlohách preferují spíše lokální znaky před globálními (Cavoto a Cook 2001; Troje a Aust 2013), jejich efekt v rozpoznávacím procesu není absolutní (Murphy et al. 2006). Například Herrstein a Loveland (1964) ukázali, že ptáci zvládají nejen jednoduchou kategoriální diskriminaci, ale umí se také učit a následně široce generalizovat. Testování holubi se naučili rozlišovat mezi fotografiemi komplexních reálných scén jen podle toho, zda na nich byla přítomna lidská bytost, která ovšem mohla mít velmi rozmanitou podobu. V rámci výzkumu rozpoznávání predátorů pak Tvardíková a Fuchs (2010) prokázali, že se při něm uplatňují i složitější kognitivní procesy, jako je „amodal completion“. Sýkory v krmítkové experimentu reagovaly na torzo krahujce (horní polovina těla – hlava a prsa s částmi křídel) odlišně v závislosti na tom, zda bylo umístěno odkryté na bidýlku, nebo zda „vyhlíželo“, ze smrkového chvojí. Prvé torzo nepovažovaly za plnohodnotného predátora, druhé však ano. Z toho plyne, že sýkory vnímají krahujce holisticky (tzn. ne jen jako soubor jednotlivých znaků), a to i v situaci, kdy je jeho část ukryta za překážkou.

Obdobné jsou i závěry Beránkové et al. (2014). Naivním sýkorám koňadrám vystavovali atrapy krahujce obecného a holuba domácího s vzájemně prohozenými klíčovými znaky (oko a zobák). Výměna očí zbavila sýkory strachu z krahujce, ale nezpůsobila strach z holuba. V obou případech se však o chiméru sýkory více zajímaly. Výměna zobáků nezbavila sýkory strachu z krahujce, holub naopak začal jistý strach vyvolávat, avšak nikoli srovnatelný s nemodifikovaným krahujcem. Autoři vyvodili, že specifické znaky krahujce (oko) jsou nezbytné pro jeho správnou identifikaci, ale obecné znaky dravce nikoliv. Zároveň platí, že specifický znak krahujce není sám o sobě dostatečným podnětem pro jeho rozpoznání, zatímco obecný znak dravce ano (ovšem pro rozpoznání dravce, nikoliv krahujce). Obecně lze konstatovat, že sýkory vnímají klíčové znaky nikoliv izolovaně, ale v kontextu. Tyto výsledky jsou v souladu s poznatky zjištěnými testováním trénovaných holubů v laboratorních experimentech, tedy že záleží nejen na samotné přítomnosti klíčových znaků, ale také na jejich poloze a vzájemné konstelaci (Wasserman et al. 1993; Kirkpatrick-Steger et al. 1996; Watanabe 2001; Goto et al. 2011). Schleidt et al. (2011) navrhují neredukovat svět na „Svět stimulů“ (World of stimuli) a doporučují místo toho „Teorii světa“ (Theory of world), kde se nesoustředíme jen na objekty samotné, nýbrž na všechno, co jakkoli vyčnívá z pozadí (k tomu citují i Komenského Svět v obrazech).

Výše uvedené studie se zaměřily výlučně na jednotlivé klíčové znaky. V naší poslední studii (Němec et al. in prep.) jsme se rozhodli otestovat současně význam potenciálních obecných klíčových znaků dravce (zahnutý zobák, silné drápy a oko s kostěným supraorbitálním hřebenem) a druhově specifického zbarvení peří pro rozpoznání poštolky obecné – ťuhýkům známého a jimi intenzivně zaháněného predátora. Klíčové dravčí znaky zůstaly u první sady atrap (vyrobených z plyše) nezměněné, dravčí. U druhé sady jsme je zaměnili za holubí (oko bez supraorbitálního hřebene, tenčí rovný zobák, růžové nohy bez drápů). Každá sada obsahovala tři barevné modifikace atrap: normálně zbarvená, zjednodušená (zbavená černého skvrnění a ostatních černých prvků ve zbarvení) a zcela odlišná (použito bylo nápadné a pro střední Evropu zcela exotické zbarvení jihoasijského luňákovce černého (*Aviceda leuphotes*). Jako kontroly sloužily vycpaniny poštolky a holuba domácího. Pokud byly na normálně zbarvené atrapě poštolky ponechány klíčové znaky dravce (původní poštolčí zobák, oko

a pařáty), byla tato atrapa řuhýky považovaná za poštolku – řuhýci na ní útočili stejně intenzivně jako na poštolku vycpanou. S o něco nižší intenzitou pak útočili na atrapu zjednodušenou. Atrapu ve zbarvení „Aviceda“ s klíčovými znaky dravce napadali již jen minimálně. Naproti tomu pokud byly klíčové znaky nahrazeny holubími, řuhýci neútočili na žádnou z atrap v jakémkoli barevném provedení. Ani když zbarvení řela zůstalo nezměněné poštolčí, řuhýci nejevili o atrapu zájem, a nevzrušeně během její přítomnosti krmili mláďata. Klíčové (lokální) znaky se tedy pro kategorizaci ukázaly jako velmi důležité, přestože řuhýci znají zbarvení poštolky a na neznámého dravce téměř neútočí. Do příštích experimentů však zatím zůstává nezodpovězeno, zda je za zařazení atrap do kategorie „neškodný druh“ zodpovědná pouhá nepřítomnost klíčových znaků dravce, nebo je nutná přítomnost klíčových znaků neškodného ptáka (holuba).

Atrapové experimenty

Antipredační chování je pro studium rozpoznávacích procesů na netréovaných ptácích velmi vhodné, neboť hrozba predace představuje pro testovaná zvířata ekologicky relevantní problém (Shettleworth 1993; Shettleworth 2010). Přítomnost predátora či jiného nepřítele vytváří pro testované zvíře silnou motivaci, na kterou je nuceno, v zájmu zachování svého fitness, adekvátně reagovat (Tvardíková a Fuchs 2010; 2012). Aby bylo možné rozpoznávací procesy detailně zkoumat, je nutné mít možnost cíleně modifikovat testované stimuly, v našem případě atrapy predátorů nebo jiných nepřátelských organismů. Přírodní preparáty (vycpaniny či mumie) jsou ovšem špatně dostupné (zejména vzácnější druhy) a lze je modifikovat jen omezeně. Gill et al. (1997), například, připevnili na mrazem vysušenou mumii vlhovce kravského zobák špačka obecného). Podobné úpravy jsou ale limitované chatrností těchto preparátů (rozpadají se) a špatnou barvitelností peří.

Dobrou alternativou by proto bylo použití umělých atrap z jiných materiálů, jež by umožňovaly výrobu různých modifikací. Umělé atrapy byly při studiu antipredačního chování ptáků dosud využívány spíše zřídka, protože většina prací studovala reakce na běžně se vyskytující reálné predátory, snadno dostupné v podobě vycpanin. Conover (1979) použil plastový model letícího jestřába lesního, (Knight a Temple 1988) pracovali s gumovým modelem vrány americké (*Corvus brachyrhynchos*) a Arroyo et

al. (2001) používali plastové modely vrány, respektive výra. Siluetu dravce vyrobenou z překližky testoval Goth (2001), a také Hartley (1950). Curio (1975) a Deppe et al. (2003) používali dřevěné modely. Kromě posledně jmenované byly ve všech výše zmíněných studiích umělé atrapy použity v pokusech spolu s vycpaninami. Autoři však případný vliv materiálu na výsledek pokusu většinou nezmiňují. Pouze Curio (1975) předkládal netrénovaným lejskům černohlavým atrapy kulíška nejmenšího lišících se mimo jiné texturou povrchu. Lejscí reagovali pouze na nemodifikovanou vycpaninu, zatímco dřevěný model v přirozených barvách reakci nevyvolal. Ve všech ostatních studiích nicméně vyvolávaly umělé atrapy u testovaných ptáků nějakou formu antipredačního chování, jako například zvýšenou ostražitost, ztuhnutí (freezing), úprk, varovnou vokalizaci, ale také útok na predátora. Zdá se tedy, že pro účely těchto experimentů sloužily umělé modely dobře, jednoznačné doklady pro to ale chybějí.

Všechny umělé modely, užití ve výše zmíněných studiích, měly shodně kompaktní povrch, který se liší od struktury, jakou vytváří obrysová pera na ptačím těle (a tedy i na vycpaninách a mumiích). Laboratorní studie s trénovanými holuby přitom ukázaly, že přítomnost geometrické textury pomáhá k rychlému rozlišení objektů od pozadí (Cook 1992a; 1992b). Holubi byli také schopni využít texturu pro kategorizaci přirozených objektů (Troje et al. 1999; Nicholls et al. 2011) či odhalit jen přítomnost lidské pokožky (Aust a Huber 2010) na digitálních fotografiích. Z těchto experimentů však jednoznačně nevyplývá, že je struktura povrchu důležitá také při rozpoznávání reálných, ekologicky relevantních stimulů netrénovanými ptáky. Struktura povrchu by přitom v tomto případě nemusela být tolik významná, pokud by platil předpoklad, že rozhodující roli hrají klíčové znaky. Opakovaně prokázán byl význam očí, zobáku (Scaife 1976; Burley a Coopersmith 1987; Gill et al. 1997) a barevných vzorů na těle (Davies a Welbergen 2008; Pincemy et al. 2009; Welbergen a Davies 2011) pro rozpoznávání predátorů (Scaife 1976; Watve et al. 2002; Davies a Welbergen 2008; Beránková et al. 2014), hnízdních parazitů (Gill et al. 1997; Welbergen a Davies 2011; Trnka et al. 2012) i sexuálních partnerů (Burley a Coopersmith 1987; Pincemy et al. 2009). Pokud byly tyto znaky ze stimulů odstraněny, testování netrénovaní ptáci je už nebyli schopni rozpoznat, nebo reagovali signifikantně slaběji.

Bylo by proto užitečné najít mez věrohodnosti, při které ještě umělý model funguje jako skutečný živočich a kdy už je příliš zjednodušený. Takové znalosti by pomohly designovat experimenty s umělými modely a interpretovat jejich výsledky. Při experimentech, v kterých mohou testování ptáci na atrapu útočit, je zároveň potřeba hledět na tvrdost materiálů, ze kterých je atrapa predátora vyrobena. Bolestivý náraz do tvrdého modelu by zapříčinil klesající ochotu ptáků nálety provádět a navíc by hrozilo i jejich vážné zranění. Rozhodli jsme se proto srovnat reakci hnízdících ťuhýků na tři typy atrap běžného středoevropského predátora hnízd, sojku obecnou (Němec et al. 2015). Použili jsme vycpanou, plyšovou a silikonovou atrapu, jež měly klesající úroveň podobnosti s živým ptákem. Všechny sice sdílely potenciální významné znaky živé sojky (silný zobák, modročerné krovky, černý vous, černobílé sekundární letky a modré oči), ale měly různý povrch. Vycpaná atrapa byla pokryta peřím, plyšová byla jemně chlupatá a silikonová atrapa hladká a lesklá. Ťuhýci bránili svá hnízda před všemi třemi atrapami. Ovšem rozdily v intenzitě obrany významně klesaly od vycpané, přes plyšovou po silikonovou atrapu. Silikonová atrapa byla navíc napadána jen tehdy, pokud nebyla v sérii pokusů zařazena jako první. Pokud netrénovaní ťuhýci neviděli nejprve věrohodnější vycpanou nebo plyšovou atrapu, silikonovou atrapu ignorovali a věnovali se péči o mláďata. Proto usuzujeme, že pouze vycpanou či plyšovou atrapu kategorizují ťuhýci jako skutečnou sojku, a že struktura povrchu atrapy má tedy na reakci testovaných ptáků velký vliv. Nezbytnost prezentace přesnějšího vzoru pro rozpoznání méně přesného připomíná proces primingu, který je znám především z lidské psychologie (pro review viz Wasserman a Zentall 2009). Priming usnadňuje rozpoznání již jednou viděného a třeba i degradovaného podnětu po delší době (Tulving a Schacter 1990). Naše studie je první, která jej identifikovala při terénních experimentech na netrénovaných ptácích.

Shrnutí

V naší první práci (Strnad et al. 2012) jsme porovnali reakci hnízdících ťuhýků obecných na více ptačích predátorů a dospěli k závěru, že ťuhýci přizpůsobují své antipredační chování tomu, jak je prezentovaný predátor nebezpečný jim samotným a nikoli jak nebezpečný je jejich mláďatům. Navíc se objevil nečekaný fenomén absolutní pasivity vůči strace.

V druhé práci (Němec a Fuchs 2014) jsme proto porovnali reakci hnízdících ťuhýků na různé krkavcovité ptáky a zjistili, že malé druhy krkavcovitých jsou napadány intenzivněji než větší druhy, a že od větších druhů udržují obránci delší vzdálenost než od neškodného holuba. Ťuhýci tedy váží svou schopnost zahnat vetřelce a nepouští se do nesmyslné agrese proti neporazitelnému soupeři.

Tyto výsledky sice podpořily hypotézu, že absence aktivního mobbingu vůči některým krkavcovitým není projevem nezájmu, nýbrž alternativní antipredační strategií, jednoznačný důkaz však poskytuje až naše zatím poslední práce (Syrová et al. in prep.). V ní vyšlo najevo, že si ťuhýci dobře uvědomují situaci kdy se „straka dívá“, a vyhýbají se riziku prozrazení svého hnízda i v situaci, kdy jejich hnízdo bezprostředně ohrožuje jiný predátor.

Posléze jsme se začali zabývat možnostmi využití umělých atrap v atrapových experimentech (Němec et al. 2014) a zjistili, že struktura jejich povrchu hraje důležitou roli v jejich rozpoznatelnosti, a že je možné použít plyšové atrapy jako náhradu za tradiční vycpané. Zaznamenali jsme efekt primingu, kdy nejméně věrohodná atrapa byla rozpoznána pouze v případě, že obránci již měli předchozí zkušenost s nějakou věrohodnější.

Nakonec jsme zjistili (Němec et al. in prep.), že pro správné rozpoznání predátora je absolutně nezbytná přítomnost obecných klíčových znaků dravce a bez jejich přítomnosti je druhově specifické zbarvení známého predátora nedostatečným podnětem k vyvolání antipredační reakce u testovaných ptáků.

Seznam literatury

- Altmann SA (1956) Avian Mobbing Behavior and Predator Recognition. *The Condor* 58:241–253. doi: 10.2307/1364703
- Amat JA, Masero JA (2004) Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour* 67:293–300.
- Antczak M, Goławski A, Kuźniak S, Tryjanowski P (2009) Costly replacement: how do different stages of nest failure affect clutch replacement in the red-backed shrikes *Lanius collurio*? *Ethology Ecology and Evolution* 21:127–136.
- Arnold KE (2000) Group Mobbing Behaviour and Nest Defence in a Cooperatively Breeding Australian Bird. *Ethology* 106:385–393. doi: 10.1046/j.1439-0310.2000.00545.x
- Arroyo B, Mougeot F, Bretagnolle V (2001) Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). *Behavioral Ecology and Sociobiology* 50:109–115. doi: 10.1007/s002650100342
- Ash J (1970) Observations on a decreasing population of red-backed shrikes. *Br Birds* 63:185–205; 225–239.
- Aust U, Huber L (2010) The role of skin-related information in pigeons' categorization and recognition of humans in pictures. *Vision Research* 50:1941–1948. doi: 10.1016/j.visres.2010.07.012
- Baker MC, Becker AM (2002) Mobbing calls of black-capped chickadees: effects of urgency on call production. *The Wilson Bulletin* 114:510–516. doi: 10.1676/0043-5643(2002)114[0510:MCOBCC]2.0.CO;2
- Beránková J, Veselý P, Sýkorová J, Fuchs R (2014) The role of key features in predator recognition by untrained birds. *Animal Cognition* 1–9. doi: 10.1007/s10071-014-0728-1
- Binazzi R, Zaccaroni M, Nespoli A, Massolo A, Dessì-Fulgheri F (2010) Anti-predator behaviour of the red-legged partridge *Alectoris rufa* (Galliformes: Phasianidae) to simulated terrestrial and aerial predators. *Italian Journal of Zoology* 78:106–112. doi: 10.1080/11250003.2010.509136
- Bruner JS, Austin GA (1986) *A Study of Thinking*. Transaction Publishers
- Buitron D (1983) Variability in the Responses of Black-Billed Magpies to Natural Predators. *Behaviour* 87:209–236.
- Bujoczek M, Ciach M (2009) Seasonal Changes in the Avian Diet of Breeding Sparrowhawks *Accipiter nisus*: How to Fulfill the Offspring's Food Demands? *Zoological studies* 48:215–222.
- Burhans D (2001) Enemy recognition by field sparrows. *Wilson Bulletin* 113:189–193.
- Burley N, Coopersmith CB (1987) Bill Color Preferences of Zebra Finches. *Ethology* 76:133–151. doi: 10.1111/j.1439-0310.1987.tb00679.x
- Burtka JL, Grindstaff JL (2013) Repeatable nest defense behavior in a wild population of Eastern bluebirds (*Sialia sialis*) as evidence of personality. *Acta Ethologica*. doi: 10.1007/s10211-013-0143-7
- Caro TM (2005) *Antipredator defenses in birds and mammals*. University of Chicago Press

- Carrillo J, Aparicio J (2001) Nest defence behaviour of the Eurasian kestrel (*Falco tinnunculus*) against human predators. *Ethology* 107:865–875.
- Carter J, Lyons NJ, Cole HL, Goldsmith AR (2008) Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. *Proceedings of the Royal Society B: Biological Sciences* 275:1709–1715. doi: 10.1098/rspb.2008.0095
- Cavoto KK, Cook RG (2001) Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 27:3–16. doi: 10.1037/0097-7403.27.1.3
- Clode D, Blumstein DT, MacDonald DW (2000) The influence of risk and vulnerability on predator mobbing by terns (*Sterna* spp.) and gulls (*Larus* spp.). *Journal of Zoology* 252:53–59.
- Conover M (1979) Response of birds to raptor models. *Bird Control Seminars Proceedings*
- Conover MR (1987) Acquisition of Predator Information by Active and Passive Mobbers in Ring-Billed Gull Colonies. *Behaviour* 102:41–57. doi: 10.2307/4534611
- Cook RG (1992a) Acquisition and transfer of visual texture discriminations by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 18:341–353. doi: 10.1037/0097-7403.18.4.341
- Cook RG (1992b) Dimensional organization and texture discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 18:354–363. doi: 10.1037/0097-7403.18.4.354
- Cramp S, Perrins CM, Brooks DJ, Dunn E, Gillmor R (1994) *Handbook of the Birds of Europe the Middle East and North Africa*. Oxford university press, Oxford, New York
- Csermely D, Casagrande S, Calimero A (2006) Differential defensive response of common kestrels against a known or unknown predator. *Italian Journal of Zoology* 73:125–128.
- Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: A study of avian visual perception. *Animal Behaviour* 23:1–115.
- Curio E (1978) The adaptive significance of avian mobbing. I. Teleonomic hypothesis and predictions. *Zeitschrift für Tierpsychologie* 69:3–18.
- Curio E, Ernst U, Vieth W (1978) The Adaptive Significance of Avian Mobbing. *Zeitschrift für Tierpsychologie* 48:184–202. doi: 10.1111/j.1439-0310.1978.tb00255.x
- Čapek M, Požgayová M, Procházka P, Honza M (2010) Repeated Presentations of the Common Cuckoo Increase Nest Defense by the Eurasian Reed Warbler but Do Not Induce It to Make Recognition Errors. *The Condor* 112:763–769. doi: 10.1525/cond.2010.100063
- D'Orazio KA, Neudorf DLH (2008) Nest defense by Carolina Wrens. *The Wilson Ornithological Society* 120:467–472.
- Dale S, Gustavsen R, Slagsvold T (1996) Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. *Behavioral Ecology and Sociobiology* 39:31–42. doi: 10.1007/s002650050264
- Davies NB, Welbergen JA (2008) Cuckoo–hawk mimicry? An experimental test. *Proceedings of the Royal Society B: Biological Sciences* 275:1817–1822. doi: 10.1098/rspb.2008.0331

- Deppe C, Holt D, Tewksbury J, Broberg L, Petersen J, Wood K (2003) Effect of Northern Pygmy-Owl (*Glaucidium gnoma*) eyespots on avian mobbing. *Auk* 120:765–771.
- Evans CS, Macedonia JM, Marler P (1993) Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. *Animal Behaviour* 46:1–11. doi: 10.1006/anbe.1993.1156
- Ficken MS, Ficken RW, Witkin SR (1978) Vocal Repertoire of the Black-Capped Chickadee. *The Auk* 95:34–48. doi: 10.2307/4085493
- Ghalambor CK, Martin TE (2000) Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Animal Behaviour* 60:263–267. doi: 10.1006/anbe.2000.1472
- Gill S, Neudorf DL, Sealy SG (1997) Host responses to cowbirds near the nest: cues for recognition. *Animal Behaviour* 53:1287–1293. doi: 10.1006/anbe.1996.0362
- Gill SA, Sealy SG (1996) Nest Defence by Yellow Warblers: Recognition of a Brood Parasite and an Avian Nest Predator. *Behaviour* 133:263–282.
- Glutz v. Blotzheim UN, Bauer KM, Bezzel E (1971) *Handbuch der Vögel Mitteleuropas*, Bd. 4. Akademische Verlagsgesellschaft Frankfurt a. M.
- Goethe F (1937) *Beobachtungen und Erfahrungen bei der Aufzucht von deutschem Auerwild*. *Deutsche Jagd* 6:97–100.
- Gołowski A, Meissner W (2007) The influence of territory characteristics and food supply on the breeding performance of the Red-backed Shrike (*Lanius collurio*) in an extensively farmed region of eastern Poland. *Ecological Research* 23:347–353. doi: 10.1007/s11284-007-0383-y
- Gołowski A, Mitrus C (2008) What is more important: nest-site concealment or aggressive behaviour? A case study of the red-backed shrike, *Lanius collurio*. *Folia Zoologica Brno* 57:403–410.
- Goth A (2001) Innate predator-recognition in Australian brush-turkey (*Alectura lathami*, Megapodiidae) hatchlings. *Behaviour* 138:117–136.
- Goto K, Lea SEG, Wills AJ, Milton F (2011) Interpreting the effects of image manipulation on picture perception in pigeons (*Columba livia*) and humans (*Homo sapiens*). *Journal of Comparative Psychology* 125:48–60. doi: 10.1037/a0020791
- Green RE, Hirons GJM, Kirby JS (1990) The effectiveness of nest defence by black-tailed godwits *Limosa limosa*. *Ardea* 78:405–413.
- Greig-Smith PW (1980) Parental investment in nest defense by Stonechats (*Saxicola torquata*). 28:604–619.
- Griffin AS, Savani RS, Hausmanis K, Lefebvre L (2005) Mixed-species aggregations in birds: zenaïda doves, *Zenaidura macroura*, respond to the alarm calls of carib grackles, *Quiscalus lugubris*. *Animal Behaviour* 70:507–515. doi: 10.1016/j.anbehav.2004.11.023
- Groom DW (1993) Magpie *Pica pica* predation on Blackbird *Turdus merula* nests in urban areas. *Bird Study* 40:55–62. doi: 10.1080/00063659309477129
- Hagelin JC, Jones IL (2007) Bird odors and other chemical substances: a defense mechanism or overlooked mode of intraspecific communication? *The Auk* 124:741–761. doi: 10.1642/0004-8038(2007)124[741:BOAOC]2.0.CO;2

- Hakkarainen H, Korpimäki E (1994) Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. *Animal Behaviour* 48:843–849. doi: 10.1006/anbe.1994.1308
- Hartley P (1950) An Experimental Analysis of Interspecific Recognition. *Symposia of the Society for Experimental Biology* 4:313–336.
- Herrnstein RJ, Loveland DH (1964) Complex Visual Concept in the Pigeon. *Science* 146:549–551. doi: 10.1126/science.146.3643.549
- Hogstad O (2004) Nest defence strategies in the Fieldfare *Turdus pilaris*: The responses on an avian and a mammalian predator. *Ardea* 92:79–84.
- Hudec K (1983) Laniidae – Ťuhýkovití. *Fauna ČSSR - Ptáci 3/II*. Academia, Praha, pp 840–873
- Chiron F, Julliard R (2007) Responses of Songbirds to Magpie Reduction in an Urban Habitat. *The Journal of Wildlife Management* 71:2624–2631. doi: 10.2193/2006-105
- Jakober H, Stauber W (2002) Why do Red-backed Shrikes not build better concealed nests? *J Ornithol* 143:397–404.
- Kirkpatrick-Steger K, Wasserman EA, Biederman I (1996) Effects of spatial rearrangement of object components on picture recognition in pigeons. *Journal of the experimental analysis of behavior* 65:465–475.
- Kis J, Liker A, Székely T (2000) Nest defence by lapwings: observations on natural behaviour and an experiment. *Ardea* 88:155–163.
- Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. *Animal Behaviour* 69:307–313.
- Kleindorfer S, Hoi H, Fessl B (1996) Alarm calls and chick reactions in the moustached warbler, *Acrocephalus melanopogon*. *Animal Behaviour* 51:1199–1206. doi: 10.1006/anbe.1996.0125
- Clump GM, Curio E (1983) Reactions of blue tits *Parus Caeruleus* to hawk models of different sizes. *Bird Behavior* 4:78–81.
- Knight RL, Temple SA (1988) Nest-defense behavior in the red-winged blackbird. *Condor* 90:193–200.
- Knight RL, Temple SA (1986a) Nest defence in American goldfinch. *Animal Behaviour* 34:887–897.
- Knight RL, Temple SA (1986b) Why Does Intensity of Avian Nest Defense Increase during the Nesting Cycle? *The Auk* 103:318–327.
- Korpimäki E (1986) Diet variation, hunting habitat and reproductive output of the kestrel *Falco tinnunculus* in the light of the optimal diet theory. *Ornis Fennica* 63:84–90.
- Krama T, Krams I (2005) Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology* 16:37–40. doi: 10.1093/beheco/arh116
- Krams I, Krama T, Igaune K, Mänd R (2007) Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology* 18:1082–1084. doi: 10.1093/beheco/arm079
- Krebs JR, Davies NB (1993) An introduction to behaviour ecology. 3rd edn. Blackwell Scientific Publications, Oxford

- Kropil L, Sládek J (1990) Contribution to the knowledge of food of some birds of prey and owls in Slovakia. *Biológia* 45:841–853.
- Kruuk H (1976) The biological function of gulls' attraction towards predators. *Animal Behaviour* 24:146–153.
- Kullberg C, Lind J (2002) An experimental study of predator recognition in great tit fledglings. *Ethology* 108:429–441.
- Kumar A (2003) Acoustic communication in birds. *Resonance* 8:44–55. doi: 10.1007/BF02837868
- Langmore NE, Feeney WE, Crowe-Riddell J, Luan H, Louwrens KM, and Cockburn A (2012) Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. *Behavioral Ecology* 23:798–805. doi: 10.1093/beheco/ars033
- Leavesley AJ, Magrath RD (2005) Communicating about danger: urgency alarm calling in a bird. *Animal Behaviour* 70:365–373. doi: 10.1016/j.anbehav.2004.10.017
- Liang W, Møller AP (2014) Hawk mimicry in cuckoos and anti-parasitic aggressive behavior of barn swallows in Denmark and China. *J Avian Biol* n/a–n/a. doi: 10.1111/jav.00515
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640. doi: 10.1139/z90-092
- Londoño GA, García DA, Martínez S (2015) Morphological and Behavioral Evidence of Batesian Mimicry in Nestlings of a Lowland Amazonian Bird. *The American Naturalist* 185:
- Lorenz KZ (1937) The Companion in the Bird's World. *The Auk* 54:245–273. doi: 10.2307/4078077
- Lyon BE, Gilbert GS (2013) Rarely parasitized and unparasitized species mob and alarm call to cuckoos: implications for sparrowhawk mimicry by brood parasitic cuckoos. *The Wilson Journal of Ornithology* 125:627–630. doi: 10.1676/12-162.1
- Magrath RD, Haff TM, Horn AG, Leonard ML (2010) Calling in the Face of Danger: Predation Risk and Acoustic Communication by Parent Birds and Their Offspring. Academic Press, pp 187–253
- Marr D, Nishihara HK (1978) Representation and Recognition of the Spatial Organization of Three-Dimensional Shapes. *Proc R Soc Lond B* 200:269–294. doi: 10.1098/rspb.1978.0020
- Martin T (1993) Nest predation among vegetation layers and habitat types: revising the dogmas. *American naturalist* 141:897–913.
- McLean IG, Rhodes G (1991) Enemy recognition and response in birds. *Current ornithology* 8:173–211.
- McLean IG, Smith JNM, Stewart KG (1986) Mobbing behaviour, nest exposure, and breeding success in the american robin. *Behaviour* 96:171–185. doi: 10.1163/156853986X00270
- Morton ES, Shalter MD (1977) Vocal Response to Predators in Pair-Bonded Carolina Wrens. *The Condor* 79:222–227. doi: 10.2307/1367165
- Müller, M, Pasinelli G, Schiegg K, Spaar R, Jenni L (2004) Ecological and social effects on reproduction and local recruitment in the red-backed shrike. *Oecologia* 143:37–50. doi: 10.1007/s00442-004-1770-5

- Murphy K, Torralba A, Eaton D, Freeman W (2006) Object Detection and Localization Using Local and Global Features. In: Ponce J, Hebert M, Schmid C, Zisserman A (eds) *Toward Category-Level Object Recognition*. Springer Berlin Heidelberg, pp 382–400
- Naguib M, Janik V, Clayton N, Zuberbühler K (2009) *Vocal Communication in Birds and Mammals*. Academic Press
- Němec M, Fuchs R (2014) Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. *Acta Ethologica* 17:149–154. doi: 10.1007/s10211-013-0175-z
- Němec M, Součková T, Fuchs R (in prep.) Red-backed Shrike *Lanius collurio* recognize predator due local not due global features.
- Němec M, Srová M, Dokoupilová L, Veselý P, Šmilauer P, Landová E, Lišková S, Fuchs R (2015) Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. *Animal Cognition* 18:259–268. doi: 10.1007/s10071-014-0796-2
- Neudorf DL, Sealy SG (1992) Reactions of Four Passerine Species to Threats of Predation and Cowbird Parasitism: Enemy Recognition or Generalized Responses? *Behaviour* 123:84–105.
- Nice MM, Pelkwyk JT (1941) Enemy Recognition by the Song Sparrow. *The Auk* 58:195–214. doi: 10.2307/4079104
- Nicholls E, Ryan CME, Bryant CML, Lea SEG (2011) Labeling and family resemblance in the discrimination of polymorphous categories by pigeons. *Anim Cogn* 14:21–34. doi: 10.1007/s10071-010-0339-4
- Olendorf R, Robinson SK (2008) Effectiveness of nest defence in the Acadian Flycatcher *Empidonax virescens*. *Ibis* 142:365–371. doi: 10.1111/j.1474-919X.2008.tb04432.x
- Opdam P (1978) Feeding ecology of a sparrowhawk population (*Accipiter nisus*). *Ardea* 66:137–155.
- Palleroni, Hauser, Marler (2005) Do responses of galliform birds vary adaptively with predator size? *Animal Cognition* 8:200–210. doi: 10.1007/s10071-004-0250-y
- Patton TB, Szafranski G, Shimizu T (2010) Male pigeons react differentially to altered facial features of female pigeons. *Behaviour* 147:757–773. doi: 10.1163/000579510X491090
- Pincemy G, Dobson FS, Jouventin P (2009) Experiments on colour ornaments and mate choice in king penguins. *Animal Behaviour* 78:1247–1253. doi: 10.1016/j.anbehav.2009.07.041
- Rauter CM, Reyer H-U, Bollmann K (2002) Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit *Anthus spinoletta*. *Ibis* 144:433–444. doi: 10.1046/j.1474-919X.2002.00013.x
- Redondo T (1989) Avian Nest Defence: Theoretical Models and Evidence. *Behaviour* 111:161–195. doi: 10.2307/4534813
- Redondo T, Carranza J (1989) Offspring reproductive value and nest defense in the magpie (*Pica pica*). *Behav Ecol Sociobiol* 25:369–378. doi: 10.1007/BF00302995
- Regelmann K, Curio (1983) Determinants of brood defence in the great tit *Parus major* L. *Behavioral Ecology and Sociobiology* 13:131–145.

- Remeš (2005) Nest concealment and parental behaviour interact in affecting nest survival in the blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis. *Behavioral Ecology and Sociobiology* 58:326–332. doi: 10.1007/s00265-005-0910-1
- Roos S (2002) Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* 133:608–615. doi: 10.1007/s00442-002-1056-8
- Roos S, Pärt T (2004) Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology* 73:117–127.
- Rytönen S, Orell M, Koivula K (1993) Sex-role reversal in willow tit nest defence. *Behavioral Ecology and Sociobiology* 33:275–282.
- Salata-Pilacinska B, Tryjanowski P (1998) Skład pokarmu pustulki *Falco tinnunculus* L. i sowy uszatej *Asio otus* [L.] współwystępujących w krajobrazie rolniczym Niziny Mazowieckiej. *Przegląd Przyrodniczy* 09:95–100.
- Scaife M (1976) The response to eye-like shapes by birds. I. The effect of context: A predator and a strange bird. *Animal Behaviour* 24:195–199. doi: 10.1016/S0003-3472(76)80115-7
- Shettleworth SJ (1993) Where Is the Comparison in Comparative Cognition? *Alternative Research Programs. Psychological Science* 4:179–184. doi: 10.1111/j.1467-9280.1993.tb00484.x
- Shettleworth SJ (2010) *Cognition, evolution, and behavior* (2nd ed.). Oxford University Press, New York, NY, US
- Shields WM (1984) Barn swallow mobbing: Self-defence, collateral kin defence, group defence, or parental care? *Animal Behaviour* 32:132–148. doi: 10.1016/S0003-3472(84)80331-0
- Scheuerlein A, Van't Hof TJ, Gwinner E (2001) Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats (*Saxicola torquata axillaris*). *Proc R Soc Lond Ser B-Biol Sci* 268:1575–1582.
- Schleidt W, Shalter MD, Moura-Neto H (2011) The hawk/goose story: The classical ethological experiments of Lorenz and Tinbergen, revisited. *Journal of Comparative Psychology* 125:121–133. doi: 10.1037/a0022068
- Smith SM (1991) *The black-capped chickadee. Behavioral ecology and natural history.* Cornell University Press, Ithaca, New York
- Sordahl TA (2009) Field evidence of predator discrimination abilities in American Avocets and Black-necked Stilts. <http://www.bioone.org/doi/full/10.1648/0273-8570%282004%29075%5B0376%3AFEOPDA%5D2.0.CO%3B2>. Accessed 28 Oct 2009
- Strnad M, Němec M, Veselý P, Fuchs R (2012) Red-backed Shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. *Ornis Fennica* 89:206–215.
- Suzuki TN (2012) Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. *Animal Behaviour* 84:53–57. doi: 10.1016/j.anbehav.2012.03.030
- Syrová M, Němec M, Fuchs R (in prep.) The cognitive aspects of the Red-backed Shrike (*Lanius collurio*) to solve the multiple predator conflict during nest defence.

- Templeton C, Greene E (2007) Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings Of The National Academy Of Sciences Of The United States Of America* 104:5479–5482. doi: 10.1073/pnas.0605183104
- Templeton CN, Greene E, Davis K (2005) Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science* 308:1934–1937. doi: 10.1126/science.1108841
- Tillmann JE (2009) An ethological perspective on defecation as an integral part of anti-predatory behaviour in the grey partridge (*Perdix perdix* L.) at night. *Journal of Ethology* 27:117–124. doi: 10.1007/s10164-008-0094-z
- Tinbergen N (1948) Social releasers and the experimental method required for their study. *Wilson Bulletin* 60:6–51.
- Toshitaka SN (2011) Parental alarm calls warn nestlings about different predatory threats. *Current Biology* 21:R15–R16. doi: 10.1016/j.cub.2010.11.027
- Trnka A, Grim T (2013) Color plumage polymorphism and predator mimicry in brood parasites. *Frontiers in Zoology* 10:1–10. doi: 10.1186/1742-9994-10-25
- Trnka A, Prokop P (2012) The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. *Animal Behaviour* 83:263–268. doi: 10.1016/j.anbehav.2011.10.036
- Trnka A, Prokop P, Grim T (2012) Uncovering Dangerous Cheats: How Do Avian Hosts Recognize Adult Brood Parasites? *PLoS ONE* 7:e37445. doi: 10.1371/journal.pone.0037445
- Troje NF, Aust U (2013) What do you mean with “direction”? Local and global cues to biological motion perception in pigeons. *Vision Research* 79:47–55. doi: 10.1016/j.visres.2013.01.002
- Troje NF, Huber L, Loidolt M, Aust U, Fieder M (1999) Categorical learning in pigeons: the role of texture and shape in complex static stimuli. *Vision Research* 39:353–366. doi: 10.1016/S0042-6989(98)00153-9
- Tryjanowski P, Goławski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. *Journal of Ethology* 22:13–16. doi: 10.1007/s10164-003-0096-9
- Tryjanowski P, Kuźniak S, Diehl B (2000) Does breeding performance of Red-backed Shrike (*Lanius collurio*) depend on nest site selection? *Ornis Fennica* 77:137–141.
- Tulving E, Schacter DL (1990) Priming and human memory systems. *Science* 247:301–306. doi: 10.1126/science.2296719
- Tvardíková K, Fuchs R (2012) Tits recognize the potential dangers of predators and harmless birds in feeder experiments. *J Ethol* 30:157–165. doi: 10.1007/s10164-011-0310-0
- Tvardíková K, Fuchs R (2011) Do birds behave according to dynamic risk assessment theory? A feeder experiment. *Behav Ecol Sociobiol* 65:727–733. doi: 10.1007/s00265-010-1075-0
- Tvardíková K, Fuchs R (2010) Tits use amodal completion in predator recognition: a field experiment. *Anim Cogn* 13:609–615. doi: 10.1007/s10071-010-0311-3
- Van Zyl AJ (1994) A comparison of the diet of the Common Kestrel *Falco tinnunculus* in South Africa and Europe. *Bird Study* 41:127–130. doi: 10.1080/00063659409477208

- Veen T, Richardson D, Blaakmeer K, Komdeur J (2000) Experimental evidence for innate predator recognition in the Seychelles warbler. *Proceedings Of The Royal Society Of London Series B-Biological Sciences* 267:2253–2258.
- Veselovský Z (2005) *Etologie: biologie chování zvířat*. Academia
- Vieth W, Curio E, Ernst U (1980) The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: Cross-species tutoring and properties of learning. *Animal Behaviour* 28:1217–1229. doi: 10.1016/S0003-3472(80)80110-2
- Walters JR (1990) Anti-Predatory Behavior of Lapwings: Field Evidence of Discriminative Abilities. *The Wilson Bulletin* 102:49–70.
- Wasserman EA, Kirkpatrick-Steger K, Van Hamme LJ, Biederman I (1993) Pigeons are sensitive to the spatial organization of complex visual stimuli. *Psychological Science* 4:336–341. doi: 10.1111/j.1467-9280.1993.tb00575.x
- Wasserman EA, Zentall TR (2009) *Comparative Cognition: Experimental Explorations of Animal Intelligence*. Oxford University Press
- Watanabe S (2001) Discrimination of cartoons and photographs in pigeons: effects of scrambling of elements. *Behavioural Processes* 53:3–9.
- Watve M, Thakar J, Kale A, Puntambekar S, Shaikh I, Vaze K, Jog M, Paranjape S (2002) Bee-eaters (*Merops orientalis*) respond to what a predator can see. *Animal Cognition* 5:253–259. doi: 10.1007/s10071-002-0155-6
- Welbergen JA, Davies NB (2008) Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. *Animal Behaviour* 76:811–822. doi: 10.1016/j.anbehav.2008.03.020
- Welbergen JA, Davies NB (2011) A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioral Ecology* 22:574–579. doi: 10.1093/beheco/arr008
- Winkler DW (1994) Anti-predator defence by neighbours as a responsive amplifier of parental defence in tree swallows. *Animal Behaviour* 47:595–605. doi: 10.1006/anbe.1994.1083
- Zawadzka D, Zawadzki J (2001) Breeding Populations and Diets of the Sparrowhawk *Accipiter nisus* and the Hobby *Falco subbuteo* in the Wigry National Park (Ne Poland). *Acta Ornithologica* 36:25–31. doi: 10.3161/068.036.0111

Jak t'uhýk obecný (*Lanius collurio*) rozpoznává nepřátele

Kapitola 2

Red-backed Shrikes (*Lanius collurio*) adjust the mobbing hazardousness, but not mobbing frequency, by assessing the potential threat to themselves from different predators

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Red-backed Shrikes (*Lanius collurio*) adjust the mobbing hazardousness, but not mobbing frequency, by assessing the potential threat to themselves from different predators

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We studied the ability to adjust nest defence to the potential threat to defending adults and their nests in the Red-backed Shrike. We presented mounts of two raptor species which predate on adult birds (Eurasian sparrowhawk, common kestrel; differing in the proportion of adult passerines in their diets), and two species of nest predators (common magpie, Eurasian jay; differing in the proportion of bird eggs and nestlings in their diets). A mounted feral pigeon was used as a control. Shrikes regularly mobbed the sparrowhawk, kestrel and jay, but not magpie or pigeon. The mobbing frequency, in terms of the number of mobbing events per 20 min, did not differ among the three regularly-mobbed predators. If shrikes tried to chase the predator away, they did not adjust the mobbing frequency to the level of threat to the nest. The proportion of mobbing events with physical contact (mobbing hazardousness) declined from the most mobbed jay to the kestrel, and to the sparrowhawk, which was considered most dangerous. Apparently the Red-backed shrikes adjusted the mobbing hazardousness by assessing the potential threat to themselves. Our results show the importance of a differentiation between mobbing hazardousness and mobbing frequency in the study of nest-defence behaviour.

1. Introduction

Predator mobbing is an important form of avian antipredator defence (Caro 2005). It can occur year round (Shedd 1982, 1983), although it is usually more intense during the breeding season (Shedd 1982; Pavel 2005) when this behaviour is used to avoid nest predation (Biermann and Robertson 1981). Predator mobbing is also connected to various trade offs. Mobbing may force the predator to leave the nest (Pettifor 1990; Flasskamp 1994). If the predator discovers a nest, mobbing may be the only chance to save the nest (Caro 2005). On the other hand, mobbing is conspicuous, and if the predator is not aware of the presence of the nest, the defence behaviour may draw attention to it, or even attract other predators (Krama and Krams 2005; Krams et al. 2007).

Like other forms of parental investment, predator mobbing is both time and energy consuming (Collias and Collias 1978; Dale et al. 1996; Scheuerlein et al. 2001); thus, the defending birds should adjust the mobbing behaviour to the existing cost/benefit trade-off (Andersson et al. 1980). The importance of some factors involved in this trade-off (i.e., age and number of offspring, sex or life span) has been extensively studied in birds, demonstrating that the investment in mobbing behaviour is positively correlated with the value of the offspring (see Lima 2009 for a review). Nevertheless, this trade-off is not the only one: different predators represent different perils. The predator represents a threat not only to the nest content but also to the defending parents (Brunton 1986; Sordahl 1990; King 1999). These two threats may not be equal at the same time. Corvids, for example, represent higher threat to the nest, while raptors often threaten the defending parents.

The responses of defending birds toward different predator guilds have been studied in several contexts, such as nest vs. adult predators (Knight and Temple 1986a; Sordahl 1990; Duckworth 1991; Jacobsen and Ugelvik 1992; Dale et al. 1996; Arroyo et al. 2001; Amat and Masero 2004; Hogstad 2005), owls vs. birds of prey (Arroyo et al. 2001), terrestrial vs. aerial predators (Sordahl 1990; Bures and Pavel 2003; Kleindorfer et al. 2005; Hogstad 2005) and predators vs. parasites (Duckworth 1991; Welbergen and Davies 2011; Trnka and Prokop 2012). Nevertheless, the dangerousness of predators may differ significantly even within a specific

guild: for example, a bird-capturing raptor represents a bigger threat for defending birds (and potentially for fledglings) than does a small mammal-catching raptor. In order for the defending birds to adequately respond to these predators, they should have the ability to discriminate particular predator species, not only groups of predators. This ability has not been tested in the above-mentioned studies, however. Comparisons of more than one species within one predator group are scarce (Curio et al. 1983).

In our study, we focused on defence responses to different predator guilds. The tested predators (both within and between guilds) differ in their degree of threat to defending birds and/or their nestlings, which allows us testing the ability of a defending bird to discriminate particular predator species. We examined the nest-defence behaviour in a 30-g passerine, the red-backed shrike (*Lanius collurio*), a good experimental model species with which to study defence behaviour, as it vigorously defends its nest even against humans (Gotzman 1967; Tryjanowski and Gołowski 2004).

We investigated variation in nest defence by using mounted individuals of four avian predators that differ in the degree of their potential threat either to the nest content or to the defending parents. We used the Eurasian sparrowhawk (*Accipiter nisus*) and the common kestrel (*Falco tinnunculus*), both of which have the ability to prey upon both adults and fledglings, and which usually do not prey upon nestlings (see below). Note, however, that some raptors at least occasionally prey on nests of Red-backed shrikes (Lefranc 1993). The risk of the two raptor species toward the nest-defending red-backed shrike differs significantly. The sparrowhawk is specialized on small birds (Opdam 1978; Simeonov 1984; Frimer 1989; Kropil and Sládek 1990; Zawadzka and Zawadzki 2001; Bujoczek and Ciach 2009), including the red-backed shrike (Glutz von Blotzheim et al. 1971), while the kestrel primarily feeds on small mammals and is less likely to prey on birds (Korpimaeki 1986; Van Zyl 1994; Salata-Pilacinska and Tryjanowski 1998). We further tested two specialized nest-content (eggs, nestlings) predators: the common magpie (*Pica pica*) and the Eurasian jay (*Garrulus glandarius*). The magpie is more often mentioned than the jay as a nest predator of various bird species (Groom 1993; Chiron and Julliard 2007), including the red-backed shrike (Roos and

Pärt 2004). Finally, as a control, we presented a non-threatening feral pigeon (*Columba livia f. domestica*).

We tested the following predictions: (1) The frequency of mobbing behaviour is adjusted to the threat to the nest content. The frequency should be lower towards raptors than towards the two corvids, and within corvids, jay should be mobbed less than magpie. (2) The hazardousness of mobbing behaviour is adjusted to the threat to the defending birds. The highest hazardousness of mobbing behaviour should occur as jay > magpie > kestrel > sparrowhawk.

2. Material and methods

2.1. Study site, and the focal species

The experiments were conducted around the village of Slapy, Central Bohemia (49°48' N, 14°23' E) during the breeding period, i.e., from June to late July, in 2002 through 2004, and near the town of Karlovy Vary, Western Bohemia (50°14' N, 12°53' E) during the same months in 2004.

The red-backed shrike is found in open habitats with scattered shrubs (including spiny species such as wild rose *Rosa* spp., blackthorn *Prunus spinosa* and hawthorn *Crataegus* spp.) where it builds an open-cup nest. Only the female incubates, and lays 3–7 eggs during 14 days, while the male feeds her. Nestlings are subsequently provisioned by both parents for approximately 14 days after hatching (Lefranc and Worfolk 1997). The red-backed shrike is insectivorous, catching larger insects in the air and on the ground using a sit-and-wait strategy; however, it also preys upon small vertebrates (Golawski 2007).

In South Bohemia, Czech Republic, the breeding success in the red-backed shrike is 51% (Šimek 2001), and the major causes of nest failure are predation and weather. The spectrum of nest and adult predators at our localities has not been studied, but magpie and jay are considered the main nest predators and sparrowhawk is presumably the main predator of adults (Lefranc and Worfolk 1997). All of the tested species are roughly equally abundant at our experimental localities (Šťastný et al. 2006). – During 2002–2004, we conducted 90 single trials on 18 nests (36 individuals).

2.2. Experimental design

All experiments were conducted at nests containing nestlings from 5 to 10 days old, so we expected both parents to show nest defence because their probability to obtain successful offspring and existing investment to the nest was significantly higher than in previous stages of development (McLean and Rhodes 1991; Halupka 1999; Rytönen 2002). We presented mounted individuals of two predators of adult birds (sparrowhawk and kestrel), two predators of nest content (jay and magpie) and one non-threatening control species (feral pigeon), all of which were in the upright posture with their wings folded. In sparrowhawk, the presented dummies were females because in this species a significant sexual size dimorphism occurs, suggesting a distinct foraging niche (Overskaug et al. 2000). Together, we used three mounted specimens of kestrel, two sparrowhawks, two magpies, five jays and two pigeons. Of these, the jays suffered most by attacks of shrikes. All used dummies were without aberrance and were new-made by the same taxidermist. The mounts were placed on a 1.5 m high pole, 1 m away from the nest, and facing toward the nest. During installation, the tested mounts were covered by a cloth to prevent early reactions of the shrikes. Each pair of shrikes was presented with all five mounts exposed individually in a randomized order during one day. Each mount trial lasted 20 minutes from the appearance of at least one parent. If the parents showed no inclination to mob a mount within 20 minutes, the trial was terminated and included into the data set with a reaction value of zero. The minimum time interval until the presentation of the next dummy was one hour. To check for the habituation or positive reinforcement, which may affect the defence behaviour significantly (Knight and Temple 1986a, 1986b), the order of presentation was used as an explanatory variable in model. The behaviour of the defending birds was taped on a VHS-C video camera on a tripod at a distance at least 30 m from the nest, so as not to disturb the parents. All experiments were conducted between 07:00 and 19:00 in conditions free of precipitation and no or light wind.

Two types of behaviour were included in the statistical analyses: (1) Mobbing frequency, i.e., the total number of mobbing events (the bird flies over the mount, decreases the flight altitude, and sometimes strikes the

mount) accomplished by a tested bird during a 20-min trial; and (2) Mobbing hazardousness, i.e., the occurrence of mobbing events with physical contact (the bird hits the mount during the mobbing event, usually with its bill).

2.3. Statistical analyses

A positive correlation in the mobbing frequency was found between males and females of the same pair (Spearman's rank correlation: $N = 36$, $r = 0.716$, $p < 0.001$), so the pair was counted as a unit of repeated measures. To filter out the individual variability in the mobbing behaviour, pairs were added to the models as a hierarchical random factor.

The mobbing frequency was tested first. The number of mobbing events towards all dummies did not meet the assumption of normality so we transformed data by $\ln(\text{number of mobbing events} + 0.01)$ to improve the data normality. Generalized linear mixed models (GLMM) with Gaussian distribution and logit link function were used to evaluate variation in mobbing frequency between the five test species. Explanatory variables were predator type, sex (within the tested pair), age of nestlings, and the order of presentation of dummies (within the tested pair and within the particular experimental day). Other explanatory variables, such as year, experimental location or dummy individual, could not be added as the model would have run out of degrees of freedom. Nevertheless, as all tested predator (and control) species were used in all years and on both localities with the same proportion, the effect of these factors should be negligible.

We then tested the mobbing hazardousness. Here, the unit of repeated measures was mobbing event (presence of a physical contact = 1, absence of a physical contact = 0). GLMMs with binomial distribution and logit link function were used to evaluate the differences in the mobbing hazardousness. The explanatory variables were predator type, sex, age of nestlings and the order of presentation. Pair was added as a random factor. Only regularly-mobbed mounts were included (sparrowhawk, kestrel and jay), as the total number of all mobbing events upon magpie and pigeon were 6 and 15, respectively, which does not allow for a balanced design.

GLMMs were used in order to include the random effect of the pair, by applying glmmPQL in R 2.12.1 (www.r-project.org). As the analysis output did not provide general effects of particular categorical explanatory variables with more than two values on the variability of tested data, these effects were assessed according to pair-wise comparisons of these variables. Therefore, results of pair-wise comparisons within a multiple-value explanatory variable (dummy type) are summarized in tables (using t tests as a criterion) and for possible interactions between tested variables, both interacting variables are listed. As pair-wise comparisons within a given model has specific vector orientations, the values of the test criterion (t) may acquire positive and negative values, depending on the position of the basal value in the comparison. As the GLMMs had to be run repeatedly, having various basal values in pair-wise comparisons, the Bonferroni adjustment was used to adjust for multiple probabilities. For more details of GLMM, see Zuur et al. (2009).

3. Results

3.1. Mobbing frequency

The age of nestlings ($t = 1.18$, $df = 16$, $p = 0.2554$) and the order of presentation of particular dummies ($t = 1.10$, $df = 156$, $p = 0.2726$) had no significant effect on the mobbing frequency; therefore, they were removed from the model. Only the dummy type, sex of the shrike individual, and their interaction was included in the newly-created model.

Only the mount type significantly influenced the number of mobbing events performed by shrikes by dividing the mounts into two groups (Fig. 1, Table 1). The first group contained sparrowhawk, kestrel and jay, all of which obtained large numbers of mobbing events, while magpie and pigeon were only occasionally, if at all, mobbed (Fig. 1). This difference was statistically significant (Table 1). Male and female shrikes mobbed the mounts with an almost equal rate ($t = -0.45$, $df = 153$, $p = 0.65$). Interaction of both tested explanatory variables showed no significant effect (Table 2).

3.2 Mobbing hazardousness

The age of nestlings and the order of presentations did not significantly affect the mobbing hazardousness ($t = 1.17$, $df = 16$, $p = 0.2574$ and $t = 0.43$, $df = 156$, $p = 0.6707$, respectively), so they were removed from the

model. Hence only sex, dummy type and their interaction was included in the newly-created model.

Both the mount type and sex of shrike significantly influenced the proportion of mobbing events with physical contact, and these factors also showed a significant interaction (Tables 3–4, Figs. 2–4). The jay was physically mobbed more often than kestrel or sparrowhawk, and kestrel more often than sparrowhawk (Table 3, Fig. 3). Male shrikes generally risked more during the mobbing behaviour than did females ($t = -3.08$, $df = 2292$, $p > 0.01$; Fig. 2) but this difference was significant only in sparrowhawk and kestrel (Table 4, Fig. 4).

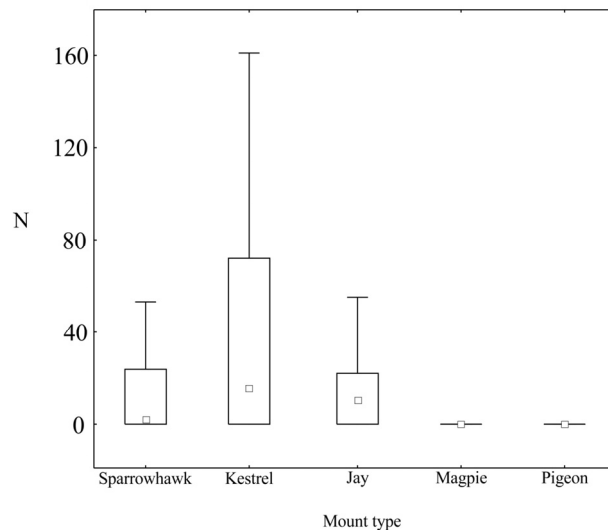


Fig. 1 Numbers of all mobbing events performed by particular shrike pairs towards particular mount types during a 20 minutes lasting trial.

Table 1 – Mobbing frequency - comparisons of the total number of mobbing events performed by shrikes to particular mounts. The lower left part of the table refers to t values; the right upper part refers to p values. The significant differences are shown in bold. Bonferroni adjustment has been used to assess the level of significance as the results of four various generalized linear mixed models (with different baselines) has been combined (critical p level = 0.05/3).

	kestrel	jay	sparrowhawk	magpie	pigeon
kestrel		0.52	0.16	>>0.01	>>0.01
jay	-0.65		0.45	>>0.01	>>0.01
sparrowhawk	1.40	0.75		>>0.01	>>0.01
magpie	-6.40	-5.75	-5.00		0.65
pigeon	5.95	5.30	4.55	-0.45	

Table 2 – Mobbing frequency in males and females towards various mounts (interaction mount type and sex of shrike) - comparisons of the total number of mobbing events performed by males and females to particular couples of mounts. Bonferroni adjustment has been used to assess the level of significance because results of three various generalized linear mixed models (with different baselines) has been combined (critical p level = 0.05/2).

Comparison	t-value	DF	p-value
Male/Female x sparrowhawk/kestrel	0.59	153	0.56
Male/Female x sparrowhawk/jay	0.74	153	0.46
Male/Female x sparrowhawk/magpie	0.89	153	0.37
Male/Female x sparrowhawk/pigeon	-1.02	153	0.31
Male/Female x kestrel/jay	0.16	153	0.88
Male/Female x kestrel/magpie	0.31	153	0.76
Male/Female x kestrel/pigeon	-0.44	153	0.66
Male/Female x jay/magpie	0.15	153	0.88
Male/Female x jay/pigeon	-0.28	153	0.78
Male/Female x magpie/pigeon	-0.13	153	0.90

Table 3 – Mobbing hazardousness - comparisons of the proportion of mobbing events with physical contact performed by shrikes to particular mounts. The lower left part of the table refers to t values; the right upper part refers to p values. The significant differences are shown in bold. Bonferroni adjustment has been used to assess the level of significance because results of three various generalized linear mixed models (with different baselines) has been combined (critical p level = 0.05/2).

	jay	kestrel	sparrowhawk
jay		>>0.01	>>0.01
kestrel	6.02		>>0.01
sparrowhawk	8.77	4.68	

Table 4 – Mobbing hazardousness in males and females towards various mounts (interaction mount type and sex of shrike) - comparisons of the proportion of mobbing events with and without physical contact performed by males and females to particular couples of mounts. The significant differences are shown in bold. Bonferroni adjustment has been used to assess the level of significance because results of three various generalized linear mixed models (with different baselines) has been combined (critical p level = 0.05/2).

Comparison	t-value	DF	p-value
Male/Female x jay/kestrel	2.79	2292	0.01
Male/Female x jay/sparrowhawk	2.46	2292	0.01
Male/Female x kestrel/Sparrowhawk	0.36	2292	0.72

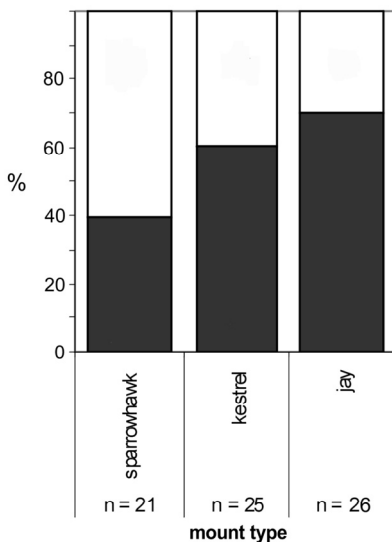


Fig. 2 Proportions of attacks with (black part of the column) and without (white part of the column) physical contact performed towards particular mount types. Number under each column represents the number of included birds out of total 36. Only dummies regularly attacked were included (without magpie and pigeon). Numbers of all attacks: sparrowhawk 419, kestrel 1316, jay 643.

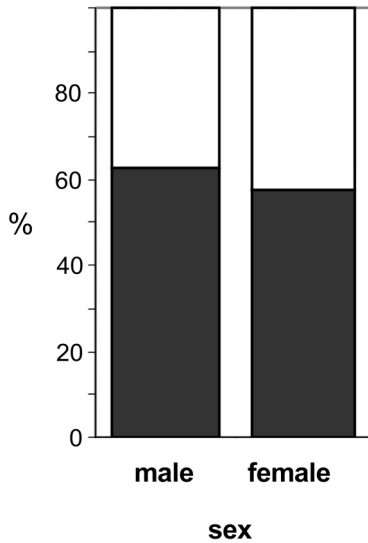


Fig. 3 Proportions of attacks with (black part of the column) and without (white part of the column) physical contact performed by both sexes towards all presented mount types together.). Numbers of all attacks: males 1411, females 872.

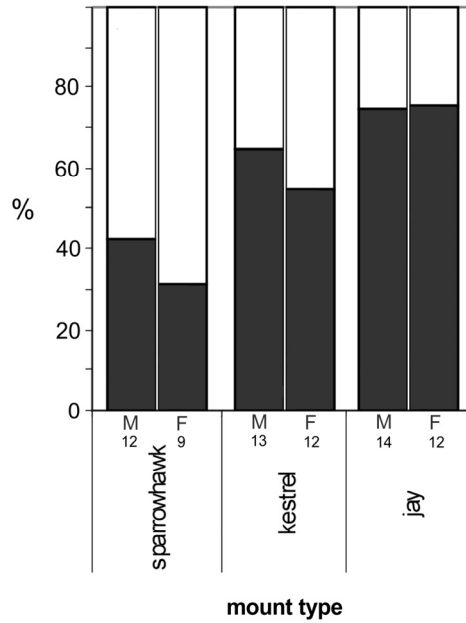


Fig. 4 Proportions of attacks with (black part of the column) and without (white part of the column) physical contact performed by both sexes towards particular mount types. Number under sex (M – male, F - female) represents the number of included birds out of total 18. Only dummies regularly attacked were included (without magpie and pigeon). Numbers of all attacks: sparrowhawk M 297, sparrowhawk F 131, kestrel M 828, kestrel F 495, jay M 287, jay F 264.

4. Discussion

We did not find clear evidence for the hypothesis that the frequency of mobbing behaviour would be adjusted to the threat to the nest content. While the jay was mobbed equally often as both raptors, the magpie was mobbed at a rate equal to the control pigeon. Thus, nest predators were not categorically mobbed more often than predators of adult birds. red-backed shrikes primarily have to decide whether to use mobbing in nest defence or not. The main criterion affecting this decision may not be the threat to nest content, as shown by the quite different responses to magpie and jay. If birds decide to use mobbing of the predator, the frequency of this behaviour appears more or less equal toward various predators. This may reflect the fact that a common objective of mobbing is to chase any predator away, which demands comparable costs and brings about equal benefits (see Dale et al. 1996).

Our second hypothesis – that the riskiness of mobbing behaviour (mobbing hazardousness) would be adjusted to the threat to the defending birds – received some support. The mobbing hazardousness – in terms of occurrence of mobbing events with physical contact – upon the three regularly-mobbed predators, steeply decreased from jay through kestrel and sparrowhawk. This suggests that the shrikes have an ability to discriminate not only corvids from raptors, but also particular species within raptors, and to assess their potential risk.

Studies on responses of breeding birds to avian predators posing different levels of risk have shown lower mobbing rates towards predators of adult birds than to nest predators (Jacobsen and Ugelvik 1992; Dale et al. 1996; Amat and Masero 2004; Hogstad 2005). The weaker mobbing of predators of adult birds has been interpreted as being both the result of a lower threat to eggs or nestlings (Dale et al. 1996) and of a greater threat to adults (Hogstad 2005). Our results agree with the above-listed studies in terms of hazardousness of mobbing. In most of these studies, the measured behavioural response of birds usually comprises alert postures, predator following and approaching, whereas in our study, the responses were fly-overs of the mount, decreases of the flight altitude and even physical attacks. Such behaviour reflects a willingness to take risks in the presence of a predator rather than an effort to chase it away. Our results

thus do not contradict with the other works, but this comparison shows the importance of a differentiation between mobbing hazardousness and mobbing frequency.

Only a few studies have tested several predators of adult birds with varying levels of threat. Curio et al. (1983) presented three species of raptors to Great Tits (*Parus major*) and found that their responses changed according to the potential threat of the raptor against themselves. Conversely, Kleindorfer et al. (2005) showed that *Acrocephalus* warblers responded to predators according to the threat to the nest. This contradiction can be explained by our results in that, besides the level of the risk to adults or nest content, the mobbing behaviour is affected also by its target. Curio et al. (1983) measured the willingness to approach the presented mount, i.e., the willingness to risk. This parameter was affected by the potential risk to defending birds, as in our shrikes. Kleindorfer et al. (2005) measured a complex reaction score of response comprising the distance from the mount, latency of response and alarm calls. Alarm calls were usually addressed to nestlings (Serra and Fernández 2010), which is why this behaviour was affected mainly by the potential threat of a presented predator to the nest.

We are puzzled by the apparent lack of willingness of the red-backed shrikes to mob the magpie, in contrast to the frequent mobbing events upon the jay. The former represents a similar if not bigger threat to the nest, compared to the jay (Chiron and Julliard 2007). The magpie is larger and more frequently preys upon adult birds than the jay (Tatner 1983; Cramp et al. 1994), so it may represent a greater threat to the adults. Some studies have shown that Blackbirds (*Turdus merula*) have higher nesting success at sites where magpies do not occur but where jays are common, compared to sites with abundant magpies (Polakova and Fuchs 2006). Nevertheless, the reaction of the shrikes to the extremely dangerous sparrowhawk was considerably stronger than to the magpie.

We hypothesize that the decision by shrikes to actively defend the nest is affected not only by the actual threat to the nest and/or the adults, but also by the likelihood of success in chasing the predator away, which may differ between the sparrowhawk and the magpie. If the former appears in the vicinity of a shrike's nest by chance and is suddenly attacked by aggressive parents, it flies away. The magpie – which often systematically

plunders birds' nests (Chiron and Julliard 2007) – may well have a priori experience on mobbing. Therefore, it may become suspicious and start to search the area after a mobbing event, an indirect signal of the nest's proximity. The effort not to disclose the location of the nest might represent an optimal antipredatory behaviour in such cases. Experimental studies have shown high conspicuousness of the mobbing behaviour and its effect on the probability of nest survival (Krama and Krams 2005; Krams et al. 2007), so the zero activity in the presence of a magpie, demonstrated here, may reflect an increased parents' fitness. This trade-off was understood also by Hogstad (2005) who found that Fieldfares (*Turdus pilaris*) ended chasing stoats (*Mustela erminea*) from their nests as it might have returned and plundered the nests when the parents were away.

Nevertheless, such an explanation assumes that the magpie is a more skilled and/or specialized nest predator than the jay, which was frequently mobbed by shrikes. No studies have compared the effect of the share of jays and magpies on nest predation; nevertheless, eggs and nestlings are more common in the diet of the latter (Cramp et al. 1994). Moreover, the magpie was found to be an extremely dangerous nest predator in an urban environment, being responsible for the population decline of various passerines, such as the blackbird (Groom 1993). Similar evidence does not exist for the jay.

Our experiment suggested no sex-related difference in the mobbing frequency, which contradicts with other studies showing higher male activity in nest defence (see Lima 2009 for a review). This pattern is common in species where the male provides food not only for nestlings but also for the incubating female, which is the case in the red-backed shrike (Lefranc and Worfolk 1997). However, in our study, we observed a sex-specific response difference when the nestlings were 5–10 days old. At this stage, the investment of the male should be greater, as it feeds an incubating female, and subsequently feeds the nestlings with the same intensity as the female (Lefranc and Worfolk 1997). This contradiction may be explained by the strong correlation in the mobbing frequency between male and female, possibly caused by stimulation of the less active partner by the more active one. Such a correlation has been shown rarely and only in birds with vigorous nest defence (Hogstad 2005). The aim of the mobbing shown by shrikes – to chase the predator away – can be more

easily achieved when both partners are active, even more so if the mobbing is aimed at warning either the younglings or the predator.

The mobbing hazardousness differed between males and females: males used to risk more than females, but only in case of predators of adult birds, suggesting the importance of a differentiation between mobbing hazardousness and mobbing frequency. Higher risk-taking by males can also be explained by the generally higher aggression of males, possibly caused by higher levels of testosterone (Wacker et al. 2009). However, Montgomerie and Weatherhead (1988) Montgomerie and Weatherhead (1988) proposed different allocation of energy in sexes with different ability to raise the offspring unaided, which is the case of red-backed shrikes (Lefranc & Worfolk 1997). Alternatively, females may be less active or more reluctant to take risks during the defence than males because of their different vulnerability. Female red-backed shrikes are more cryptically coloured than males (Lefranc and Worfolk 1997), which may more often cause a furtive behaviour and therefore lower activity during the nest defence.

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Selostus

Pikkulepinkäinen säätelee häirinnän voimakkuutta muttei siihen panostettua aikaa arvioimalla saalistajan itseensä kohdistamaa uhkaa.

Tutkimme pikkulepinkäisen (*Lanius collurio*) kykyä säädellä aikuisten ja pesän puolustustaan. Käytimme pesien vierelle tuotuja, täytettyjä, aikuisia lintuja saalistavia petolintu- (varpus- ja tuulihaukka) sekä pesiä ryöstäviä varislintu- (harakka ja närhi) ja yhtä kontrollilintulajia (kesykyhky). Pikkulepinkäiset hätistivät säännöllisesti varpus- ja tuulihaukkaa sekä närheä, mutteivät harakkaa tai kesykyhkyä. Hätistelyyn käytetty aika

(hätistelykertoja/20 min) ei vaihdellut mainittujen hätisteltyjen lajien välillä. Jos taas lepinkäiset yrittivät hätistää saalistajan pois, voimakkuuteen ei vaikuttanut itse pesään kohdistuva potentiaalinen uhka (suurempi varis- kuin petolinnuilla). Päinvastoin fyysisen kontaktin sisältävien hätistely-yrityksien osuus väheni närhestä ja tuulihaukasta varpushaukkaan, vaikka viime mainittua voidaan pitää vaarallisimpana. Ilmeisesti pikkulepinkäiset säätelivät hätistelyn voimakkuutta arvioimalla itseensä kohdistunutta uhkaa. Tuloksemme kertovat hätistelyn voimakkuuden ja ajallisen panostuksen erottamisen merkityksestä pesäpuolustuksen tutkimuksessa.

References

- Amat JA, Masero JA (2004) Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour* 67:293–300.
- Andersson M, Wiklund CG, Rundgren H (1980) Parental defence of offspring: A model and an example. *Animal Behaviour* 28:536–542. doi: 10.1016/S0003-3472(80)80062-5
- Arroyo B, Mougeot F, Bretagnolle V (2001) Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). *Behavioral Ecology and Sociobiology* 50:109–115. doi: 10.1007/s002650100342
- Biermann GC, Robertson RJ (1981) An increase in parental investment during the breeding season. *Animal Behaviour* 29:487–489.
- Brunton DH (1986) Fatal Antipredator Behavior of a Killdeer. *The Wilson Bulletin* 98:605–607.
- Bujoczek M, Ciach M (2009) Seasonal Changes in the Avian Diet of Breeding Sparrowhawks *Accipiter nisus*: How to Fulfill the Offspring's Food Demands? *Zoological studies* 48:215–222.
- Bures S, Pavel V (2003) Do birds behave in order to avoid disclosing their nest site? *Bird Study* 50:73–77.
- Caro TM (2005) *Antipredator defenses in birds and mammals*. University of Chicago Press
- Collias NE, Collias EC (1978) Group territory, co-operative breeding in birds, and a new dominance factor. *Animal Behaviour* 26:308–309.
- Cramp S, Perrins CM, Brooks DJ, Dunn E, Gillmor R (1994) *Handbook of the Birds of Europe the Middle East and North Africa*. Oxford university press, Oxford, New York
- Curio E, Klump G, Regelman K (1983) An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? *Oecologia* 60:83–88.
- Dale S, Gustavsen R, Slagsvold T (1996) Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. *Behavioral Ecology and Sociobiology* 39:31–42. doi: 10.1007/s002650050264
- Duckworth JW (1991) Responses of breeding Reed Warblers *Acrocephalus scirpaceus* to mounts of Sparrowhawk *Accipiter nisus*, Cuckoo *Cuculus canorus* and Jay *Garrulus glandarius*. *Ibis* 133:68–74.

- Flasskamp A (1994) The adaptive significance of avian mobbing .5. an experimental test of the move on hypothesis. *Ethology* 96:322–333.
- Frimmer O (1989) Food and predation in suburban Sparrowhawks *Accipiter nisus* during the breeding season. *Dansk Orn Foren Tidsskr* 83:35–44.
- Glutz v. Blotzheim UN, Bauer KM, Bezzel E (1971) *Handbuch der Vögel Mitteleuropas*, Bd. 4. Akademische Verlagsgesellschaft Frankfurt a. M.
- Golawski A (2007) Does the red-backed shrike (*Lanius collurio* L.) benefit from nesting in the association with the barred warbler (*Sylvia Nisoria bechst.*)? *Polish Journal of Ecology* 55:601–604.
- Gotzman J (1967) Remarks on ethology of the red-backed shrike, *Lanius collurio* L.-nest defence and nest desertion. *Acta Ornithologica* 10:83–96.
- Groom DW (1993) Magpie *Pica pica* predation on Blackbird *Turdus merula* nests in urban areas. *Bird Study* 40:55–62. doi: 10.1080/00063659309477129
- Halupka L (1999) Nest defence in an altricial bird with uniparental care: the influence of offspring age, brood size, stage of the breeding season and predator type. *Ornis Fennica* 76:97–105.
- Hogstad O (2005) Sex-differences in nest defence in Fieldfares *Turdus pilaris* in relation to their size and physical condition. *Ibis* 147:375–380. doi: 10.1111/j.1474-919x.2005.00416.x
- Chiron F, Julliard R (2007) Responses of Songbirds to Magpie Reduction in an Urban Habitat. *The Journal of Wildlife Management* 71:2624–2631. doi: 10.2193/2006-105
- Jacobsen O, Ugelvik M (1992) Antipredator behavior of breeding eurasian wigeon. *Journal of Field Ornithology* 63:324–330.
- King DI (1999) Mortality of an adult veery incurred during the defense of nestlings. *The Wilson bulletin* 111:576–577.
- Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. *Animal Behaviour* 69:307–313.
- Knight RL, Temple SA (1986a) Nest defence in American goldfinch. *Animal Behaviour* 34:887–897.
- Knight RL, Temple SA (1986b) Why Does Intensity of Avian Nest Defense Increase during the Nesting Cycle? *The Auk* 103:318–327.
- Korpimäeki E (1986) Diet variation, hunting habitat and reproductive output of the kestrel *Falco tinnunculus* in the light of the optimal diet theory. *Ornis Fennica* 63:84–90.
- Krama T, Krams I (2005) Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology* 16:37–40. doi: 10.1093/beheco/arh116
- Krams I, Krama T, Igaune K, Mänd R (2007) Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology* 18:1082–1084. doi: 10.1093/beheco/arm079
- Kropil L, Sládek J (1990) Contribution to the knowledge of food of some birds of prey and owls in Slovakia. *Biológia* 45:841–853.

- Lefranc N (1993) Les Pies-grieches d'Europe, d'Afrique du Nord et du Moyen-Orient. Delachaux et Niestlé, Lausanne and Paris (in French with English summary)
- Lefranc N, Worfolk T (1997) Shrikes: a guide to the shrikes of the world. Pica Press
- Lima SL (2009) Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* 84:485–513. doi: 10.1111/j.1469-185X.2009.00085.x
- McLean IG, Rhodes G (1991) Enemy recognition and response in birds. *Current ornithology* 8:173–211.
- Montgomerie RD, Weatherhead PJ (1988) Risks and Rewards of Nest Defence by Parent Birds. *The Quarterly Review of Biology* 63:167–187.
- Opdam P (1978) Feeding ecology of a sparrowhawk population (*Accipiter nisus*). *Ardea* 66:137–155.
- Overskaug K, Sunde P, Stuve G (2000) Inter-sexual differences in the diet composition of Norwegian raptors. *Ornis Norvegica* 23:24–31.
- Pavel V (2005) When do altricial birds reach maximum of their brood defence intensity? *Journal of Ethology* 24:175–179. doi: 10.1007/s10164-005-0178-y
- Pettifor RA (1990) The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. *Animal Behaviour* 39:821–827. doi: 10.1016/S0003-3472(05)80945-5
- Polakova S, Fuchs R (2006) Where to breed? Advice for Eurasian Blackbirds in Ceske Budejovice, Czech Republic. *Journal of Ornithology* 147:
- Roos S, Pärt T (2004) Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology* 73:117–127.
- Rytkönen S (2002) Nest defence in great tits *Parus major*: support for parental investment theory. *Behavioral Ecology and Sociobiology* 52:379–384. doi: 10.1007/s00265-002-0530-y
- Salata-Pilacinska B, Tryjanowski P (1998) Skład pokarmu pustułki *Falco tinnunculus* L. i sowy uszatej *Asio otus* [L.] współwystępujących w krajobrazie rolniczym Niziny Mazowieckiej. *Przegląd Przyrodniczy* 09:95–100.
- Serra C, Fernández GJ (2010) Reduction of nestlings' vocalizations in response to parental alarm calls in the Southern House Wren, *Troglodytes musculus*. *Journal of Ornithology* 152:331–336. doi: 10.1007/s10336-010-0595-8
- Shedd D (1982) Seasonal variation and function of mobbing and related antipredator behaviors of the american robin (*Turdus migratorius*). *Auk* 342–352.
- Shedd D (1983) Seasonal variation in mobbing intensity in the black-capped chickadee. *Wilson Bulletin* 343–348.
- Scheuerlein A, Van't Hof TJ, Gwinner E (2001) Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats (*Saxicola torquata axillaris*). *Proceedings of the Royal Society of London Series B-Biological Sciences* 268:1575–1582.
- Simeonov SD (1984) On the diets and the numbers of the hawks (genus *Accipiter*) in Bulgaria. *Ekologiya (Sofia)* 13:83–95.

- Sordahl TA (1990) The Risks of Avian Mobbing and Distraction Behavior: An Anecdotal Review. *The Wilson Bulletin* 102:349–352.
- Šimek J (2001) Patterns of breeding fidelity in the Red-backed Shrike (*Lanius collurio*). *Ornis Fenn* 78:61–71.
- Šťastný K, Bejček V, Hudec K (2006) Atlas hnízdního rozšíření ptáků v České republice. Aventinum, Praha
- Tatner P (1983) The diet of urban Magpies *Pica pica*. *Ibis* 125:90 – 107.
- Trnka A, Prokop P (2012) The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. *Animal Behaviour* 83:263–268. doi: 10.1016/j.anbehav.2011.10.036
- Tryjanowski P, Goławski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. *Journal of Ethology* 22:13–16. doi: 10.1007/s10164-003-0096-9
- Van Zyl AJ (1994) A comparison of the diet of the Common Kestrel *Falco tinnunculus* in South Africa and Europe. *Bird Study* 41:127–130. doi: 10.1080/00063659409477208
- Wacker DW, Coverdill AJ, Bauer CM, Wingfield JC (2009) Male territorial aggression and androgen modulation in high latitude populations of the Sooty, *Passerella iliaca sinuosa*, and Red Fox Sparrow, *Passerella iliaca zaboria*. *J Ornithol* 151:79–86. doi: 10.1007/s10336-009-0428-9
- Welbergen JA, Davies NB (2011) A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioral Ecology* 22:574–579. doi: 10.1093/beheco/arr008
- Zawadzka D, Zawadzki J (2001) Breeding Populations and Diets of the Sparrowhawk *Accipiter nisus* and the Hobby *Falco subbuteo* in the Wigry National Park (Ne Poland). *Acta Ornithologica* 36:25–31. doi: 10.3161/068.036.0111
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media

Jak t'uhýk obecný (*Lanius collurio*) rozpoznává nepřátele

Kapitola 3

Nest defense of the red-backed shrike *Lanius collurio* against five corvid species predators

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Michal Němec, disertační práce

Title: Nest defense of the red-backed shrike *Lanius collurio* against five corvid species

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Abstract

We compared the antipredation behavior of the red-backed shrike against five European corvids including the jay, nutcracker, rook, crow, and raven. These species differ in body size and in the proportion of eggs and nestlings in their diets. The jay and nutcracker are the smallest, the rook and crow are middle-sized, the raven being the largest corvid of all. The jay, crow, and raven are habitual nest plunderers, whereas the nutcracker and rook are not. The harmless pigeon was presented as a control. We analyzed (1) the number of attacks executed by shrikes against intruder presented close to shrike nests and (2) the distance between the intruder and the shrikes during the trial. The small corvids (the jay and nutcracker) were attacked significantly more intensively than the other, larger, corvids (the rook, crow, and raven) and pigeon control. All three large corvids were attacked as exceptionally as the pigeon. Shrikes approached closer to the small corvids and the pigeon than to the large corvids. These results imply that shrike antipredation strategy is adjusted to intruder size, but not to the level of intruder nest plundering specialization. Shrikes weigh up their ability to chase a given intruder away and avoid pointless aggression against large, undefeatable, intruders. This suggests that shrikes are able to assess not only the dangerousness of the intruder, but also the potential advantageousness, or otherwise, of active defense.

Key words: red-backed shrike; *Lanius collurio*; nest defense strategy; antipredation behavior; corvids

Introduction

Although corvids are not specialized predators, but mainly generalized omnivores (Lockie 1956; Holyoak 1968), many studies describe heavy predation pressure on avian nest content caused by them (Robert and Kenneth 1972; Andrén 1992; Groom 1993; Söderström et al. 1998; Schaefer 2004; Eggers et al. 2005; Bolton et al. 2007; Stevens et al. 2008; Weidinger 2009). The defense of nests against corvids has thus been investigated in many experimental studies (see Caro 2005 for review). Of the European corvids, the crow – *Corvus corone* (Röell and Bossema 1982; Buitron 1983; Siderius 1993; Hogstad 2004), jay – *Garrulus glandarius* (Gottfried 1979; Förschler 2002; Olendorf and Robinson 2008), raven – *Corvus corax* (Bures and Pavel 2003; Csermely et al. 2006), and magpie – *Pica pica* (Drachmann et al. 2002; Kryštofková et al. 2011), have been used most often in these studies. Other European corvids, including the jackdaw (*Corvus monedula*), nutcracker (*Nucifraga caryocatactes*), and rook (*Corvus frugilegus*) have never been tested in such a manner.

In passerines, most often a form of passive defense, such as alarm calls (McLean et al. 1986; Knight and Temple 1988; Hatch 1997; Förschler 2002; D’Orazio and Neudorf 2008), or approaching close to the intruder (Olendorf and Robinson 2008) have been observed. Physical attacks by passerines against corvids are apparently less frequent (Gottfried 1979; Siderius 1993; Hogstad 2004; Olendorf and Robinson 2008; Kryštofková et al. 2011). The absence of antipredation behavior is very rare (Drachmann et al. 2002). Overall, nest defense against corvids seems to be a universal phenomenon among passerines.

In a previous study (Strnad et al. 2012) we investigated the antipredation behavior of the red-backed shrike (*Lanius collurio*), a medium-sized insectivorous passerine, against various predators. We found that shrikes physically attacked the predators of adult birds (the kestrel, *Falco tinnunculus* and sparrowhawk, *Accipiter nisus*). In addition, from among corvids, the jay was attacked as intensively as both raptors; on the contrary, the magpie was almost never attacked – similarly to the harmless control (pigeon, *Columba palumbus*).

We suggest two explanations for the unexpected difference in shrike defense against the jay and magpie: 1) Shrikes avoid drawing magpie attention to the nest. We hypothesize that as the magpie is more

specialized in nest plundering than the jay and that active defense would notify it of the presence of a nest in the close vicinity, the magpie would then be motivated to search for the nest later, while the parents are not present. Skutch (1949) already proposed that parental activities around the nest could increase nest predation. Recently, this hypothesis has been supported by the results of Krama and Krams (2005) and Krams et al. (2007) which show that conspicuous mobbing behavior increases the probability of nest predation by a specialized predator. 2) Shrikes are unable to chase magpies away. The magpie is slightly heavier and probably stronger than the jay (Cramp et al. 1994) and moreover it often occurs in groups (Vines 1981; Díaz and Asensio 1991; Cramp et al. 1994), so there is a smaller chance of chasing it/them away from the nest. These two hypothesized explanations are not strictly mutually exclusive. Shrikes may try to keep the nest unknown to magpies because they are unable to chase them away.

To gain a better understanding of the shrike's antipredation behavior against the corvids, we tested its response against other corvids known from Central Europe including the nutcracker, rook, crow, and raven. For comparison with the previous study, the jay was also included. These species differ in body size but also in the proportion of eggs and nestlings in their diets (see Methods for details). We tested three hypotheses: Shrikes will use active defense against: 1) small corvids only (the jay and nutcracker); 2) all corvids, which are dangerous for nestlings only (the jay, crow, and raven); 3) the small corvid, which is dangerous for nestlings only (the jay).

Methods

Study area

The study took place in the Doupovské hory Mountains, near the town of Karlovy Vary, in the west of the Czech Republic. The experiments were conducted in the breeding season (from June to late July) during the years 2005 to 2007. The study area is located on the border of the Hradiště military area (50°10'N, 13°9'E). The prevalent landscape is that of farmland (old meadows or pastures with many shrubs), but without settlements. In the study area, the red-backed shrike reaches high breeding densities (up to 18 pairs/km²; Němec, personal observation).

Study species

The red-backed shrike (*Lanius collurio*) was chosen as the model species. It is a medium-sized insectivorous passerine, but it is also able to hunt small mammals, other songbirds, or lizards (Tryjanowski et al. 2003). It possesses a strong bill enabling it to defend its nest quite vigorously, via physical attacks (Tryjanowski and Golawski 2004, Strnad et al. 2012).

Five corvid species differing in size as well as in threat to nest content were used as intruders in our experiment. The jay (170.3 g) and nutcracker (164.8 g) are the smallest of the five, the rook (560 g) and crow (515 g) are middle-sized, the raven (1330 g) being the largest corvid of all (all mentioned weights refer to the average male, Hudec 1983). In general, corvids are considered to be potential nest predators (Lockie 1956; Holyoak 1968; Cramp et al. 1994). Indeed, the jay, crow, and raven are confirmed as habitual nest plunderers (Henze 1979; Ewins 1991; Andr n 1992; Bayne and Hobson 1997; Schaefer 2004; Zduniak 2006; Bolton et al. 2007; Stevens et al. 2008; Weidinger 2009), whereas the rook plunders nests only rarely (Holyoak 1968; Kalot s 1986 ex Cramp et al. 1994) and the nutcracker has never been recorded to do so (Cramp et al. 1994). The crow and raven occasionally chase adult birds or mammals (Hendricks and Schlang 1998; Zduniak et al. 2008), whereas the other tested corvids hunt adult birds very rarely (Hollyer 1970; Ehrlich and McLaughlin 1988; Guex 1986 ex Cramp et al. 1994).

Experimental design

We tested the response of shrikes to the stuffed dummies of the five aforementioned corvids and one non-threatening control species (the pigeon). From 2005 through 2007, we examined 25 nests containing nestlings aged between 5 to 13 days. All dummies were placed in an upright position, with their wings folded, on a 1.5 m high pole, 1 m away from, but facing, the nest. During installation, the tested dummies were covered with a cloth to prevent early responses. All dummies used were without aberrance and were freshly-made by the same taxidermist. All six intruders were presented to each tested pair of shrikes in random order. The time interval until the presentation of the next dummy was one hour. Each trial (the presentation of one dummy) lasted 20 minutes from the appearance of at least one parent. If the parents did not appear within

20 minutes, the trial was terminated and included into the data set as a zero response. The shrikes' response was recorded on a DV Camera placed on a tripod c. 50 m from the nest to exclude its effects upon the birds' behavior. All experiments took place between 10:00 a.m. and 18:00 p.m. CEST, as long as the weather was suitable.

Direct attack is the most ostentatious feature of shrike active defense. We analyzed the number of attacks executed against the dummy, both with and without physical contact with the dummy. Further, we evaluated the distance between the dummy intruder and the individual perches used by the shrikes after each change of position during the trial. The behavior of females and males were analyzed separately.

Statistical analyses

Both analyzed variables (the number of attacks as well as the distances between the intruder and tested shrikes) were log-transformed [$\log(\text{no. of attacks or meters} + 1)$] in order to bring their distributions closer to that of a normal distribution. To assess the level of cooperation between mates within each pair, we tested the correlation of the number of attacks between males and females within the pairs by Pearson's correlation coefficient. Since we found a strong correlation between mates within a pair ($r = 0.826$, $t = 17.84$, $df = 148$, $p << 0.001$), we decided to use pair identity as a random factor in both of the statistical models described below.

The dependent variable in the first statistical model was the total number of attacks executed by individual shrikes against the dummy. We used a linear mixed effect model (LME, Pinheiro et al. 2012) with five variables used as fixed-effect factors: the intruder (with values 'jay', 'nutcracker', 'rook', 'crow', 'raven', and 'pigeon'); the order of the dummy (continuous variable), the sex of the parent (values 'male' and 'female'); the date in the season (continuous variable); and the age of nestlings (continuous variable).

The dependent variable in the second statistical model was the distance between the dummy of the intruder and individual perches used by the tested shrikes after each change of position during the trial. We used LME (Pinheiro et al. 2012) with two variables used as fixed-effect factors: the intruder (with values 'jay', 'nutcracker', 'rook', 'crow', 'raven', and 'pigeon')

and the sex of the parent (values 'male' and 'female'). Because the sample size for this model was huge (tested individuals used 1–184 perches during the trial, in total 2783 perches were used), we decided to shift the level of significance to 0.01.

The significance of the model terms were evaluated by ANOVA using a partial F-test. The Tukey HSD post-hoc test was used to evaluate the differences among intruder species. All statistical analyses were computed in R 2.15.0 (R Development Core Team 2012), and all graphs were done in Statistica 9.0 (StatSoft Inc. 2010).

Results

The number of attacks

Twenty of twenty-five tested shrike pairs attacked at least one of the tested intruders. Only the intruder species (LME ANOVA: $F_{5,264} = 32.028$, $p < 0.001$) significantly influenced the number of attacks executed against the presented dummy. The order of dummies (LME ANOVA: $F_{5,264} = 1.458$, $p = 0.204$), the sex of the parent (LME ANOVA: $F_{1,264} = 1.196$, $p = 0.275$), the date within the season (LME ANOVA: $F_{1,22} = 1.206$, $p = 0.284$), and the age of nestlings (LME ANOVA: $F_{1,22} = 3.237$, $p = 0.086$) were not significant.

Both the jay and nutcracker were attacked significantly more often than all the large corvids and the pigeon ($p < 0.001$ in all comparisons); the jay was attacked significantly more often than the nutcracker ($p < 0.019$). All the larger corvids were attacked as exceptionally as the pigeon (rook $p = 0.982$; crow $p = 0.771$; raven $p = 0.451$, respectively). There were no differences within the large corvids (rook vs. crow: $p = 0.988$; rook vs. raven: $p = 0.884$; crow vs. raven: $p = 0.997$). All aforementioned p -values refer to the Tukey HSD post hoc test and pertain to Fig 1.

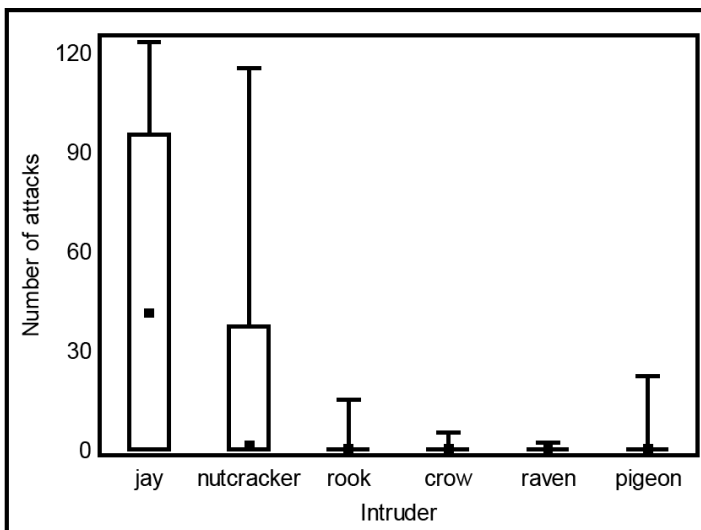


Fig. 1 Number of attacks executed by nesting pairs of the red-backed shrike ($n = 25$) against intruders presented individually close to shrikes nest. The filled-in square within each box-and-whisker drawing represents the median; the vertical span of the box represents the range from the lower to the upper quartile; the range of whiskers represents the 5% and 95% percentiles

The distance from the dummy

Only the intruder species significantly influenced the distance between the dummy of the intruder and the individual perches used by the tested individuals during the trial (LME ANOVA: $F_{5,2752} = 88.889$ $p < 0.001$). The sex of the parent was not significant (LME ANOVA: $F_{1,2752} = 0.906$, $p = 0.341$). Shrikes sat closer to the jay and nutcracker than to the pigeon and the large corvids ($p < 0.001$ in all comparisons). Moreover, they kept a greater distance from the large corvids (the rook, crow, and raven) than from the pigeon ($p < 0.001$ in all comparisons). Hence, distance kept from the jay or nutcracker was much shorter than from the large corvids ($p < 0.001$ in each comparison). All aforementioned p-values refer to Tukey HSD post hoc test and pertain to Fig 2.

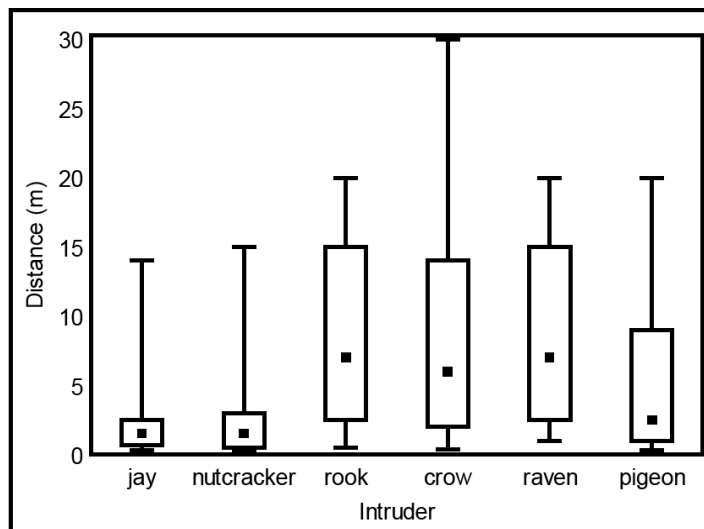


Fig. 2 The distances of sitting individuals of the red-backed shrike after each change of their position during the presence of the intruder close to their nests ($n = 2783$). The filled-in square within each box-and-whisker drawing represents the median; the vertical span of the box represents the range from the lower to upper quartile; the range of whiskers represents the 5% and 95% percentiles

Discussion

The tested shrikes attacked only the jay and nutcracker regularly. Attacks against other corvids (the rook, crow, and raven) occurred only sporadically and the number of attacks executed against these larger corvids did not differ from the number of attacks executed against the harmless pigeon. Shrike behavior towards the rook, crow, and raven was similar to behavior towards the magpie in the previous study (Strnad et al. 2012).

The simplest explanation for why shrikes do not attack the rook, crow, and raven is that shrikes assess them as dangerous to themselves. However, this is in conflict with our previous study where shrikes attacked even raptors, including the most dangerous middle European predator of small adult passerines – the sparrowhawk (Strnad et al. 2012). An alternative explanation is that, to the contrary, shrikes assess them as not dangerous. However, shrikes keep a greater distance from the rook, crow, and raven than from harmless pigeon during the trials. Moreover, shrikes never fed nestlings during the presence of any corvid, whereas they sometimes fed them during the presence of the pigeon (22 cases in total). Therefore, we can probably exclude the explanation that the shrikes assessed the tested large corvids as harmless and thus uninteresting.

Hence, we suggest that the third explanation is the most likely, that shrike passive behavior is an alternative antipredation strategy used to keep the nest unnoticed if a pair is unable to expel the intruder by force. All non-attacked corvids, including the magpie from previous study, (average male weight 208.6 g – Hudec 1983) had greater body measurements than attacked ones (see Methods for details). Thus, attacks against them probably would not be very effective. On the contrary – ineffective aggression against a large undefeatable intruder may be counterproductive, because a long and noisy fight around the nest may increase the interest of the expelled intruder or other predators in the vicinity to search for the nest (Krama and Krams 2005; Krams et al. 2007).

The effect of predator size on the choice of antipredation behavior has been studied only sporadically. Palleroni et al. (2005) tested the responses of domestic fowl (*Gallus gallus*) to three predators of differing size, but with similar proportions, coloration, and foraging strategies: a small raptor

– the male of the sharp-shinned hawk (*Accipiter striatus* – 23 cm), medium – the female of Cooper’s hawk (*Accipiter cooperii* – 51 cm), and large – the female of the goshawk (*Accipiter gentilis* – 62 cm). While the large hawk is a danger to adults, the small one is a danger only to chicks. In response to the goshawk, adults tended to crouch, to look away, and to give aerial alarm calls. In response to the sharp-shinned hawk, they tended to look towards the predator with an upright, often ruffled posture and were more likely to give ground alarm calls. There was an intermediate response to the middle-sized hawk. Evans et al. (1993) also confronted fowl with a similar task, but they used variously sized, computer-generated silhouettes of raptors presented on an overhead video monitor. Big silhouettes elicited more alarm calls than small ones. The magnitude of non-vocal responses also increased significantly with stimulus size – small silhouettes elicited visual fixation by the fowl, big silhouettes elicited crouching. Klump and Curio (1983) passed large and small models of the sparrowhawk (*Accipiter nisus*) over the blue tit (*Cyanistes caeruleus*). A life-size model inhibited locomotion for up to 3 min, and elicited the “scolding” alarm call. A small model inhibited locomotion for a shorter time (less than 1 min) and elicited the “seeet” alarm call. Curio et al. (1983) found seemingly opposite results – the great tit (*Parus major*) approaching a relatively large raptor, the tawny owl – (*Strix aluco*) at a shorter distance than the relatively smaller pigmy owl (*Glaucidium perlatum*). However, the pigmy owl is much more dangerous than the tawny owl, since small passerines prevail in the pigmy owl diet, whereas small rodents do so in that of the tawny owl (Curio et al. 1983). All aforementioned studies investigated responses towards the predators of adult birds. Tested individuals responded with only avoidance behavior or passive mobbing. Our results show that the usage of active defense against the predators of nestlings can be strongly affected by predator size. The red-backed shrike is able to anticipate the effectiveness of its attack and use the attack only in anticipation of a successful result.

It seems the shrike’s choice of nest defense strategy is not affected by the given predator’s preponderance to nest plundering. Firstly, responses (including passive sitting at a distance) to all larger corvids were identical; even though they do not represent an identical risk regarding nest predation (nor the predation of adult birds). Whereas the rook is herbivorous (Holyoak 1968; Holyoak 1972; Feare et al. 1974;

Kasprzykowski 2003), the crow and raven often plunder nests and occasionally hunt adult birds (Klicka and Winker 1991; Hendricks and Schlang 1998; Opermanis et al. 2001; Zduniak 2006; Zduniak et al. 2008; Austin and Mitchell 2010). Secondly, both of the smaller corvids were attacked vigorously, although only the jay plunders passerine nests regularly (Söderström et al. 1998; Förschler 2002; Schaefer 2004; Stevens et al. 2008). The nutcracker has never been observed to plunder nests (Cramp et al. 1994), thus shrikes probably have no individual experience with the nutcracker as a predator. Therefore, it seems that shrikes assess the nutcracker as a potential danger according to its overall appearance, namely regarding its heavy beak, which it shares with other corvids.

Ethical note

This study was conducted in the accordance with the valid laws and regulations of the Czech Republic; in compliance with ethic committee of the Faculty of Science, University of South Bohemia. Behavioral experiments on the wild birds were enabled by accreditation no. 9103/2009-17210 offered by the Ministry of the Environment of the Czech Republic. We have observed that our activities influenced neither the life of tested birds nor fate of their nests.

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References

- Andrén H (1992) Corvid Density and Nest Predation in Relation to Forest Fragmentation: A Landscape Perspective. *Ecology* 73:794–804. doi: 10.2307/1940158
- Austin JE, Mitchell CD (2010) Characteristics of Common Raven (*Corvus corax*) Predation on Sandhill Crane (*Grus canadensis*) EGGS. *Northwestern Naturalist* 91:23–29. doi: 10.1898/NWN09-01.1
- Bayne EM, Hobson KA (1997) Comparing the Effects of Landscape Fragmentation by Forestry and Agriculture on Predation of Artificial Nests. *Conservation Biology* 11:1418–1429. doi: 10.1046/j.1523-1739.1997.96135.x

- Bolton M, Butcher N, Sharpe F, Stevens D, Fisher G (2007) Remote monitoring of nests using digital camera technology. *Journal of Field Ornithology* 78:213–220. doi: 10.1111/j.1557-9263.2007.00104.x
- Buitron D (1983) Variability in the Responses of Black-Billed Magpies to Natural Predators. *Behaviour* 87:209–236.
- Bures S, Pavel V (2003) Do birds behave in order to avoid disclosing their nest site? *Bird Study* 50:73–77.
- Caro TM (2005) Antipredator defenses in birds and mammals. University of Chicago Press
- Cramp S, Perrins CM, Brooks DJ, Dunn E, Gillmor R (1994) *Handbook of the Birds of Europe the Middle East and North Africa*. Oxford university press, Oxford, New York
- Csermely D, Casagrande S, Calimero A (2006) Differential defensive response of common kestrels against a known or unknown predator. *Italian Journal of Zoology* 73:125–128.
- Curio E, Klump G, Regelman K (1983) An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? *Oecologia* 60:83–88.
- D’Orazio KA, Neudorf DLH (2008) Nest defense by Carolina Wrens. *The Wilson Ornithological Society* 120:467–472.
- Díaz JA, Asensio B (1991) Effects of group size and distance to protective cover on the vigilance behaviour of Black-billed Magpies *Pica pica*. *Bird Study* 38:38–41. doi: 10.1080/00063659109477064
- Drachmann J, Broberg MM, Sogaard P (2002) Nest predation and semicolonial breeding in Linnets *Carduelis cannabina*: Nest predation in Linnets in Denmark was caused mainly by Hooded Crows *Corvus corone cornix* and Magpies *Pica pica* with no experimental evidence of antipredator aggression. *Bird Study* 49:35–41. doi: 10.1080/00063650209461242
- Eggers S, Griesser M, Andersson T, Ekman J (2005) Nest predation and habitat change interact to influence Siberian jay numbers. *Oikos* 111:150–158. doi: 10.1111/j.0030-1299.2005.13802.x
- Ehrlich PR, McLaughlin JF (1988) Scrub Jay Predation on Starlings and Swallows: Attack and Interspecific Defense. *The Condor* 90:503–505.
- Evans CS, Macedonia JM, Marler P (1993) Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. *Animal Behaviour* 46:1–11. doi: 10.1006/anbe.1993.1156
- Ewins P (1991) Egg predation by corvids in gull colonies on Lake Huron. *Colon Waterbirds* 14:186–189.
- Feare C, Dunnet G, Patterson I (1974) Ecological studies of the Rook (*Corvus frugilegus* L.) in North-East Scotland: Food intake and feeding behaviour. *Journal of Applied Ecology* Vol. 11:867–896.
- Förschler MI (2002) Predation strategy of the Eurasian Jay *Garrulus glandarius* and antipredator response by the Citril Finch *Serinus citrinella*. *Revista Catalana d’Ornitologia* 19:41–43.
- Gottfried BM (1979) Anti-predator aggression in birds nesting in old field habitats: an experimental analysis. *The Condor* 81:251–257. doi: 10.2307/1367626

- Groom DW (1993) Magpie *Pica pica* predation on Blackbird *Turdus merula* nests in urban areas. *Bird Study* 40:55–62. doi: 10.1080/00063659309477129
- Hatch MI (1997) Variation in song sparrow nest defense: individual consistency and relationship to nest success. *The Condor* 99:282–289. doi: 10.2307/1369934
- Hendricks P, Schlang S (1998) Aerial attacks by Common Ravens, *Corvus corax*, on adult feral pigeons, *Columbia livia*. *Can Field-Nat* 112:702–703.
- Henze O (1979) Tonband zur Eichelhäherbekämpfung. *Anzeiger für Schädlingskunde* 52:136–136.
- Hogstad O (2004) Nest defence strategies in the Fieldfare *Turdus pilaris*: The responses on an avian and a mammalian predator. *Ardea* 92:79–84.
- Hollyer J (1970) The invasion of Nutcrackers in autumn 1968. *British Birds* 63:353–373.
- Holyoak D (1968) A comparative study of the food of some British Corvidae. *Bird Study* 15:147. doi: 10.1080/00063656809476194
- Holyoak DT (1972) Food of the Rook in Britain. *Bird Study Volume* 19:59 – 68.
- Hudec K (1983) Laniidae – Ťuhýkovití. *Fauna ČSSR - Ptáci 3/II*. Academia, Praha, pp 840–873
- Kasprzykowski Z (2003) Habitat preferences of foraging rooks *Corvus frugilegus* during the breeding period in the agricultural landscape of eastern Poland. *Acta Ornithologica* 38:27–31. doi: 10.3161/068.038.0107
- Klicka J, Winker K (1991) Observations of ravens preying on adult kittiwakes. *The Condor* 93:755–757. doi: 10.2307/1368209
- Klump GM, Curio E (1983) Reactions of blue tits *Parus Caeruleus* to hawk models of different sizes. *Bird Behavior* 4:78–81.
- Knight R, Temple S (1988) Nest-defense behavior in the red-winged blackbird. *Condor* 90:193–200.
- Krama T, Krams I (2005) Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology* 16:37–40. doi: 10.1093/beheco/arh116
- Krams I, Krama T, Igaune K, Mänd R (2007) Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology* 18:1082–1084. doi: 10.1093/beheco/arm079
- Kryštofková M, Haas M, Exnerová A (2011) Nest defense in blackbirds *Turdus merula*: effect of predator distance and parental sex. *Acta Ornithologica* 46:55–63. doi: 10.3161/000164511X589938
- Lockie JD (1956) The food and feeding behaviour of the jackdaw, rook and carrion crow. *Journal of Animal Ecology* 25:421–428.
- McLean IG, Smith JNM, Stewart KG (1986) Mobbing behaviour, nest exposure, and breeding success in the american robin. *Behaviour* 96:171–185. doi: 10.1163/156853986X00270
- Olendorf R, Robinson SK (2008) Effectiveness of nest defence in the Acadian Flycatcher *Empidonax virens*. *Ibis* 142:365–371. doi: 10.1111/j.1474-919X.2000.tb04432.x
- Opermanis O, Mednis A, Bauga I (2001) Duck nests and predators: interaction, specialisation and possible management. *Wildlife Biology* 7:87–96.

- Palleroni, Hauser, Marler (2005) Do responses of galliform birds vary adaptively with predator size? *Animal Cognition* 8:200–210. doi: 10.1007/s10071-004-0250-y
- Pinheiro J, Bates D, DebRoy S, et al. (2012) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103.
- R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Robert JE, Kenneth HE (1972) Evaluation of nesting cover as protection from magpie predation. *The Journal of Wildlife Management* 36:727–732.
- Röell A, Bossema I (1982) A comparison of nest defence by jackdaws, rooks, magpies and crows. *Behavioral Ecology and Sociobiology* 11:1–6. doi: 10.1007/BF00297658
- Schaefer T (2004) Video monitoring of shrub-nests reveals nest predators: Capsule Jays *Garrulus glandarius* are the most common predators, but carnivorous mammals and some other species also predate nests. *Bird Study* 51:170. doi: 10.1080/00063650409461349
- Siderius JA (1993) Nest defense in relation to nesting stage and response of parents to repeated model presentations in the eastern kingbird (*Tyrannus tyrannus*). *The Auk* 110:921–923.
- Skutch AF (1949) Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–455. doi: 10.1111/j.1474-919X.1949.tb02293.x
- Söderström B, Pärt T, Rydén J (1998) Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia* 117:108–118. doi: 10.1007/s004420050638
- Stevens DK, Anderson GQA, Grice PV, et al. (2008) Predators of Spotted Flycatcher *Muscicapa striata* nests in southern England as determined by digital nest-cameras: Capsule Avian predators are principally responsible. *Bird Study* 55:179–187. doi: 10.1080/00063650809461520
- Strnad M, Němec M, Veselý P, Fuchs R (2012) Red-backed Shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. *Ornis Fennica* 89:206–215.
- Vines G (1981) A Socio-Ecology of Magpies *Pica Pica*. *Ibis* 123:190–202. doi: 10.1111/j.1474-919X.1981.tb00924.x
- Weidinger K (2009) Nest predators of woodland open-nesting songbirds in central Europe. *Ibis* 151:352–360. doi: 10.1111/j.1474-919X.2009.00907.x
- Zduniak P (2006) The prey of hooded crow (*Corvus cornix* L.) in wetland: Study of damaged egg shells of birds. *Polish Journal of Ecology* 54:491–498.
- Zduniak P, Kosicki J, Goldyn B (2008) Un-paint it black: Avian prey as a component of the diet of nestling Hooded Crows *Corvus cornix*. *Belgian Journal of Zoology* 138:85–89.

Jak tuhýk obecný (*Lanius collurio*) rozpoznává nepřátele

Kapitola 4

The red-backed shrike *Lanius collurio* recognize the predator due local, not due global features

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Manuskript for Animal Congition

Michal Němec, disertační práce

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Michal Němec, Tereza Součková, and Roman Fuchs

Abstract

Birds are strongly motivated to discriminate among various predators to ensure survival and reproductive success. Thus, predator discrimination provides an occasion to investigate the process of categorisation via non-trained animals. The most important role in categorization processes is usually attributed to the prominent features shared by all members within the category (a.k.a. salient cues/features), but absent in the other categories. However, it is known that birds are also able to discriminate variously dangerous raptors according species-specific components of colouration. In this study, we simultaneously manipulated general raptor salient features (hooked beak, talons with claws, and eyes with supraorbital ridges) and species-specific plumage colouration on a kestrel dummy to investigate if both types of cues are necessary for proper categorisation of the predator by the red-backed shrike. We found, that the presence of general raptor salient features is necessary for the categorization of the predator. The kestrel dummy with natural species-specific colouration but without general raptor salient features were treated by shrikes as uninteresting objects; whereas the dummy with identical colouration and general raptor salient features were recognized as a kestrel and elicited strong anti-predator behaviour.

Introduction

Animals perceive their surrounding, recognize familiar objects such as food, mates or predators, and respond appropriately to them. If encounter novel object, the animal tries to generalize it with some known one into which it can respond. Such a generalization is conditioned by the ability of categorization. In absence of categorization, each object or event would be identified as unique, and the generalization would be impossible (Bekoff et al. 2002). The process of category formation is one of the fundamental topics within the animal cognitive research. Since avian dominant sense is sight, birds, especially pigeons, are the most frequent model species for this research. In the eighties, two opposing concepts were proposed. The “Particulate feature theory” assumes birds see objects as non-organized set of abstract local features. Only the presence of these features, but not their absolute or relative position, is required for categorization (Cerella 1980). On the other hand, “Recognition by components theory” assumes each object is defined not only by contained local features (geons), but also by their mutual positions (Biederman 1987). The results of laboratory experiments endorsing the relevance of “Particulate feature theory” (Cerella 1979; Cerella 1980; Herrnstein 1984; Cerella 1986; Delius and Hollard 1995; Cavoto and Cook 2001) or “Recognition by components” theory (Steele 1990; Watanabe and Ito 1991; Brown and Dooling 1993; Kirkpatrick-Steger et al. 1996; Kirkpatrick-Steger et al. 1998) were found. It seems that pigeons perceive both local (elemental) and global (configural, spatial) features of complex cues in similar way, as humans do. They are probably able to switch between these two attempts according to the type and quality of the presented cue (Kirkpatrick-Steger et al. 1998; Soto and Wasserman 2012; Troje and Aust 2013).

Most of experimental studies investigating categorization processes in animals were realized mainly via laboratory experiments with pigeons based on the operant conditioning (see Jitsumori and Delius 2001 for review). Allen and Hauser (1991) criticized the common laboratory technique, which use responses to photographs (often photographs of irrelevant stimuli for tested animal) to investigate categorization processes in non-human animal, because the animal reactions to relevant or irrelevant stimuli can be different (Pashler and Yantis 2004).

Another approach in categorization research is to focus on natural behaviour of non-trained animals. It means to confront the animal with natural task which must be solved to ensure future reproductive success (Bolles and Beecher 1988). Predator recognition and categorization is an excellent example of such a problem. Wide array of predator species represents various types of peril, therefore the animal necessarily needs to be able to faultlessly discriminate among them (Allen and Bekoff 1999). It was demonstrated many times, that birds are able to discriminate nest predators from nest parasites (D’Orazio and Neudorf 2008) or predators of adults from predators of the young (Onnebrink and Curio 1991; Strnad et al. 2012). They can also discern the predators of different taxa (Strnad et al. 2012; Suzuki and Ueda 2012; Tvardíková and Fuchs 2012) as well as sizes (Klump and Curio 1983; Palleroni et al. 2005; Němec and Fuchs 2013). However, processes of predator categorisation alone used by non-trained birds were not investigated in detail.

In classical ethology, the most important role in recognition and categorization processes is usually attributed to salient cues – prominent features shared by all members within the category, but absent in the other categories (Schleidt et al. 2011). The crucial role of salient cues in predator recognition was firstly detected in experiments with cardboard silhouette of “short necked” bird. This dummy elicits escape behaviour in tested birds independently of its colour or shape of wings and tail (Krätzig 1940, Lorenz 1940 ex Tinbergen 1948). The experiments with stuffed dummies consequently confirmed the importance of the eyes (Scaife 1976; Watve et al. 2002; Trnka et al. 2012; Beránková et al. 2014), beak (Burley and Coopersmith 1987; Gill et al. 1997), and salient components of colouration (Davies and Welbergen 2008; Pincemy et al. 2009; Welbergen and Davies 2011) for recognition of predators (Scaife 1976; Watve et al. 2002; Davies and Welbergen 2008), nest parasites (Gill et al. 1997; Welbergen and Davies 2011; Trnka et al. 2012), and sexual partners (Burley and Coopersmith 1987; Pincemy et al. 2009). If these features were removed from tested species, non-trained birds were unable to recognize them, or their responses were significantly minor.

However, birds are also able to distinguish particular species of raptors and respond adequately to various perils they represent. Once the stuffed dummy of kestrel (*Falco tinnunculus*) is exposed close to the red-backed

shrike (*Lanius collurio*) nest, it is audaciously attacked by parent shrikes. On the contrary, the dummy of the sparrowhawk (*Accipiter nisus*), the other common small raptor, is attacked cautiously, which implies that shrikes can subtly discriminate variously dangerous raptors according species-specific components of colouration (Strnad et al. 2012).

Hence, there persist questions if both types of salient cues – general raptor (hooked beak, talons with claws, and eyes with supraorbital ridges) and species-specific (plumage colouration) – are necessary for proper categorisation of enemy and what is superior to proper discrimination of species. To examine these questions, we decided to manipulate simultaneously potential general raptor salient features and species-specific colour pattern in this study. As a model species, the kestrel, a common small middle European raptor, was chosen. Two groups of kestrel dummies were used. Whereas dummies in ‘raptor’ group, possessed general raptor salient features (normal kestrel beak, claws and eyes with supraorbital ridges), dummies in ‘harmless’ group had these features changed to the beak, talons and eyes of harmless bird species, the pigeon (*Columba livia*). In both groups, three different colour patterns were applied on the kestrel bodies: ‘natural’ (unmodified colouration of the kestrel), ‘brown’ (only underlay colours of the natural colouration of kestrel, without back spots and streaks), and ‘aviceda’ (the colouration of the black baza, *Aviceda leuphotes* – the south-Asian raptor, which is unfamiliar to the red-backed shrike). We tested following hypotheses.

1) Both general raptor salient features and species-specific colouration are necessary for proper categorisation of the kestrel. Therefore, the red-backed shrike will attack unmodified kestrel dummy (‘raptor-natural’) more intensively than any other dummy.

2) Only general raptor salient features are sufficient for proper categorisation of raptor. Therefore, the red-backed shrike will attack all dummies with general raptor salient features (‘raptor-natural’, ‘raptor-brown’, and ‘raptor-aviceda’) with higher intensity than harmless control, ‘stuffed-pigeon’.

3) Only species-specific colouration is sufficient cue for proper categorization of the kestrel. Therefore, the red-backed shrike will attack both dummies with unmodified species-specific kestrel colouration (‘raptor-natural’ and ‘harmless-natural’) with similar intensity.

4) Only basic components of species-specific colouration are sufficient for proper categorisation of the kestrel. Therefore, the red-backed shrike will attack the dummies with simplified species-specific kestrel colouration ('raptor-brown' and 'harmless-brown') with similar intensity as the dummies with unmodified kestrel colouration ('raptor-natural' and 'harmless-natural').

Methods

Study area

The study took place in the Doupov Mountains, nearby the town of Karlovy Vary, in the west of the Czech Republic. The experiments were conducted during the breeding season from June to late July in years 2009 to 2010. The study area is located on the south border of the Hradiště military area (50°10'N, 13°9'E). The prevalent landscape is that of farmland (old meadows or pastures with many shrubs), but without settlements. In the study area, the red-backed shrike reaches high breeding densities (up to 18 pairs per km²; Němec, personal observation).

Study species

The red-backed shrike, that was chosen to be the tested species, is a medium-sized mainly insectivorous passerine, which is able to hunt also small mammals, lizards and other songbirds (Tryjanowski et al. 2003). The red-backed shrike defends its nest quite vigorously, via physical attacks (Tryjanowski and Goławski 2004; Strnad et al. 2012), and is able to adjust the defence intensity according to the predator dangerousness (Strnad et al. 2012).

As predator species, a kestrel was chosen. It is small-sized avian raptor (Falconidae), which possesses common raptor features like hooked beak, relatively strong yellow talons with claws, and "frown" eyes with supraorbital ridges. Its colouration is unmistakable for human observer. The background colours are rusty brown on the dorsal and rusty to ochre on the ventral part of the body. Further, there are black spots and streaks on the dorsal (head, back, wings, and tail) as well as ventral (breast, flanks) part of body. Moreover, male has greyish head. Kestrel hunts mainly on rodents and occasionally small passerines (Riegert and Fuchs 2011). The

red-backed shrike is familiar with kestrel and attacks it in order to expel it from own territory (Strnad et al. 2012).

Experimental design

We tested the response of the shrikes to the kestrel dummies, placed close to shrike nest. From 2009 to 2010, we examined 38 nesting pairs, containing nestlings aged between 2–14 days. Two groups of the kestrel dummies were established (Figure 1). The dummies in the group ‘raptor’ possess normal (not adjusted) hooked beak, strong yellow talons with black claws, and eyes with supraorbital ridges. These general ‘raptor’ salient features were removed and replaced in the group ‘harmless’ by pigeons beak (straight and weak), talons (pinkish, with smoother whitish legs without hooked claws), and eyes (without the supraorbital ridges).

There were three patterns of body colouration within both groups of kestrel dummies: a) ‘normal’ – natural kestrel female colouration; b) ‘brown’ – only the background brown and rusty colours of kestrel female natural colouration preserved – without black spots and streaks; c) ‘aviceda’ – body colouration of south Asian raptor black baza, resembles none of European raptors – thus unfamiliar to shrikes. All dummies were made from the plush. The usability of plush dummies in anti-predator experiment was verified by (Němec et al. 2015). The red-backed shrike responded equally to plush jay dummy and stuffed jay dummy – the response was only just non-significantly weaker. Therefore, we used two stuffed dummies as controls in this study – the kestrel as the raptor control and the pigeon as the harmless control. All dummies used were freshly-made.

In order to prevent tested birds from effusive intrusion, each tested shrike pair was confronted only with dummies from either group ‘raptor’ (19 tested pairs), or ‘harmless’ (19 tested pairs), but always with both stuffed control dummies. All five dummies pertaining to one set were presented subsequently in random order. Each presented dummy was placed in an upright position, with its wings folded, on a 1.5 m high pole, 1 m away from, but facing, the nest. During installation, the tested dummy was covered with a cloth to prevent early responses. Each trial (presentation of single dummy) lasted 20 minutes starting from the appearance of at least one parent. If neither parent appeared within 20

minutes, the trial was terminated and included into the dataset as a zero response. This approach was used, because shrikes tend to visit the nest relatively rarely (the feeding frequency is usually 5–10 minutes, at least, parents keep visiting the nest during the 20 minutes; personal observation) when foraging far from the nest, and they might simply not to be aware of the presence of the dummy. The time interval until the presentation of the next dummy was one hour from the experimenter disappearance from shrikes' territory. The shrikes' response was recorded on a DV Camera placed on a tripod c. 50 m from the nest to exclude its effects upon the birds' behaviour. All experiments took place between 10:00 a.m. and 18:00, as long as the weather was suitable.

A direct attack (defined as a flight over the dummy with apparent decrease of bird's height above the dummy) is the most ostentatious feature of the parent shrike active nest defence. We recorded the number of attacks executed against the dummy, both with and without physical contact with the dummy. The behaviour of females and males were monitored separately.

Statistical analyses

The analyzed variable was the number of the attacks performed by the parent shrikes against individually presented dummy. The values of this variable were log-transformed [$\log(\text{no. of attacks} + 1)$] in order to bring their distribution closer to that of a normal distribution. To assess the level of cooperation between mates within each pair, we tested the correlation of the number of the attacks between males and females within the pairs by Pearson's correlation coefficient. Since we found a strong correlation between mates within a pair ($r = 0.641$, $t = 11.45$, $df = 188$, $p \ll 0.001$), we decided to use a pair identity as a random factor in the subsequent linear mixed-effect model (LME, Pinheiro et al. 2012). To test given hypotheses it is necessary to evaluate interaction of two factors – the type of salient features and colouration of the dummy. However, both controls (the 'stuffed-kestrel' and 'stuffed-pigeon') are not describable by this interaction, so we merged all combinations of both factors into one factor "dummy". Four variables were included into the model in the following order: the dummy (with values 'raptor-natural', 'raptor-brown', 'raptor-aviceda', 'harmless-natural', 'harmless-brown', 'harmless-aviceda',

'stuffed-kestrel', 'stuffed-pigeon'), the sex of parent (values 'male' and 'female'), the age of nestlings (continuous variable), and the order of the dummy (values 'first', 'second', 'third', 'fourth', 'fifth'). The effect of particular variables was evaluated by Likelihood ratio test using ANOVA with a partial F-test. The Tukey HSD post-hoc test was used to evaluate the differences among levels of particular categorical variables. All statistical analyses were computed in R 2.15.0 (R Development Core Team 2012), and all graphs were created in Statistica 9.0 (StatSoft, Inc. 2011).

Results

Seven of thirty-eight tested shrike pairs did not attack any of tested dummies. The rest of tested shrike pairs (31) attacked at least one of presented dummies. The number of attacks was influenced only by the presented dummy (LME ANOVA: $F_{7,329} = 14.038$, $p < 0.001$) and by sex of the parents (LME ANOVA: $F_{1,329} = 11.799$, $p < 0.001$). The effect of the age of nestlings (LME ANOVA: $F_{1,329} = 0.718$, $p = 0.397$) and the order of the dummies presentation (LME ANOVA: $F_{4,329} = 0.747$, $p = 0.561$) were not significant.

Tukey HSD post hoc test (Table 1, Figure 2) detected that only the 'raptor-natural' attacked significantly more often than the harmless control 'stuffed-pigeon'. Simultaneously, the 'raptor-natural' dummy was attacked as often as the raptor control 'stuffed-kestrel'. The 'raptor-brown' dummy was attacked significantly less often than raptor control 'stuffed-kestrel', however, on contradiction to all other tested dummies, equally as 'raptor-natural' dummy. All dummies with harmless salient features were almost not attacked. The number of the attacks against 'raptor-aviceda' dummy was not significantly different from the number of attacks against dummies with harmless salient features. Males attacked all dummies more often than females (Figure 3).

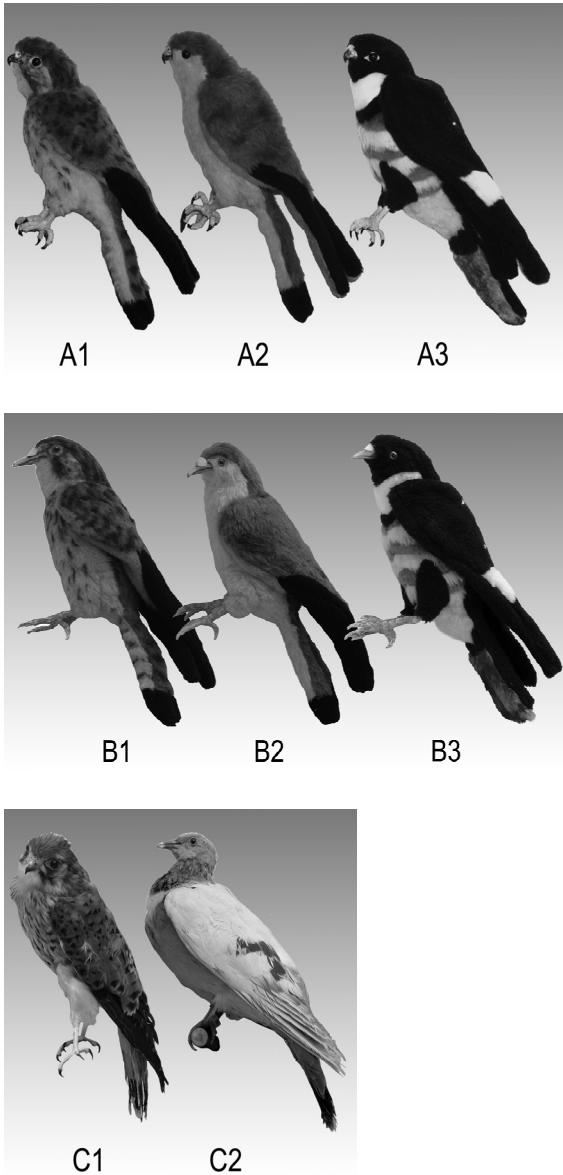


Figure 1: The kestrel dummies, presented close to the red-backed shrike's nests. Three different colour patterns were applied on the kestrel body:

'natural' (unmodified colouration of the kestrel), 'brown' (only underlay colours of the natural colouration of kestrel, without back spots and streaks), and 'aviceda' (the colouration of the black baza, *Aviceda leuphotes* – the south-Asian raptor, which is unfamiliar to the red-backed shrike).

A) The dummies with general raptor salient features: A1 raptor-natural, A2 raptor-brown, A3 raptor-aviceda.

B) The dummies, which had general raptor salient features changed to the beak, talons and eyes of the pigeon: B1 harmless-natural, B2 harmless-brown, B3 harmless-aviceda.

C) Control stuffed dummies: C1 the kestrel, C2 the pigeon.

Table 1 Results of Tukey HSD post-hoc test showing the differences in the red-backed shrike anti-predator response against particular dummies. The *p* values are above the diagonal, the *Z* statistics are under the diagonal.

	stuffed kestrel	raptor natural	raptor brown	raptor aviceda	harmless natural	harmless brown	harmless aviceda	stuffed pigeon
stuffed kestrel	-	n.s.	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
raptor natural	n.s.	-	n.s.	0.010	0.008	0.026	0.023	< 0.001
raptor brown	4.157	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.
raptor aviceda	5.600	3.494	n.s.	-	n.s.	n.s.	n.s.	n.s.
harmless natural	6.367	3.584	n.s.	n.s.	-	n.s.	n.s.	n.s.
harmless brown	5.900	3.227	n.s.	n.s.	n.s.	-	n.s.	n.s.
harmless aviceda	5.983	3.263	n.s.	n.s.	n.s.	n.s.	-	n.s.
stuffed pigeon	-8.165	< 0.001	n.s.	n.s.	n.s.	n.s.	n.s.	-

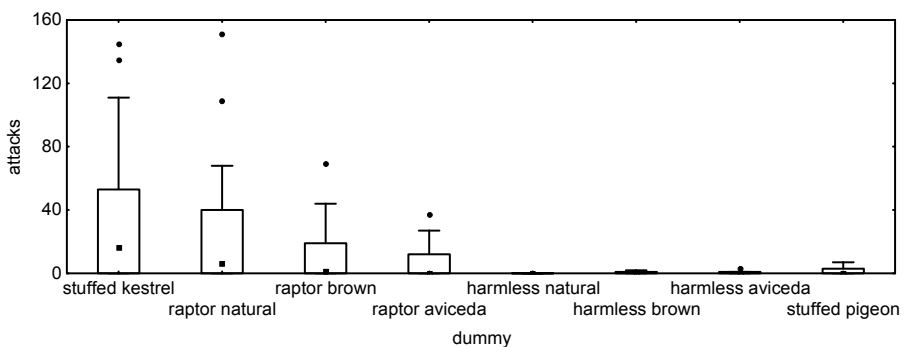


Figure 2: Number of the attacks performed by the red-backed shrikes against presented dummies (*n* = 38). The filled square within each box-and-whisker drawing represents the median; the vertical span of the box represents the non-outlier values, and the rounded spots represent the outliers.

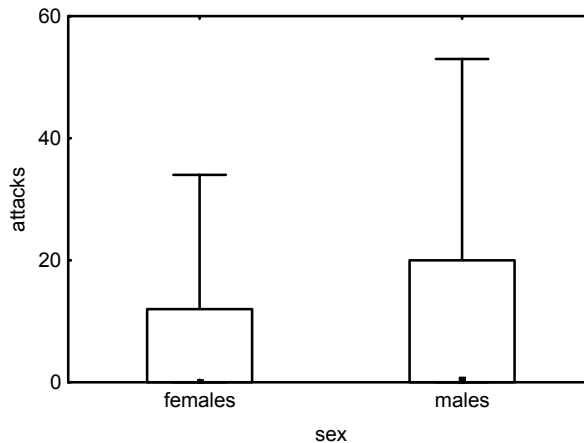


Figure 3: Number of attacks performed by the males and females of the red-backed shrike against presented kestrel dummies with general raptor salient features and control stuffed dummies ($n = 19$). The filled square within each box-and-whisker drawing represents the median; the vertical span of the box represents the range from the lower to upper quartile; the range of whiskers represents the 10 % and 90 % percentile.

Discussion

Only ‘raptor-natural’ dummy (unmodified kestrel dummy with both general raptor salient features and species-specific kestrel colouration) was attacked as intensively as a raptor control (‘stuffed-kestrel’). This result validates the hypothesis no. 1 that both general raptor salient features (hooked beak, yellow talons with claws, and eyes with supraorbital ridges) and species-specific colouration are necessary for proper categorisation of the kestrel.

None of the dummies with harmless salient features was attacked more intensively than the harmless control ‘stuffed-pigeon’. From dummies with general raptor salient features, only the ‘raptor-natural’ was attacked by shrikes more intensively than ‘stuffed-pigeon’. These results can imply that general raptor salient features alone are not sufficient cue for proper categorization of the predator. However, we cannot exclude the possibility that the red-backed shrikes recognized the ‘raptor-aviceda’ dummy as a raptor, but they might have not considered it as dangerous predator towards which the defence is necessary. The active mobbing is the very last option in the anti-predator response (Caro 2005) and shrikes may use it only against familiar enemies. Thus, we cannot exclude for a certainty

the hypothesis no. 2, which presume that only general raptor salient features are sufficient for proper categorization of raptor.

On the other hand, we can obviously refuse the hypothesis no. 3, which supposed that only species-specific colouration was sufficient for proper categorization of the kestrel, because even 'harmless-natural' dummy with complete species-specific colouration was not categorized as the kestrel. The red-backed shrike almost ignored this dummy, which lacked general raptor salient features, and treated it like a harmless control 'stuffed-pigeon'.

The 'raptor-brown' dummy was not attacked significantly more intensively than control dummy 'stuffed-pigeon', however also not less intensively than 'raptor-natural' dummy. It means that we can carefully validate the hypothesis no. 4, because if general raptor salient features were present, also simplified (i.e. incomplete) colouration of kestrel was sufficient cue for categorization of this dummy as the kestrel at least by some tested shrikes. Nevertheless, it seems that substantial decrease of discrimination accuracy appeared in this case.

The most surprising result of our study is that presence of general raptor salient features is absolutely necessary for the categorization of the predator, even in the case its species-specific colouration, which is present, is used for discrimination of this predator among others by the red-backed shrike. It can seem paradoxically. At the first glance, it is the same as if the human observer could not recognize a car without wheels as a car. On the other hand, the car without wheels is unable to serve for transportation. Thus, we guess that the shrikes possibly recognized the kestrel, but they did not expect it as a danger for their nestlings, because it had neither hooked beak nor claws. However, this explanation assumes that the process of predator recognition is not only about the registration of the cues, but it is much more sophisticated process in shrikes. Similar processes are speculated by the Theory of mind. However, it handles with the ability of one animal to anticipate the intention of the other one (Bugnyar 2007), and it is focused on intraspecific relationships. Other possibility is that predator recognition proceeds in two levels. Firstly, the predator is detected according to the presence of general raptor salient features and after that, the species-specific features are used for recognition that determines the type of risk more accurately. If the dummy

lacks general raptor salient features, the more accurate species-specific recognition does not pass.

The role of general salient features in predator recognition towards various silhouette shapes of birds was firstly detected in responses of willow ptarmigan (*Lagopus lagopus*) and domesticated fowl (*Gallus domesticus*). The length of the neck essentially affected the anti-predator response. If the silhouette was moved in the direction, which induced impression of the bird with short neck and long tail, tested fowls perceived it as a raptor and responded by escape behaviour. On the contrary, if the silhouette was moved in the direction which induced the impression of the bird with long neck and short tail, anti-predator behaviour did not occur in tested birds (Goethe 1937) (Krätzig 1940; Lorenz 1940 ex Tinbergen 1948). However, when Schleidt et al. (2011) revised Tinbergen and Lorenz's experiments he concluded that the releaser of the anti-predator response was probably not "a short neck" but rather "a slow relative speed of flight".

The importance of the eyes as the salient feature was documented repeatedly. Curio (1975) presented stuffed dummy of the pigmy owl (*Glaucidium passerinum*) with modified eyes to the pied flycatcher (*Ficedula hypoleuca*). A strong response occurred against the unmodified control dummy as well as the dummy with triangular eyes. If one eye was covered by feathers, flycatchers almost ignored the dummy. If both of eyes were hidden, it elicited some anti-predator response, but the difference between no-eyed and one-eyed dummy was not significant. The author explained the slight increase via restored symmetry and added that the shape of eyes was less critical than their number. Scaife (1976) also tested the importance of eyes and found that yellow raptor eyes elicited stress response (escape to the cover) in chicks, even if placed on harmless stuffed kiwi. There are few recent studies, which also claim the importance of eyes as anti-predation starter in birds. Trnka et al. (2012) tested the response of the great reed warbler (*Acrocephalus arundinaceus*) towards the dummy of cuckoo (*Cuculus canorus*) and found out that the mobbing response was significantly stronger against the unmodified stuffed dummy of cuckoo with yellow eyes, than against the dummy with black eye.

On the other hand, just the presence of salient feature is not the only one considerable explanation of why the absence or modification of the

intruders' eyes might have affected the behaviour of mobbers. Watve et al. (2002) found, that bee-eaters (*Merops orientalis*) were able to assess the angle of the predator's gaze and anticipate what the predator can or cannot see. The angle of predator's gaze and the nest affected the bee-eaters response more strongly than the angle formed by predator's body with the nest. Bee-eaters entered the nest more frequently when the predator was unable to see the nest. Similar findings described Carter et al. (2008), who tested the effect of human gaze to the European starlings (*Sturnus vulgaris*), placed in aviary. If the human's gaze was averted from the food, starlings resumed feeding sooner, at a higher rate, and consumed more food too.

The role of the beak as the salient feature in predator recognition and categorization was tested surprisingly rarely, and moreover, never in the raptors, although shape of their beak has been understood as characteristic and relatively uniform feature within the genus. Gill et al. (1997) removed the beak from a freeze-dried brown-headed cowbird (*Molothrus ater*) and replaced it with a beak of a juvenile starling (*Sturnus vulgaris*), which was blackish like cowbird's one, but shorter and thicker. Yellow warblers (*Dendroica petechia*) responded more intensively towards control dummy with original longer, thinner beak, which suggested that beak shape was a salient sign in recognition of this nest parasite.

The conspicuous and species-specific elements of plumage colouration could serve as salient features for the recognition of particular predator or nest parasite species or conspecifics. Already in 1946 Lack found out that only a bunch of red feathers elicited an aggressive response of a robin (*Erithacus rubecula*) male (Tinbergen 1948).

One of the most extensive anti-predator investigations was conducted by Curio (1975) with pied flycatchers. In first experiment, he presented them the dummies of the red-backed shrike with colour modification of eye strip. The strongest responses elicited only the control unmodified dummy. Except the dummy with red eye stripe, which elicited the same response as unmodified dummy, all other modifications of dummies (eye strip green, white on black head, black on white head, without strip, resp. without strip and eye) caused strong decrease of intensity in flycatcher's response. Then, the contrast between eye strip and head was tested. Curio either decreased the saturation of the strip, or in contrary saturated the

colour of the head. The desaturation of the stripe did not elicit any changes in flycatcher's response until the stripe was fully merged with the background. After that, the anti-predator response ceased. The response also changed in dependence on the saturation of the bird's head. The richer coloured head was, the stronger anti-predation response appeared. However, when the head was totally black, no reaction occurred. The location of the stripe was also important. The flycatchers responded strongly to the unmodified control dummy and even more strongly to the dummy, which had the eye stripe shifted from the front to the nape. Other modifications (the stripe on the neck, on the belly, vertically on the vertex) elicited only slight anti-predator responses in tested flycatchers. Another experiment included the presentation of dummies of the red-backed shrike male with modified colouration of body to the flycatchers. However, the flycatchers responded strongly only towards the unmodified control dummy. If the original colour body pattern was substituted by white colour only with the black eye stripe, the anti-predator response of tested flycatchers decreased dramatically. Further, if the eye stripe was completely removed, the dummy elicited no anti-predator response in tested flycatchers.

Taken together, the results of Curio indicate that the flycatcher perceived the predator as an integer entity; nevertheless, it focused more attention on salient species-specific features (the eye strip in the red-backed shrike). The flycatcher lost their ability to recognize the red-backed shrike after the modification of whole body colouration as well as the removing the eye strip. These findings are in exact accordance with our results, which showed, that tested shrikes responded to the kestrel only if it possessed species-specific colouration as well as general raptor salient features.

Recently, the effect of colouration resemblance between the predator of adult passerines, the sparrowhawk, and nest parasite, the cuckoo, have been investigated repeatedly. One of two colour forms of European cuckoo has barred belly and yellow eye. Therefore, it was hypothesized that the nest parasite mimics the most dangerous predator of small birds in Europe, the sparrowhawk, which facilitate the access to the hosts nest (Welbergen and Davies 2011). However, Welbergen and Davies (2008) showed that reed warbler (*Acrocephalus scirpaceus*), a species, which is

commonly parasited by the cuckoo, mobbed the dummy of cuckoo with alarm calls more strongly than the dummy of sparrowhawk or harmless control, the teal (*Anas crecca*). This result implied that the reed warbler was able to discriminate among particular intruders. On the other hand, in experiments with plumage manipulation, the reed warbler was more reluctant to approach the common cuckoos with barred rather than unbarred underparts (Welbergen and Davies 2011). Therefore, the barred belly protects the cuckoo before the active mobbing from host species. In addition, also the harmless control, the dove (*Streptopelia decaocto*), was approached significantly more closely unbarred than barred (Welbergen and Davies 2011). However, the bared belly did not induce the anti-predator response unconditionally, because there was no difference in approach to barred and unbarred hawks (Welbergen and Davies 2011). Authors considered that the reed warblers discriminated the sparrowhawk probably according to the typical raptor features, sited on the sparrowhawk body.

The removal of the barred belly from the dummy of sparrowhawk could be considered being comparable with simplification of the colour pattern of our 'raptor-brown' dummy, which was also not attacked significantly less intensively than unmodified dummy in the red-backed shrikes. However, in contradiction to our finding that the species-specific colouration in 'harmless-natural' dummy was not sufficient feature without general raptor salient feature for release of mobbing response, the species-specific colouration of the sparrowhawk used on cuckoo dummy, caused fear in the reed warbler from the cuckoo dummy, although it did not possess general raptor salient features. This discrepancy could be explained by various manners of anti-predator behaviour of the reed warblers and red-backed shrikes. Whereas the warblers responded by the change of the distance from the intruder, the shrikes changed the intensity of the active mobbing. However, the passive and the active mobbing differ in costs and risks.

Moreover, Trnka et al. (2012) support, that the yellow iris and yellow eye ring of the cuckoo are more important cues than its barred belly for the great warbler. The authors explain that host looks to cuckoo mostly from above, so it could see rather the eye than the belly. They also noted that the same cue could induce aggressive response in one population or

escape response in other, according to their experience with presented intruders.

On the other hand, Trnka and Prokop (2012) found that the great warbler (*Acrocephalus arundinaceus*) attacked both the cuckoo and the sparrowhawk with similar intensity, however, only when they were presented in sequence. Since they were presented simultaneously, the great warblers could distinguish between them and attacked the cuckoo more intensively. The authors explained that the cuckoo's hawk mimicry was not thorough; however, the great warblers generalized the danger among all intruders during the nest defence. It could be caused by strong physique of the great warbler, which increased the probability of successful mobbing against the cuckoo.

Whereas the reed warblers could distinguish between the cuckoo and sparrowhawk, species, which were not parasited by the cuckoo (the swallow, *Hirundo rustica*), and species, which had no experiences with it (the bushtits, *Psaltriparus minimus*) were mystified by the hawk mimicry and treated it like it was the sparrowhawk (Lyon and Gilbert 2013). Also the great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) responded to the cuckoo similarly cautiously as to the sparrowhawk (Langmore et al. 2012).

On the other hand, in feeder experiments the tits showed similarly strong alarm to barred and unbarred hawks, and little alarm to barred doves (Davies and Welbergen 2008). These results imply that the barred belly alone is not sufficient feature for recognition of the sparrowhawk. There have to be present also another species-specific (the yellow eyes) and/or general-raptor (hooked beak, or strong talons) features. These variations in behaviour among various species depend probably on the context in several levels. The effect of one particular feature is affected by the presence of other features, by the relevance of their holder for receiver, by the ability of the receiver to act towards the holder, and by the individual receiver experience with the holder.

Only few studies distinguished manipulation with general and species-specific salient features. Beránková et al. (2014) presented dummies of the sparrowhawk and the pigeon with mutually exchanged salient features (the eye and the beak) to naïve great tits. The exchange of the eyes removed the fear from the sparrowhawk from the tits response, but did

not cause the fear from the pigeon. Tits were interested in both chimeras, which suggest they considered the chimeras as “weird enemies”. The exchange of beaks did not remove the fear from the sparrowhawk, however caused some fear from pigeon (but not as intensive as from unmodified sparrowhawk). The authors deduced that species-specific features of the sparrowhawk were necessary for proper identification, whereas general raptor salient features were not. At the same time, species-specific feature of the sparrowhawk alone was not the sufficient cue for the determination, whereas general raptor salient feature was (for the recognition of the “raptor”, not “sparrowhawk”, of course).

Although birds use rather local than global cues (Wasserman et al. 1993; Cavoto and Cook 2001; Troje and Aust 2013) the effect of salient features in recognition process is not unconditional. Although the black eye stripe is an important cue for recognition of the red-backed shrike, the flycatchers did not respond to the white coloured dummy of the red-backed shrike, as well as to the white stick, lacking the shape of avian body, although they both possess stylised black eye stripe (Curio 1975). Similarly, the white coloured pigmy owl did not elicit almost any mobbing response in pied flycatchers; although the dummy possessed unmodified eyes, whose presence appeared to be utterly crucial for the recognition of unmodified dummy of the pigmy owl (Curio 1975). On the other hand, pygmy owl eyes placed on the dummy of the red-backed shrike with unmodified colour pattern had no effect to the response of tested pied flycatchers. Curio (1975) recapped from his extensive experiments that for red-backed shrike recognition by the pied flycatchers, the facial mask as well as the ‘rest’ of the colour pattern (grey back), body size, and spatial orientation were important, while movement and other features were found to be irrelevant.

Numerous laboratory studies (see Dukas and Ratcliffe 2009 for review) showed, that birds are able not only to discriminate by categories, but also easily to learn and generalize. Tvardíková and Fuchs (2010) proved that also complex mechanisms like “amodal completion” occur during predator recognition and categorisation process. The great tits in feeder-experiment respond differently according circumstances to the upper part torso of sparrowhawk, cut off the rest of the body (only the head and breast with parts of wings). If the torso was placed revealed on the perch, tits behaved

just a little feared, but if the torso was “looking out” from the tuft of branches, tits recognized it as real sparrowhawk. It implies, that tits perceive the sparrowhawk holistic, not as set of particular features, also in the situation if it is covered by another object.

Generally, our results show that birds do not perceive salient features apart, but in context. Thus, we can agree with (Schleidt et al. 2011) that suggest to overcome the simplistic attempt to reduce our world to a “world of stimuli” and propose a “theory of world”. Here we take into account not only objects, but also everything that sticks out from the background noise, and are distinguishable from the clutter as something relevant to that individual’s survival.

References

- Allen C, Bekoff M (1999) *Species of Mind: The Philosophy and Biology of Cognitive Ethology*. MIT Press
- Allen C, Hauser MD (1991) Concept Attribution in Nonhuman Animals: Theoretical and Methodological Problems in Ascribing Complex Mental Processes. *Philosophy of Science* 58:221–240.
- Bekoff M, Allen C, Burghardt G (2002) *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition*, First Edition. A Bradford Book
- Beránková J, Veselý P, Sýkorová J, Fuchs R (2014) The role of key features in predator recognition by untrained birds. *Anim Cogn* 1–9. doi: 10.1007/s10071-014-0728-1
- Biederman I (1987) Recognition-by-components: A theory of human image understanding. *Psychological Review* 94:115–147. doi: 10.1037/0033-295X.94.2.115
- Bolles RC, Beecher MD (1988) *Evolution and learning*. Lawrence Erlbaum Associates
- Brown SD, Dooling RJ (1993) Perception of conspecific faces by budgerigars (*Melopsittacus undulatus*): II. Synthetic models. *J Comp Psychol* 107:48–60.
- Bugnyar T (2007) An integrative approach to the study of “theory-of-mind”-like abilities in ravens. *The Japanese Journal of Animal Psychology* 57:15–27. doi: 10.2502/janip.57.1.2
- Burley N, Coopersmith CB (1987) Bill Color Preferences of Zebra Finches. *Ethology* 76:133–151. doi: 10.1111/j.1439-0310.1987.tb00679.x
- Caro TM (2005) *Antipredator defenses in birds and mammals*. University of Chicago Press
- Carter J, Lyons NJ, Cole HL, Goldsmith AR (2008) Subtle cues of predation risk: starlings respond to a predator’s direction of eye-gaze. *Proceedings of the Royal Society B: Biological Sciences* 275:1709–1715. doi: 10.1098/rspb.2008.0095
- Cavoto KK, Cook RG (2001) Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 27:3–16. doi: 10.1037/0097-7403.27.1.3
- Cerella J (1980) The pigeon’s analysis of pictures. *Pattern Recognition* 12:1–6.

- Cerella J (1979) Visual classes and natural categories in the pigeon. *Journal of Experimental Psychology: Human Perception and Performance* 5:68–77. doi: 10.1037/0096-1523.5.1.68
- Cerella J (1986) Pigeons and perceptrons. *Pattern Recognition* 19:431–438.
- Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: A study of avian visual perception. *Animal Behaviour* 23:1–115.
- D’Orazio KA, Neudorf DLH (2008) Nest defense by Carolina Wrens. *The Wilson Ornithological Society* 120:467–472.
- Davies NB, Welbergen JA (2008) Cuckoo–hawk mimicry? An experimental test. *Proceedings of the Royal Society B: Biological Sciences* 275:1817–1822. doi: 10.1098/rspb.2008.0331
- Delius JD, Hollard VD (1995) Orientation invariant pattern recognition by pigeons (*Columba livia*) and humans (*Homo sapiens*). *Journal of Comparative Psychology* 109:278–290. doi: 10.1037/0735-7036.109.3.278
- Dukas R, Ratcliffe JM (2009) *Cognitive Ecology II*. University of Chicago Press
- Gill S, Neudorf DL, Sealy SG (1997) Host responses to cowbirds near the nest: cues for recognition. *Animal Behaviour* 53:1287–1293. doi: 10.1006/anbe.1996.0362
- Goethe F (1937) Beobachtungen und Erfahrungen bei der Aufzucht von deutschem Auerwild. *Deutsche Jagd* 6:97–100.
- Herrnstein RJ (1984) Objects, categories, and discriminative stimuli. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.) *Animal Cognition*. Psychology Press, Hillsdale, NJ: Erlbaum., pp 233–261
- Jitsumori M, Delius JD (2001) Object Recognition and Object Categorization in Animals. In: Matsuzawa T (ed) *Primate Origins of Human Cognition and Behavior*. Springer Japan, pp 269–293
- Kirkpatrick-Steger K, Wasserman EA, Biederman I (1996) Effects of spatial rearrangement of object components on picture recognition in pigeons. *Journal of the experimental analysis of behavior* 65:465–475.
- Kirkpatrick-Steger K, Wasserman EA, Biederman I (1998) Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 24:34–46. doi: 10.1037/0097-7403.24.1.34
- Klump GM, Curio E (1983) Reactions of blue tits *Parus Caeruleus* to hawk models of different sizes. *Bird Behavior* 4:78–81.
- Lack D (1946) *The life of the robin*. London HF & G. Witherby
- Langmore NE, Feeney WE, Crowe-Riddell J, Luan H, Louwrens KM, and Cockburn A (2012) Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. *Behavioral Ecology* 23:798–805. doi: 10.1093/beheco/ars033
- Lyon BE, Gilbert GS (2013) Rarely parasitized and unparasitized species mob and alarm call to cuckoos: implications for sparrowhawk mimicry by brood parasitic cuckoos. *The Wilson Journal of Ornithology* 125:627–630. doi: 10.1676/12-162.1
- Němec M, Fuchs R (2014) Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. *acta ethol* 17:149–154. doi: 10.1007/s10211-013-0175-z

- Němec M, Syrová M, Dokoupilová L, Veselý P, Šmilauer P, Landová E, Lišková S, Fuchs R (2015) Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. *Animal Cognition* 18:259-268. doi: 10.1007/s10071-014-0796-2
- Onnebrink H, Curio E (1991) Brood Defense and Age of Young: A Test of the Vulnerability Hypothesis. *Behavioral Ecology and Sociobiology* 29:61-68. doi: 10.2307/4600584
- Palleroni, Hauser, Marler (2005) Do responses of galliform birds vary adaptively with predator size? *Animal Cognition* 8:200-210. doi: 10.1007/s10071-004-0250-y
- Pashler H, Yantis S (2004) *Stevens' Handbook of Experimental Psychology, Sensation and Perception*. John Wiley and Sons
- Pincemy G, Dobson FS, Jouventin P (2009) Experiments on colour ornaments and mate choice in king penguins. *Animal Behaviour* 78:1247-1253. doi: 10.1016/j.anbehav.2009.07.041
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2012) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103.
- R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Riegert J, Fuchs R (2011) Fidelity to Roost Sites and Diet Composition of Wintering Male Urban Common Kestrels *Falco tinnunculus*. *Acta Ornithologica* 46:183-189. doi: 10.3161/000164511X625955
- Scaife M (1976) The response to eye-like shapes by birds. I. The effect of context: A predator and a strange bird. *Animal Behaviour* 24:195-199. doi: 10.1016/S0003-3472(76)80115-7
- Schleidt W, Shalter MD, Moura-Neto H (2011) The hawk/goose story: The classical ethological experiments of Lorenz and Tinbergen, revisited. *Journal of Comparative Psychology* 125:121-133. doi: 10.1037/a0022068
- Soto FA, Wasserman EA (2012) Visual object categorization in birds and primates: Integrating behavioral, neurobiological, and computational evidence within a "general process" framework. *Cogn Affect Behav Neurosci* 12:220-240. doi: 10.3758/s13415-011-0070-x
- StatSoft, Inc. (2011) *Electronic Statistics Textbook*, WEB: <http://www.statsoft.com/textbook/>. StatSoft, Tulsa, OK
- Steele KM (1990) Configural processes in pigeon perception. *Quantitative analyses of behavior: Behavioral approaches to pattern recognition and concept formation* 8:111-125.
- Strnad M, Němec M, Veselý P, Fuchs R (2012) Red-backed Shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. *Ornis Fennica* 89:206-215.
- Suzuki T, Ueda K (2012) Great Tit mobbing calls signal predator type to both parents and nestlings. 14:
- Tinbergen N (1948) Social releasers and the experimental method required for their study. *Wilson Bulletin* 60:6-51.

- Trnka A, Prokop P (2012) The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. *Animal Behaviour* 83:263–268. doi: 10.1016/j.anbehav.2011.10.036
- Trnka A, Prokop P, Grim T (2012) Uncovering Dangerous Cheats: How Do Avian Hosts Recognize Adult Brood Parasites? *PLoS ONE* 7:e37445. doi: 10.1371/journal.pone.0037445
- Troje NF, Aust U (2013) What do you mean with “direction”? Local and global cues to biological motion perception in pigeons. *Vision Research* 79:47–55. doi: 10.1016/j.visres.2013.01.002
- Tryjanowski P, Goławski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. *Journal of Ethology* 22:13–16. doi: 10.1007/s10164-003-0096-9
- Tryjanowski P, Karg MK, Karg J (2003) Diet composition and prey choice by the red-backed shrike *Lanius collurio* in western Poland. *Belg J Zool* 133:157–162.
- Tvardíková K, Fuchs R (2012) Tits recognize the potential dangers of predators and harmless birds in feeder experiments. *J Ethol* 30:157–165. doi: 10.1007/s10164-011-0310-0
- Tvardíková K, Fuchs R (2010) Tits use amodal completion in predator recognition: a field experiment. *Anim Cogn* 13:609–615. doi: 10.1007/s10071-010-0311-3
- Wasserman EA, Kirkpatrick-Steger K, Van Hamme LJ, Biederman I (1993) Pigeons are sensitive to the spatial organization of complex visual stimuli. *Psychological Science* 4:336–341. doi: 10.1111/j.1467-9280.1993.tb00575.x
- Watanabe S, Ito Y (1991) Discrimination of individuals in pigeons. *Bird Behavior* 9:20–29.
- Watve M, Thakar J, Kale A, Puntambekar S, Shaikh I, Vaze K, Jog M, Paranjape S (2002) Bee-eaters (*Merops orientalis*) respond to what a predator can see. *Animal Cognition* 5:253–259. doi: 10.1007/s10071-002-0155-6
- Welbergen JA, Davies NB (2008) Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. *Animal Behaviour* 76:811–822. doi: 10.1016/j.anbehav.2008.03.020
- Welbergen JA, Davies NB (2011) A parasite in wolf’s clothing: hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioral Ecology* 22:574–579. doi: 10.1093/behco/arr008

Jak ťuhýk obecný (*Lanius collurio*) rozpoznává nepřátele

Kapitola 5

Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments

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Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments

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Abstract

We compared the responses of the nesting red-backed shrikes (*Lanius collurio*) to three dummies of a common nest predator, the Eurasian jay (*Garrulus glandarius*), each made from a different material (stuffed, plush, and silicone). The shrikes performed defensive behaviour including attacks on all three dummies. Nevertheless, the number of attacks significantly decreased from the stuffed dummy through the plush dummy and finally to the silicone dummy. Our results show that wild birds use not only colours but also other surface features as important cues for recognition and categorization of other bird species. Moreover, the silicone dummy was attacked only when presented after the stuffed or plush dummy. Thus, we concluded that the shrikes recognized the jay only the stuffed (with feathered surface) and plush (with hairy surface) dummies during the first encounter. Recognition of the silicon dummy (with glossy surface) was facilitated by previous encounters with the more accurate model. This process resembles the effect of perceptual priming, which is widely described in the literature on humans.

Key words: anti-predator behaviour, artificial dummies, surface texture, categorization, recognition, priming

Introduction

Animals perceive their surrounding and categorize objects such as food, mates, and predators in order to respond adaptively. Experimental studies investigating cognitive processes like categorization (reviewed in Jitsumori and Delius 2001) or concept formation (reviewed in Zentall et al. 2008) have been conducted mainly in laboratory conditions, using a limited array of tested species (among birds, the pigeon has been used most often). The majority of studies examining object categorization has been based on discrimination learning using an operant conditioning method and picture stimuli (Bovet and Vauclair 2000; Friedman et al. 2003; Spetch and Friedman 2006).

To validate the universality of cognitive processes found in laboratory conditions it is necessary to present ecologically meaningful stimuli to wild animals and to focus the research effort on the cognitive processes that occur in animals during ecologically relevant issues (Shettleworth 1993; 2010). Predators represent an example of such a type of ecologically relevant stimuli (Tvardíková and Fuchs 2010; 2012). Some animals possess an innate ability (Lombardi and Curio 1985) to avoid specific predators, while other animals learn to avoid them (Kullberg and Lind 2002) during their lives. The number of threatening predators a prey animal might meet is very large (Blumstein 2006), and includes novel predators. To react adequately to all of them, prey animals possess the ability to generalize predator recognition. This phenomenon has been described in species belonging to various taxa from all vertebrate classes: mammals (Griffin et al. 2001; Stankowich and Coss 2007), reptiles (Webb et al. 2009), amphibians (Ferrari et al. 2009) and fishes (Ferrari et al. 2007; Brown et al. 2011).

Numerous studies have shown the ability of birds to differentiate predators from harmless animals (see Caro 2005 for review). However recognition of predators differing in the level of danger they represent has been subjected by behavioural studies less often (Patterson et al. 1980; Curio et al. 1983; Buitron 1983; Clemmons and Lambrechts 1992; Jacobsen and Ugelvik 1992; Rytönen and Soppela 1995; Kleindorfer et al. 2005; Tvardíková and Fuchs 2011; Strnad et al. 2012; Němec and Fuchs 2014). One way to studying how animals form the “predator” category in the

field, it is necessary to measure the level of generalization between various modifications of the same species of predator.

Most experimental studies examining anti-predator behaviour of birds make use of stuffed dummies representing the tested predators (see Caro 2005 for review). However, stuffed dummies are not easily adjustable for cognitive experiments, which require colour, shape and/or surface modifications. Artificial models of avian predators, which provide a broader array of modifiability, have been used occasionally and in combination with stuffed dummies; these have included rubber (Knight and Temple 1988), plastic (Arroyo et al. 2001), and wooden (Hartley 1950; Deppe et al. 2003) dummies. Some types of anti-predator response, such as vigilance, freezing, escape flight, alarm calls, or even attacks towards artificial dummies have emerged in all of these studies. Thus, it seems that the use of artificial models on birds in anti-predator experiments is a valid option.

Nevertheless, comparison of birds' responses to stuffed dummies and artificial models of the same predator in the same experiment has not been done. It would be very important to find the threshold of difference (the point at which the artificial dummies start to differ from the original model too much) at which the birds stop recognizing it as the real model. Such a finding would be valuable for refining the methodology for future experiments in the field.

All the artificial models used in the aforementioned studies had compact surfaces, markedly different from the structure that is created by contour feathers on stuffed dummies. Laboratory studies with trained pigeons have shown that the presence of a geometric texture results in very quick differentiation of objects from background, which is enabled by grouping perceptually similar elements within the object (Cook 1992a; Cook 1992b). Pigeons were also able to utilize the texture for categorization of natural (Troje et al. 1999; Nicholls et al. 2011) as well as artificial (Cook 1993; Cook et al. 1995; Cook et al. 1996; Cook et al. 1997; Katz and Cook 2000; Young et al. 2001; Kelly and Cook 2003) objects occurring in digital photographs. However it is not evident whether the surface texture is also important in the recognition of ecologically relevant stimuli by wild birds. If the presumption of using the key features in conspecifics (red feathers of a robin, Lack 1946), predator (short neck and

long tail on a raptor silhouette, Krätzig 1940; Lorenz 1940 as cited by Tinbergen 1948) or prey (striped yellow and black pattern, Dittrich et al. 1993) recognition is valid, the effect of the surface texture should be lower.

We decided to test the importance of texture cues for predator recognition by wild birds in field experiments. We compared the responses of the breeding red-backed shrike (*Lanius collurio* L., 1758) to three types of dummy of the common European nest predator, the Eurasian jay (*Garrulus glandarius* L., 1758). Shrikes are familiar with the Eurasian jay as a nest predator and they mob them intensively if they appeared in the proximity of the nest (Strnad et al. 2012; Němec and Fuchs 2014). We used stuffed, plush, and silicone dummies of the Eurasian jay, which together represent a gradient of a decreasing level of similarity with the living predator. All dummies shared potential key features (strong bill and conspicuous colouration – blue and black striped coverts, black moustache, black and white secondaries, and blue eyes) of the real jay; however, they had different surface textures. The stuffed dummy was feathered, the plush dummy hairy, and the silicone dummy glossy. We presumed that both artificial dummies would be imperfect, and that the silicone dummy with its shiny surface would be much worse mimic of the feathered dummy than the hairy plush dummy. Thus, we tested the hypotheses that the anti-predator response would diminish from the stuffed dummy (real plumage) through the plush dummy (hairy surface) to the silicone dummy (glossy surface).

Methods

Study area

The study took place in the Doupov Mountains (50°10'N, 13°9'E), near the town of Karlovy Vary in the Czech Republic. The experiments were conducted during the breeding season (from June to late July) within the years 2008 to 2010.

Study species

The red-backed shrike, chosen as the model species, is a medium-sized insectivorous songbird able to hunt small mammals, other songbirds, and lizards (Tryjanowski et al. 2003). It possesses a strong bill enabling it to defend its nest quite vigorously, including physical attacks (Strnad et al.

2012). From 2008 through 2010, we examined 27 breeding pairs with nestlings aged between 3 to 12 days. The Eurasian jay, chosen as a predator, is considered a significant nest predator of the Czech populations of small passerines (Weidinger and Kocvara 2010). The majority of shrikes nesting in our study area intensively attacked the stuffed dummy of the jay if it was placed close to their nests (Strnad et al. 2012; Němec and Fuchs 2014).

Experimental design

We successively tested the responses of shrikes to three different Eurasian jay dummy types. The stuffed one possessed a feathered surface, the plush one a hairy surface (similar to birds' feathers), and the silicone one a glossy surface (Fig. 1). All dummies were new and used only in this study. They were placed in an upright position, with their wings folded, on a 1.5 m high pole, 1 m away from but facing the nest. The dummy was brought to the nest covered by a cloth, so that birds present at the nest could not see the connection of the human intruder and the dummy. Birds flew away from the nest during the installation. The experimenter then removed the cloth and started recording the birds' behaviour.

The three dummy types were presented to each tested pair in a random sequence. Each trial (presentation of one dummy) lasted 20 minutes starting from the appearance of at least one parent. If neither parent appeared within 20 minutes, the trial was terminated and included in the data set as a zero response. We used this approach because shrikes tend to visit the nest relatively rarely (the feeding frequency is 5 to 10 minutes) when foraging far from the nest, and they might simply not be aware of the presence of the dummy. However, we did not record any case when neither of the parents appeared at the nest during the 20 minutes. The experimenter interrupted the experiment after 20 minutes. The time interval until the presentation of the next dummy was one hour.

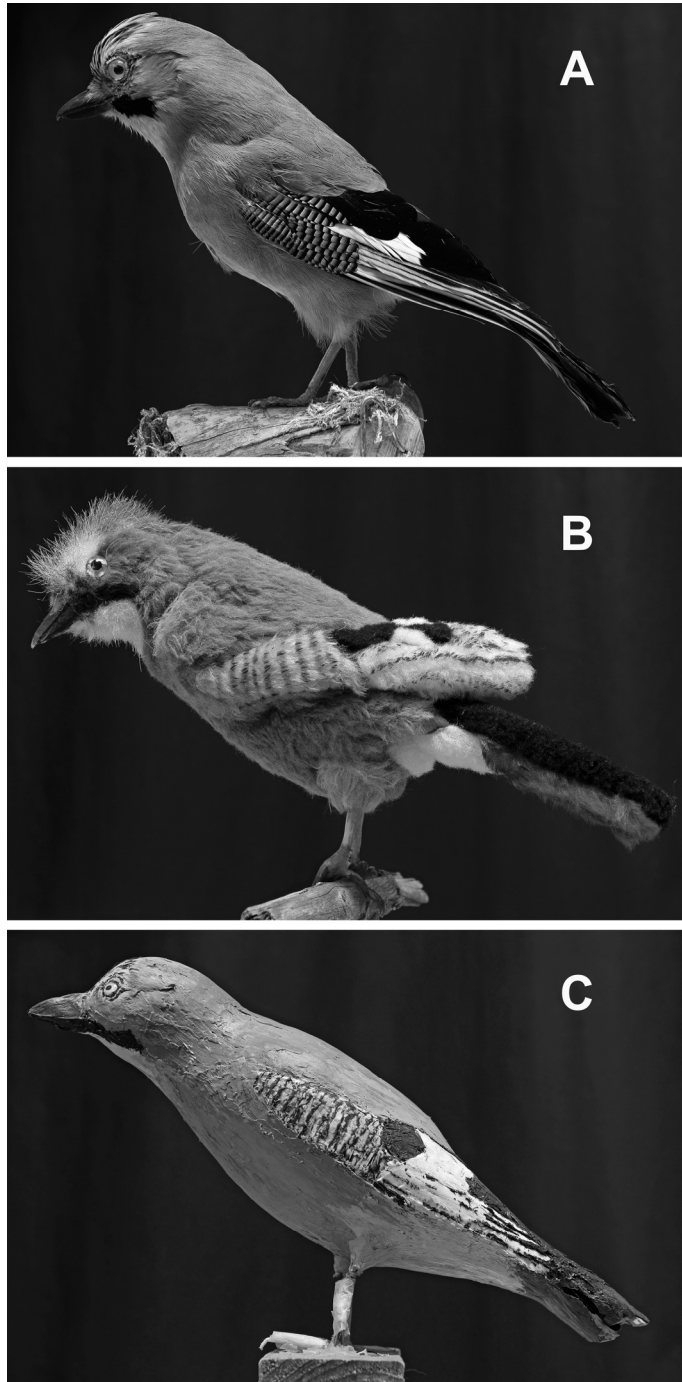


Figure 1 Three dummy types of the Eurasian jay presented close to the red-backed shrikes' nests. A) Stuffed dummy; B) Plush dummy; C) Silicone dummy.

Dummy reflectance measurement

We aimed to create dummies of the same colour as the stuffed dummy in terms of colour. However, the paint used in creating the artificial dummies differed from the pigments (and structural colouration) of the stuffed dummy. To be able to assess the effect of the surface texture on the birds' behaviour, we needed to compare it to the effect of the colouration. To quantify colour differences, the reflectance spectra of the three dummies were measured using equipment that allowed us to measure the reflectance in both the UV and visible wavelengths (spectrophotometer USB 2000, Ocean Optics, Dunedin, Florida, USA). The light source was emitted by a DT-Mini-GS device (Ocean Optics), and the light was conducted by a QR400-7-UV/VIS-BX optical cable (Ocean Optics). The measurements were stored using OOIBase 32 software (Ocean Optics). There were two calibrations of the device; the first using the white standard WS-2 (Ocean Optics), and the other using a completely dark environment. Seven body parts of each dummy were measured: white throat, black moustaches, brown side of the neck, grey back, black tail, white belly and blue coverts of the wing. Five measurements were conducted for each body part and the mean of these measurements (which showed minimal variation) was used in the subsequent evaluation of the colour's reflectance. The measured data ranged from 300 to 700 nm.

Measuring the colour differences

To assess the differences between the particular colours measured, the avian colour discrimination model (Vorobyev and Osorio 1998) was used. This model calculates the distance in avian colour space (ΔS), defined by the quantum catches of each receptor type in the avian retina. We used the *pavo* package (Maia et al. 2013) for software R 2.15.0 (© 2012 The R foundation for statistical computing) to create a visual model (command *vismodel*). We used the spectral sensitivity data from the blue tit (*Cyanistes caeruleus*; Hart et al. 2000) and Vorobyev et al. (1998) estimate of the Weber fraction for each cone type based on an empirical estimate of behavioural data from the red-billed leiothrix (*Leiothrix lutea*). The command *coldist* was used to count the distances (ΔS) between all measured body parts on all three dummies. Units of ΔS are jnd (just noticeable differences), where 1.0 jnd is the threshold value for

discrimination of colours. In general, at 1.0 jnd two colours are barely distinguishable under ideal conditions, and as the number of jnds increases, the two colours become more easily discernible under worsening viewing conditions (Siddiqi et al. 2004).

Statistical analysis of shrike behaviour

We recorded the attacks of the shrikes to the presented dummies. An attack was counted when the shrike flew at the dummy with a significant decrease of height above the dummy (both with and without physical contact with the dummy). This activity was used in subsequent analyses in four ways. Firstly, we used the occurrence of any attack during the 20 minutes, scored dichotomously for each trial (0/1). Secondly, we used the number of attacks against the dummy performed during the 20 minutes. This variable was log-transformed [$\log(\text{no. of attacks} + 1)$] in order to bring its distribution closer to normal. Thirdly, we used the latency to the first attack (in seconds). In this analysis, only trials where at least one attack occurred were included. This variable was log-transformed in order to bring its distribution closer normal. Lastly, we calculated the rate of attack as the quotient of the number of attacks and the time from the first attack to the end of the trial. In this analysis, only trials where at least one attack occurred were included. These data followed the normal distribution.

We used generalized linear mixed effect models (GLME; Pinheiro et al. 2012) to assess the effect of the following categorical variables (fixed-effect factors): the type of the dummy (with values 'stuffed', 'plush', and 'silicone'); the 'sequential position' as the point of sequence when the dummy was presented (values 'first', 'second', and 'third'), the sex of the attacker (values 'male' and 'female'); and the age of the nestlings (with values '3–4 days', '6–9 days', and '10–12 days') on each dependent variable. Individual trials were used as the unit of replication. There was a strong correlation between the male and female within a pair (Pearson's correlation coefficients, occurrence of attack: $r = 0.718$, $t = 5.44$, $df = 52$, $P \ll 0.001$; number of attacks: $r = 0.678$, $t = 6.64$, $df = 52$, $P \ll 0.001$; attack latency: $r = 0.325$, $t = 3.89$, $df = 52$, $P \ll 0.001$; attack rate: $r = 0.821$, $t = 8.85$, $df = 52$, $P \ll 0.001$). Thus, we decided to use pair identity instead of individual identity as a random factor in all statistical mixed effects models to avoid pseudoreplication. The same procedure was used by Tryjanowski

and Goławski (2004) for analysis of similar data with the red-backed shrike. Likelihood ratio tests (based on the appropriate distribution binomial or Gaussian, followed by χ^2 or F test respectively) were used to assess the effect of particular variables. The Tukey HSD post-hoc test (in case of normal data) or Fisher LSD post hoc test (for binomial data) were used to evaluate the differences between particular types of dummies or between particular trials in sequence. The effects of sequence within each dummy type (effect of the interaction dummy * sequential position) were compared using a multiple comparison general linear hypothesis, with pre-specified contrasts (Hothorn et al. 2008). All statistical analyses were computed in R 2.15.0 (R Development Core Team 2012).

Results

The occurrence of an attack

The occurrence of an attack was significantly influenced by the dummy type ($\chi^2 = 15.94$, $df = 2$ and 126 , $P < 0.001$; Fig. 2), by the sequence of the dummy ($\chi^2 = 10.18$, $df = 2$ and 126 , $P = 0.006$, Fig. 2) and by the sex of the parent ($\chi^2 = 8.87$, $df = 1$ and 126 , $P = 0.003$). The silicone dummy was attacked by fewer birds than the stuffed (Fisher LSD post hoc test, $P < 0.001$) or than the plush dummy (Fisher LSD post hoc test, $P = 0.020$). Dummies were attacked by fewer birds in the first trial than in the second (Fisher LSD post hoc test, $P = 0.033$) or than in the third trial (Fisher LSD post hoc test, $P = 0.007$). More males than females attacked the presented dummies at least once.

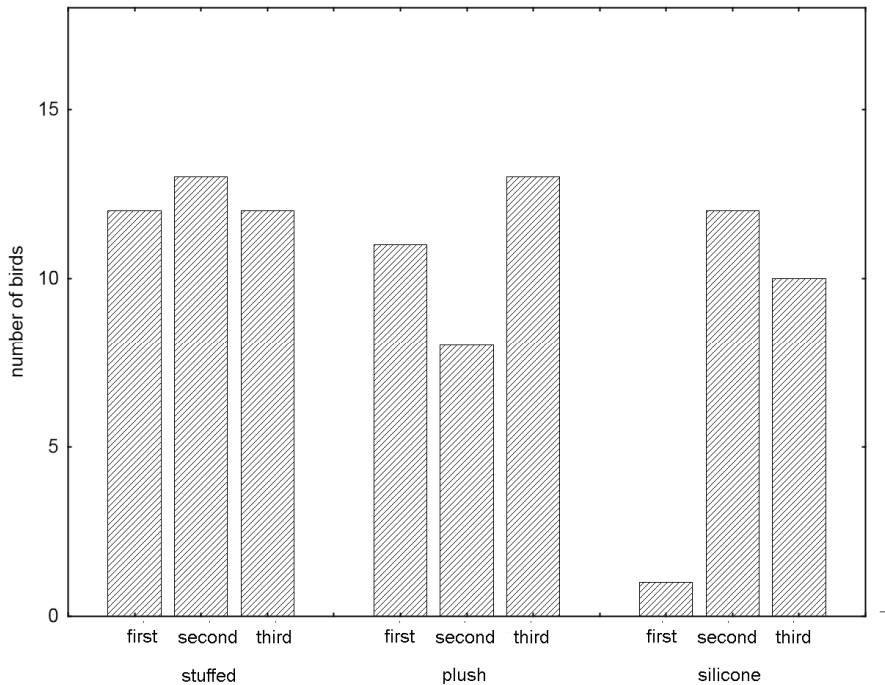


Figure 2 Numbers of birds performing attacks against particular dummies, exposed in various order in the sequence.

Number of attacks

The number of attacks was significantly influenced by the dummy type ($F = 20.14$, $df = 2$ and 126 , $P < 0.001$) and the sex of the parent ($F = 9.43$, $df = 1$ and 126 , $P < 0.001$). The interaction of the type of the dummy and the sequential position of the dummy bordered on significance ($F = 2.15$, $df = 6$ and 126 , $P = 0.052$). The number of attacks decreased significantly from the stuffed, through plush to silicone dummy (Tukey HSD post hoc test: stuffed vs. plush: $z = 2.99$, $P = 0.007$; stuffed vs. silicone: $z = 5.57$, $P < 0.001$; plush vs. silicone: $z = -2.77$, $P = 0.015$). Males performed more attacks than females.

When the silicone dummy was presented as the first one in the sequence of dummies, it was attacked only by one bird; however, whereas when the silicone dummy was presented second or third in the sequence, the shrikes attacked it significantly more often (Fig. 3, Tab. 1). There were no significant effects of sequence within the stuffed and plush dummies (Fig. 3, Tab. 1).

Table 1 Results of multiple comparisons on the interaction terms for dummy type and the order of its exposure, using linear contrasts. The statistic is followed by a parenthesized estimate of Type I error.

	as first – as second	as first – as third	as second – as third
Stuffed	1.03 (n.s.)	1.59 (n.s.)	0.55 (n.s.)
Plush	-0.43 (n.s.)	-1.06 (n.s.)	-0.63 (n.s.)
Silicone	-2.71 (0.054)	-2.69 (0.057)	0.02 (n.s.)

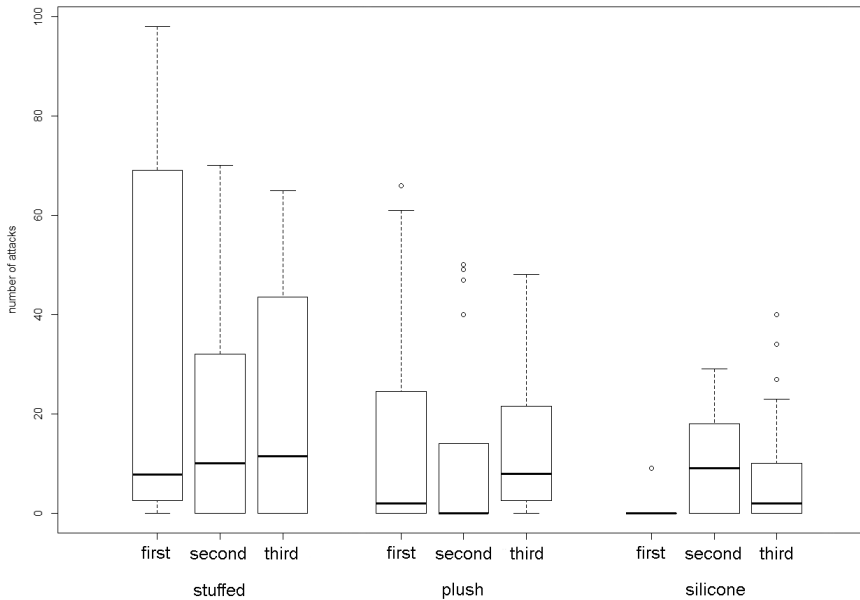


Figure 3 Number of attacks performed by the red-backed shrikes against particular dummies, exposed in various order in the sequence. The thick line within each box-and-whisker drawing represents the median; the vertical span of the box represents the range from the lower to upper quartile; the range of whiskers represents the 5% and 95% percentile, circles represent extremes.

First attack latency

The latency to the first attack (trials with attack only) was not affected by any of the tested variables.

The attack rate

The rate of attacks was significantly affected only by the sequential position of the dummy ($F = 9.61$, $df = 2$ and 126 , $P = 0.008$). Dummies presented in the first trial were attacked as a higher rate than dummies presented in the second (Tukey HSD post hoc test: $z = 2.73$, $P = 0.017$) as well as than in the third trial (Tukey HSD post hoc test: $z = 2.77$, $P = 0.016$).

Colour differences

We found significant differences among all three dummies regarding the reflectance of particular parts of the body (Tab. 2). However, the overall differences between the stuffed and silicone dummies and between the stuffed and plush dummies were slightly smaller than the difference between the plush and silicone dummies. The biggest individual differences were found for the blue coverts (among all three dummies). Other body parts were i) significantly distinct in one dummy only (silicone throat or plush tail) or ii) quite similar among all dummies (back, neck, belly, moustaches). Only the colouration of the stuffed and silicone tail should not be recognizable by birds according to statistical significance within the avian visual model (see Tab. 2).

Considering the reflectance curves (Fig. 4), we may conclude that out of all three dummies, the silicone dummy reflects the complete visible light spectrum the most (i.e., is perceived as the lightest), and the plush dummy the least (i.e., is perceived as the darkest). Only the stuffed dummy reflected the whole bird-visible spectrum, including a significant portion of UVa radiation, within the belly and throat bodily parts. This was not true for the silicone, or for the plush dummy (i.e., these are perceived as darker than the stuffed dummy by the birds). The peak reflectance of the blue coverts on the stuffed dummy is also shifted into the UV part of the spectrum (peaking at 370 nm). The silicone blue does not reflect UVa radiation and its reflectance peak is about 470 nm (blue light). The plush blue generally reflects only a little, but it does so in the whole measured spectrum including the UV part. The blue colour on the stuffed dummy is

thus sensed as brighter than the blue on the silicone dummy, and the blue on the plush dummy has lower saturation and is perceived as rather greyish or whitish.

Table 2 Distances (ΔS) between particular spots on each dummy type based on the reflectance data in respect to the avian visual system. Presented units are dimensionless just noticeable differences. Values lower than 1 should not be recognizable for birds under optimal light conditions.

body part	stuffed-plush	comparison	
		stuffed-silicone	plush-silicone
back (grey)	2.74	1.32	2.81
neck (rusty)	3.02	3.42	1.91
throat (white)	1.03	7.58	8.43
belly (white)	2.19	5.79	3.82
coverts (blue)	8.96	11.09	8.10
moustache (black)	1.16	1.65	2.68
tail (black)	9.76	0.43	9.57
sum	28.86	31.28	37.32

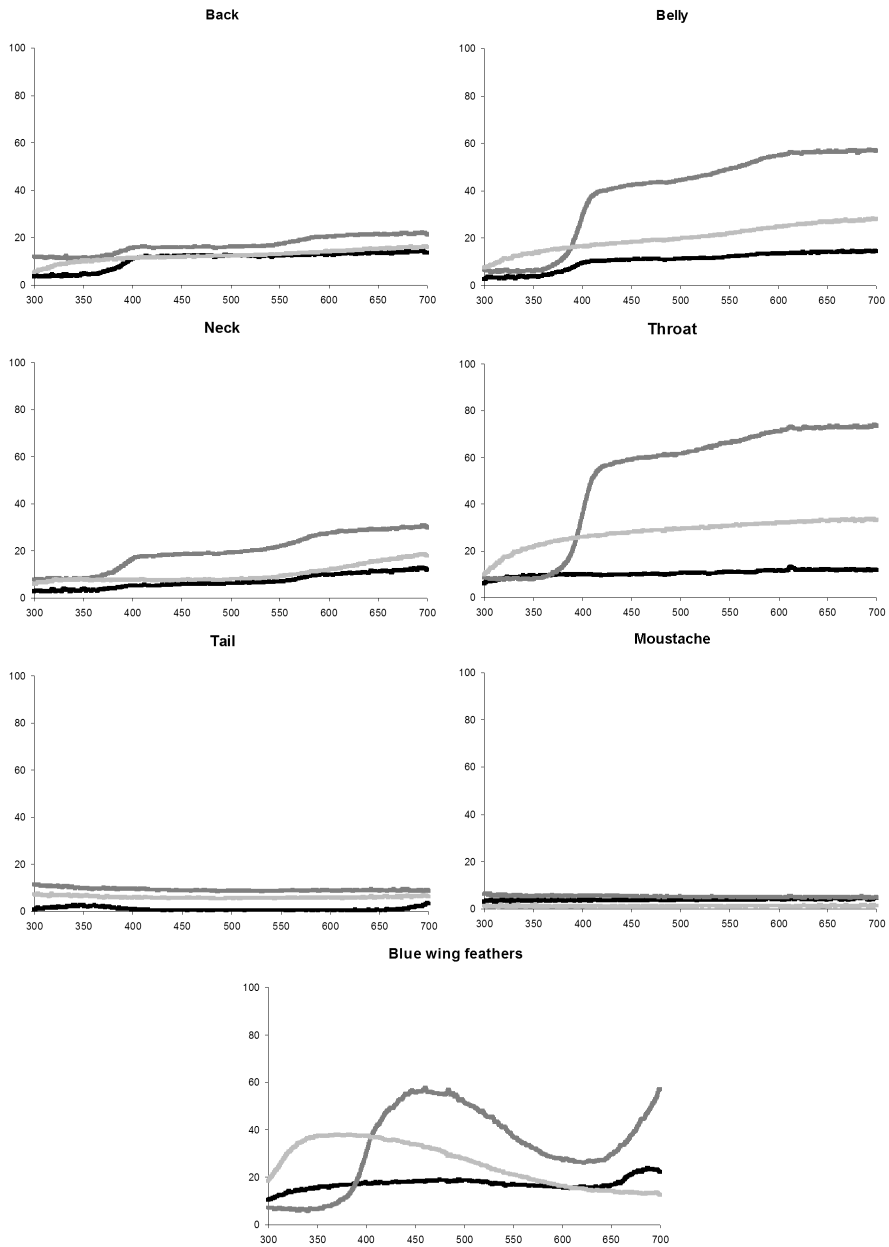


Figure 4 Average spectral reflectance (mean of five independent measurements on each body part) of seven body parts on each dummy type as depicted in Figure 1. 100% reflectance is defined as the light reflected from 'white standard' (WS-2, Ocean Optics). Light grey line refers to the stuffed dummy, dark grey line to the silicone dummy and black line to the plush dummy.

Discussion

The red-backed shrikes attacked all three of the stuffed, plush, and silicone dummies. Nevertheless, the silicone dummy was attacked by fewer birds than the more accurate (in terms of surface texture) plush and stuffed dummies although all dummies were designed to share all potential key features with the real predator. The number of birds attacking the plush and stuffed dummies did not differ significantly. On the other hand, the number of attacks performed against particular dummies decreased from the most accurate stuffed dummy through the plush dummy to the least accurate silicone dummy. When attacking the birds inspected the dummies from close proximity and we suggest that they might notice the dissimilarity between the stuffed and plush dummies and consequently stop attacking. The latency to the first attack and the attack rate did not differ between the presented dummies. This implies that once the birds recognize the dummy as a predator, the attack intensity remains the same, because the target is to chase the predator away as fast as possible. A similar defensive tactic was found in our previous study (Strnad et al. 2012).

The dummies presented in our study did not differ only in their surface texture. The results of the reflectance comparisons from the avian point of view suggest that the colouration may be the cue for recognition of particular dummies by birds. All three dummies differed significantly in the most conspicuous trait within the jay colouration – the blue coverts. Nevertheless, we did not find a closer similarity between the plush and stuffed dummies than between the silicone and stuffed dummies (as would be expected based on the anti-predation behaviour intensity). UV reflectance, which may be especially important, was present only in the stuffed dummy. The brightness of the stimulus has been shown to be one of the important cues for stimulus recognition in pigeons (Young et al. 2001). If we compare the colouration of other parts of the body (especially the white throat and belly), their brightness decreases from the silicone, through stuffed to the plush dummy. It seems thus that the brightness of the colouration corresponds with the surface texture and decreases from the most compact to the most ragged texture.

In summary, we cannot exclude some effect of the colour differences of the tested dummies on their recognition; nevertheless, the differences in the surface texture explain the variation in the bird anti-predatory behaviour better than the colour differences do. Moreover, the surface texture affects the reflectance, and thus, we cannot separate the effect of these two factors.

Experiments with pigeons (Cook 1992a) have shown a very high ability to learn to discriminate stimuli with homogenous internal texture, because they have the capacity for global perception of contrasting texture regions. This enables rapid visual perception during flight (Cook 1992b). Troje et al. (1999) showed that pigeons use information contained in the texture rather than in the shape for discrimination of sex in digital photographs of human faces. In the experiments of Aust and Huber (2002; 2006; 2010), pigeons had problems with human recognition in photographs depicting only silhouettes of humans. On the other hand, the texture did not serve to pigeons as an exclusive cue, but only as an alternative cue for discrimination of photographs of houses and cars (Nicholls et al. 2011). This might be because the shapes of houses and cars are more different from each other than shapes of men's and women's faces as studied in Troje et al. (1999). Our experiments show that texture is an important cue for recognition of ecologically relevant stimuli by wild birds.

At first sight, it may seem that the shrikes recognized a jay in all of the dummies, though in the case of the silicone dummy this was only true for a smaller portion of the tested birds. However, this conclusion is not acceptable because only one of the tested birds defended the nest in trials in which the glossy silicone dummy was presented to the shrikes first in the trial sequence. In all other trials, the aggressive response towards the silicone dummy had to be preceded by the presentation of a more accurate dummy (stuffed or plush) in a previous trial. There was no similar effect of the plush dummy when it was presented first in trial sequence. We can exclude the potential simple effect of sensitisation or habituation of the shrikes during trials, because in a previous experiment shrikes did not attack a harmless pigeon even when presented after various predators, including a jay (Strnad et al. 2012).

The necessity for a presentation of a more accurate dummy (stuffed or plush) before the least accurate dummy (silicone) to evoke recognition of

the latter resembles the process of perceptual priming (sometimes referred to as sequential or repetition priming) described in the psychological literature on humans (for a review see Wasserman and Zentall 2009). Perceptual priming is implicit (unconscious) and occurs when a degraded or reduced set of cues is readily identified after an exposure to a related object (Tulving and Schacter 1990). In other words, once an object has been seen and recognized, it is easier to recognize it again (Basile and Hampton 2013). In a series of studies, (Blough 1989; 1991; 1992) investigated the presence of a similar effect in pigeons showing that priming modifies the mechanism of attention. However, only one paper has described the presence of perceptual priming using a similar method as in human studies (Brodbeck 1997), and Basile and Hampton (2013) were not able to show this process in macaque monkeys. No paper has previously described the presence of perceptual priming in any field study.

A phenomenon similar to priming is studied within behavioural ecology under the name of search image. A search image involves the utilization of knowledge about prey (how it looks, smells etc.) for faster and more successful searching even though the prey may be cryptic or mimetic (for reviews see Edmunds 1974; Dukas 1998; Caro 2005). In an ecological concept, the search image is usually reported in the context of a predator more readily recognizing its prey, but the reverse case may be equally be applicable, our shrikes' recognition of the predator was facilitated after seeing the dummy and thus forming its image to search for.

However, priming and search image are probably not identical processes. Priming should be a long-term effect lasting for weeks or even years (Basile and Hampton 2013). The search image, on the opposite, is momentary, persisting only in the short-term (Langley et al. 1996) and diminished by divided attention (Dukas and Kamil 2001). In our experiments, the effect of more accurate dummy presentation lasted at least for an hour. We may speculate, that it is not a very long term effect because tested shrikes are familiar with living jays and could therefore transfer this knowledge to the silicone dummy as well, (which did not happen).

However, faster location and identification of a predator (or a nest parasite, competitor, or even sexual mate), which occurs in the surrounding and has already been observed, may considerably increase the

probability of successful results in a repeated encounter. Our study shows that perceptual priming may facilitate the categorisation of ecologically relevant objects by wild non-trained birds in the field.

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Ethical note

All experiments were conducted in accordance with the valid laws and regulations of the Czech Republic and in compliance with the Ethic Committee of the Faculty of Science, University of South Bohemia. Behavioural experiments on the wild birds were enabled by the certificate no. 13842/2011-30 offered by the Ministry of the Environment of the Czech Republic and licence for experimenting with birds (Czech animal welfare commission, licence no. ČZU 486/01). The authors declare they have no conflict of interest.

References

- Arroyo B, Mougeot F, Bretagnolle V (2001) Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). *Behavioral Ecology and Sociobiology* 50:109–115. doi: 10.1007/s002650100342
- Aust U, Huber L (2002) Target-defining features in a “people-present/people-absent” discrimination task by pigeons. *Animal Learning & Behavior* 30:165–176. doi: 10.3758/BF03192918
- Aust U, Huber L (2006) Picture-object recognition in pigeons: Evidence of representational insight in a visual categorization task using a complementary information procedure. *Journal of Experimental Psychology: Animal Behavior Processes* 32:190–195. doi: 10.1037/0097-7403.32.2.190
- Aust U, Huber L (2010) The role of skin-related information in pigeons' categorization and recognition of humans in pictures. *Vision Research* 50:1941–1948. doi: 10.1016/j.visres.2010.07.012

- Basile BM, Hampton RR (2013) Monkeys show recognition without priming in a classification task. *Behavioural Processes* 93:50–61. doi: 10.1016/j.beproc.2012.08.005
- Blough PM (1989) Attentional priming and visual search in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 15:358–365. doi: 10.1037/0097-7403.15.4.358
- Blough PM (1991) Selective attention and search images in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 17:292–298. doi: 10.1037/0097-7403.17.3.292
- Blough PM (1992) Detectability and choice during visual search: joint effects of sequential priming and discriminability. *Animal Learning & Behavior* 20:293–300. doi: 10.3758/BF03213383
- Blumstein DT (2006) The Multipredator Hypothesis and the Evolutionary Persistence of Antipredator Behavior. *Ethology* 112:209–217. doi: 10.1111/j.1439-0310.2006.01209.x
- Bovet D, Vauclair J (2000) Picture recognition in animals and humans. *Behavioural Brain Research* 109:143–165. doi: 10.1016/S0166-4328(00)00146-7
- Brodbeck DR (1997) Picture fragment completion: priming in the pigeon. *Journal of Experimental Psychology Animal Behavior Processes* 23:461–468.
- Brown GE, Ferrari MCO, Malka PH, Russo S, Tressider M, Chivers DP (2011) Generalization of predators and nonpredators by juvenile rainbow trout: learning what is and is not a threat. *Animal Behaviour* 81:1249–1256. doi: 10.1016/j.anbehav.2011.03.013
- Buitron D (1983) Variability in the Responses of Black-Billed Magpies to Natural Predators. *Behaviour* 87:209–236.
- Caro TM (2005) Antipredator defenses in birds and mammals. University of Chicago Press
- Clemmons JR, Lambrechts MM (1992) The Waving Display and Other Nest Site Anti-Predator Behavior of the Black-Capped Chickadee. *The Wilson Bulletin* 104:749–756.
- Cook RG (1992a) Acquisition and transfer of visual texture discriminations by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 18:341–353. doi: 10.1037/0097-7403.18.4.341
- Cook RG (1992b) Dimensional organization and texture discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 18:354–363. doi: 10.1037/0097-7403.18.4.354
- Cook RG (1993) The Experimental Analysis of Cognition in Animals. *Psychological Science* 4:174–178. doi: 10.1111/j.1467-9280.1993.tb00483.x
- Cook RG, Cavoto BR, Katz JS, Cavoto KK (1997) Pigeon perception and discrimination of rapidly changing texture stimuli. *Journal of Experimental Psychology: Animal Learning and Cognition* 23:390–400.
- Cook RG, Cavoto KK, Cavoto BR (1995) Same-different texture discrimination and concept learning by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 21:253–260. doi: 10.1037/0097-7403.21.3.253
- Cook RG, Cavoto KK, Cavoto BR (1996) Mechanisms of multidimensional grouping, fusion, and search in avian texture discrimination. *Animal Learning & Behavior* 24:150–167. doi: 10.3758/BF03198963
- Curio E, Klump G, Regelman K (1983) An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? *Oecologia* 60:83–88.

- Deppe C, Holt D, Tewksbury J, Broberg L, Petersen J, Wood K (2003) Effect of Northern Pygmy-Owl (*Glaucidium gnoma*) eyespots on avian mobbing. *Auk* 120:765–771.
- Dittrich W, Gilbert F, Green P, McGregor P, Grewcock D (1993) Imperfect Mimicry: A Pigeon's Perspective. *Proceedings of the Royal Society of London Series B-Biological Sciences* 251:195–200. doi: 10.1098/rspb.1993.0029
- Dukas R (1998) *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making*. University of Chicago Press
- Dukas R, Kamil AC (2001) Limited attention: the constraint underlying search image. *Behavioral Ecology* 12:192–199. doi: 10.1093/beheco/12.2.192
- Edmunds M (1974) *Defence in animals: a survey of anti-predator defences*. Longman Publishing Group
- Ferrari MCO, Brown GE, Messier F, Chivers DP (2009) Threat-sensitive generalization of predator recognition by larval amphibians. *Behavioral Ecology and Sociobiology* 63:1369–1375. doi: 10.1007/s00265-009-0779-5
- Ferrari MCO, Gonzalo A, Messier F, Chivers DP (2007) Generalization of learned predator recognition: an experimental test and framework for future studies. *Proceedings of the Royal Society of London B: Biological Sciences* 274:1853–1859. doi: 10.1098/rspb.2007.0297
- Friedman A, Spetch ML, Lank I (2003) An automated apparatus for presenting depth-rotated three-dimensional objects in human and animal object recognition research. *Behavior Research Methods, Instruments, & Computers* 35:343–349. doi: 10.3758/BF03202563
- Griffin A, Evans C, Blumstein D (2001) Learning specificity in acquired predator recognition. *Animal Behaviour* 62:577–589. doi: 10.1006/anbe.2001.1781
- Hartley P (1950) An Experimental Analysis of Interspecific Recognition. *Symposia of the Society for Experimental Biology* 4:313–336.
- Jacobsen O, Ugelvik M (1992) Antipredator behavior of breeding eurasian wigeon. *Journal of Field Ornithology* 63:324–330.
- Jitsumori M, Delius JD (2001) Object Recognition and Object Categorization in Animals. In: Matsuzawa T (ed) *Primate Origins of Human Cognition and Behavior*. Springer Japan, pp 269–293
- Katz JS, Cook RG (2000) Stimulus repetition effects on texture-based visual search by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 26:220–236. doi: 10.1037/0097-7403.26.2.220
- Kelly DM, Cook RG (2003) Differential effects of visual context on pattern discrimination by pigeons (*Columba livia*) and humans (*Homo sapiens*). *Journal of Comparative Psychology* 117:200–208. doi: 10.1037/0735-7036.117.2.200
- Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. *Animal Behaviour* 69:307–313.
- Knight R, Temple S (1988) Nest-defense behavior in the red-winged blackbird. *Condor* 90:193–200.
- Kullberg C, Lind J (2002) An experimental study of predator recognition in great tit fledglings. *Ethology* 108:429–441.

- Lack D (1946) The life of the robin. London HF & G. Witherby
- Langley CM, Riley DA, Bond AB, Goel N (1996) Visual search for natural grains in pigeons (*Columba livia*): Search images and selective attention. *Journal of Experimental Psychology: Animal Behavior Processes* 22:139–151. doi: 10.1037/0097-7403.22.2.139
- Lombardi CM, Curio E (1985) Social Facilitation of Mobbing in the Zebra Finch *Taeniopygia guttata*. *Bird Behavior* 6:34–40. doi: 10.3727/015613885792335338
- Maia R, Eliason C, Bitton P (2013) Perceptual analysis, visualization and organization of spectral color data in R. CRAN Project, The R foundation for statistical computing
- Němec M, Fuchs R (2014) Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. *Acta Ethologica* 7:149–154. doi: 10.1007/s10211-013-0175-z
- Nicholls E, Ryan CME, Bryant CML, Lea SEG (2011) Labeling and family resemblance in the discrimination of polymorphous categories by pigeons. *Animal Cognition* 14:21–34. doi: 10.1007/s10071-010-0339-4
- Patterson TL, Petrinovich L, James DK (1980) Reproductive value and appropriateness of response to predators by White-Crowned Sparrows. *Behavioral Ecology and Sociobiology* 7:227–231. doi: 10.1007/BF00299368
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2012) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103.
- R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rytkönen S, Soppela M (1995) Vicinity of Sparrowhawk Nest Affects Willow Tit Nest Defense. *The Condor* 97:1074–1078. doi: 10.2307/1369550
- Shettleworth SJ (1993) Where Is the Comparison in Comparative Cognition? *Alternative Research Programs. Psychological Science* 4:179–184. doi: 10.1111/j.1467-9280.1993.tb00484.x
- Shettleworth SJ (2010) *Cognition, evolution, and behavior* (2nd ed.). Oxford University Press, New York, NY, US
- Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K (2004) Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *Journal of Experimental Biology* 207:2471–2485. doi: 10.1242/jeb.01047
- Spetch ML, Friedman A (2006) Comparative Cognition of Object Recognition. *Comp Cogn Behav Rev* 12–35.
- Stankowich T, Coss RG (2007) The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. *Proceedings of the Royal Society of London B: Biological Sciences* 274:175–182. doi: 10.1098/rspb.2006.3716
- Strnad M, Němec M, Veselý P, Fuchs R (2012) Red-backed Shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. *Ornis Fennica* 89:206–215.
- Tinbergen N (1948) Social releasers and the experimental method required for their study. *Wilson Bulletin* 60:6–51.

- Troje NF, Huber L, Loidolt M, Aust U, Fieder M (1999) Categorical learning in pigeons: the role of texture and shape in complex static stimuli. *Vision Research* 39:353–366. doi: 10.1016/S0042-6989(98)00153-9
- Tryjanowski P, Goławski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. *Journal of Ethology* 22:13–16. doi: 10.1007/s10164-003-0096-9
- Tryjanowski P, Karg K, Karg J (2003) Assessing Red-backed Shrike *Lanius collurio* diet: a comparison of collar, pellet and prey remain methods of analysis. *Acta Ornithologica* 38:59–64.
- Tulving E, Schacter DL (1990) Priming and human memory systems. *Science* 247:301–306. doi: 10.1126/science.2296719
- Tvardíková K, Fuchs R (2010) Tits use amodal completion in predator recognition: a field experiment. *Animal Cognition* 13:609–615. doi: 10.1007/s10071-010-0311-3
- Tvardíková K, Fuchs R (2012) Tits recognize the potential dangers of predators and harmless birds in feeder experiments. *Journal of Ethology* 30:157–165. doi: 10.1007/s10164-011-0310-0
- Tvardíková K, Fuchs R (2011) Do birds behave according to dynamic risk assessment theory? A feeder experiment. *Behavioral Ecology and Sociobiology* 65:727–733. doi: 10.1007/s00265-010-1075-0
- Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London B: Biological Sciences* 265:351–358. doi: 10.1098/rspb.1998.0302
- Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC (1998) Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A* 183:621–633. doi: 10.1007/s003590050286
- Wasserman EA, Zentall TR (2009) *Comparative Cognition: Experimental Explorations of Animal Intelligence*. Oxford University Press
- Webb JK, Pike DA, Shine R (2009) Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. *Behavioral Ecology* 152. doi: 10.1093/beheco/arp152
- Weidinger K, Kocvara R (2010) Repeatability of nest predation in passerines depends on predator species and time scale. *Oikos* 119:138–146. doi: 10.1111/j.1600-0706.2009.17649.x
- Young ME, Peissig JJ, Wasserman EA, Biederman I (2001) Discrimination of geons by pigeons: The effects of variations in surface depiction. *Animal Learning & Behavior* 29:97–106. doi: 10.3758/BF03192819
- Zentall TR, Wasserman EA, Lazareva OF, Thompshon RKR, Rattermann MJ (2008) Concept Learning in Animals. *Comparative Cognition & Behavior Reviews*. doi: 10.3819/ccbr.2008.30002

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PUBLIKACE

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Němec M, Surová M, Dokoupilová L, Veselý P, Šmilauer P, Landová E, Lišková S, Fuchs R (2014) Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. *Animal Cognition* 18:259-268. doi: 10.1007/s10071-014-0796-2

Němec M, Fuchs R (2014) Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. *Acta Ethologica* 17:149–154. doi: 10.1007/s10211-013-0175-z

Strnad M, **Němec M**, Veselý P, Fuchs R (2012) Red-backed Shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. *Ornis Fennica* 89:206–215.

Němec M, Bušek O, Lípa M (2009) Chřástal polní (*Crex crex*) na kraslicku a v karlovarském kraji v letech 2005–2009. *Příroda Kraslicka* 2: 157–170

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Surová M, Bendová L, Poláková S, Němec M, Fuchs R (2011) Artificial dummies as stimuli in field mobbing experiments. *The Association for the Study of Animal Behaviour; Summer Conference 2011; St Andrews, Scotland. 18-19 August; Collection of abstracts, pp. 53*

Němec M, Fuchs R (2009) Shrikes vs. Corvids: Nest defense of red backed strike (*Lanius collurio*) *31st International Ethological Conference, 2009, Rennes, France, Collection of abstracts p. 349*

Poláková S, Strnad M, Němec M, Fuchs R (2006) How Shrikes defend their nests? *Animal Behavior Society Annual Meeting, srpen 2006, Snowbird, USA.*

Orální prezentace v češtině

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